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TREATISE ON
MARINE ECOLOGY AND PALEOECOLOGY

Volume 1

ECOLOGY

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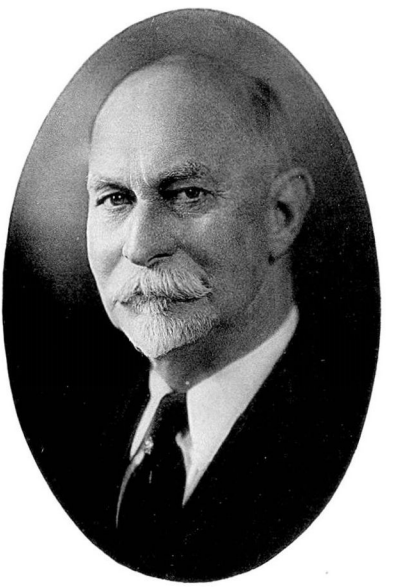
EDWARD FORBES (1815–1854)
From Wilson and Geikie:
Memoir of Edward Forbes, F. R. S.

KARL MÖBIUS (1825–1908)
From a painting at Kiel:
courtesy Adolf Remane

C. G. JOHANNES PETERSEN
(1860–1928)
Photograph courtesy Gunnar Thorson



T. WAYLAND VAUGHAN (1870–1952)

PIONEERS OF MARINE ECOLOGY AND PALEOECOLOGY

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Dedicated to
Thomas Wayland Vaughan
who organized the group responsible for this Treatise
and who served as a member until a few months before his death.

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Foreword

The late Dr. T. Wayland Vaughan, who had long been interested in marine ecology and paleoecology, in 1940 planned and organized a Subcommittee on the Ecology of Marine Organisms as a part of the Committee on Geologic Research (Norman L. Bowen, Chairman) in the Division of Geology and Geography of the National Research Council of the National Academy of Sciences. The members of this Subcommittee were: C. H. Edmondson, Remington Kellogg, Harry S. Ladd (Chairman), Kenneth E. Lohman, Roger Revelle, F. W. Rolshausen, H. C. Stetson, T. Wayland Vaughan. The first annual report, which attempted to summarize current activities in marine ecology and paleoecology, was issued in 1941. In this report the possibility of preparing an ecological treatise was mentioned. In 1942 the Subcommittee was made a full Committee and its title was changed to Committee on Marine Ecology As Related to Paleontology to emphasize the paleontological nature of its interests. With the encouragement and assistance of Walter H. Bucher, Chairman of the Division of Geology and Geography, the Committee in its second report, issued at the close of 1942, briefly listed its aims. There were six of these, the last of which read: "Possibly, at a later date, to prepare a special treatise on ecology that would stress geological interpretation." World War II greatly curtailed most activities in marine ecology and also curtailed the activities of the Committee. Serious consideration was given to the possibility of recessing the work, but the members felt that it might be difficult to revive the program if work was stopped. Interest in the *Treatise* continued at a low level until the war was over, but in 1946 in its sixth annual report the Committee published a tentative outline for the *Treatise* and invited criticism. In this same year Kenneth E. Lohman was made Vice-Chairman of the Committee.

During the first 5 years of its existence the group that formed the original Subcommittee continued to serve. Gordon Gunter was added as a member in 1942 and Earl H. Myers in 1944. In 1946, the sixth year, H. C. Stetson resigned because of the pressure of other duties, and three new members were added: K. O. Emery, of California, A. W. B. Powell, of New Zealand, and H. G. Schenck, then stationed in Japan. In 1947 four more members were added: R. H. Fleming, Julia Gardner, J. B. Reeside, Jr., and Waldo L. Schmitt. At a two-day meeting held in March 1947, Gordon Gunter was named Vice-Chairman for Biology, Kenneth E. Lohman Vice-Chairman for Geology, and Roger Revelle Vice-Chairman for Oceanography; and concrete plans for the completion of the *Treatise* were formulated. In 1948 Frank C. Whitmore was made a member, and in the following year Roland W. Brown and Joel W. Hedgpeth were added and assumed editorial duties. These additions brought the total membership of the Committee to 19. In 1951 Doctor Vaughan asked that his name be dropped from the Committee because of his failing eyesight. The Committee accepted his resignation reluctantly, and John W. Wells was appointed to fill the vacancy.

Most of the members of the Committee have prepared one or more units of the text or the accompanying bibliographies, but the Committee alone could not have produced the *Treatise* in its present form. To obtain as nearly complete coverage as

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possible the aid of nearly 100 specialists was enlisted, each of whom prepared one or more units in his particular field. To this large group the Committee extends its deepest thanks. Formal titles of the contributors are not given but the field of interest of each is indicated, together with his address at the time of going to press.

The Committee wishes to express its thanks to the Office of Naval Research, whose support made it possible for Vice-Chairman Gunter to make an extended stay at the University of California, Scripps Institution of Oceanography and a short visit to the Woods Hole Oceanographic Institution in 1948–1949. Later, through a similar co-operative arrangement between the Scripps Institution of Oceanography and the Office of Naval Research, Joel W. Hedgpeth was able to spend several years at Scripps assembling and organizing the materials for volume I and writing certain of the units. During the summer of 1953, again with the support of the Scripps Institution and the Office of Naval Research, he was able to travel in Europe and consult with many of the contributors to the *Treatise*. The Committee also desires to express its appreciation to the United States Geological Survey for encouragement and support; six members of the Committee and many of the other contributors to the *Treatise* are on the staff of the Geological Survey. Many members of the staff of the Geological Survey, the Scripps Institution, the National Museum and of other organizations have assisted the Committee in the critical review of manuscripts; this help is gratefully acknowledged. We also wish to thank Karl P. Schmidt for translating Chapter 25, which was submitted in German.

Messrs. Walter H. Bucher, W. W. Rubey, Arthur Bevan, Ernst Cloos, and Francis Birch, who have successively served as Chairman of the Division of Geology and Geography—now known as the Division of Earth Sciences—since the formation of the Committee have encouraged and supported the work in every way possible. The Committee desires to express its special thanks to Miss Margaret L. Johnson, Secretary to the Division, for great assistance particularly in assembling and duplicating of the Annual Reports, and to Mr. G. D. Meid, Business Manager of the National Academy of Sciences, National Research Council, for aid in making publication arrangements for the *Treatise*.

From the start the *Treatise* has been planned as an appraisal of accomplishments in the fields of marine ecology and paleoecology, particularly those ecological investigations related directly or indirectly to paleontology. In attempting to obtain broad coverage the Committee and its collaborators discovered several blank areas in the paleoecological field and thus initiated several investigations that otherwise might not have been started until some time later. These developments were gratifying and have served to bridge the gap between past and present work in the field. Paleoecology, though it deals with the past, is a comparatively youthful but active branch of paleontology.

With these thoughts in mind it was decided to supplement the appraisals of past work with some sort of prophetic look into the future. In what direction is paleoecology going, how far may it hope to go, and what sorts of tools may be used in the future? Some of the new techniques developed in recent years in borderline fields such as biochemistry, biophysics, and geochemistry exhibit great promise and may be successfully applied to paleoecological investigations. These prospects are discussed in a concluding chapter in Volume 2.

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Chapter 1

Introduction*

JOEL W. HEDGPETH

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Ecology has no aim, but ecologists have. The problems of the ecologist are not fundamentally different from those of any other kind of naturalist. The superficial differences in aim are due to the different points of view, or methods of approach, rather than to any essential difference in the character of the problems.

—Charles C. Adams, *Guide to the Study of Animal Ecology*, 1913

Since the early history of ecology has been discussed in some detail by Allee *et al.* (1949), among others, there is no need to repeat it here. Our concern is with the development of marine ecology in general, especially as it may be related to paleoecology. Gislén (1930) traced the study of "marine sociology," in particular of intertidal zonation, as far back as 1812, although Wahlenberg's pioneer effort to describe zonation was overlooked until 1917. The early work of d'Orbigny (1820) was also for the most part neglected, and it is not until the decades 1830–1840 that we find the unmistakable beginnings of modern marine ecology. In France it was the work of Audouin and Milne Edwards (1832), whose scheme of zonation of the life of the shore and shallow sea persisted for 50 years. In England, it was the influence of the Manxman Edward Forbes that gave marine ecology its start. In Norway Michael Sars, in Sweden Sven Lovén, and in Germany Johannes Müller turned their attention to the animals of the sea. Dredging for bottom animals was the fashion of the day, and in 1839 the British Association appropriated £60 to defray the expenses of "researches with the dredge, with a view to the investigation of the marine zoology of Great Britain, the illustration of the geographical distribution of marine animals, and the more accurate determination of the fossils of the pleistocene period." Forbes was the leading spirit on this dredging committee, and gave its activities a strong ecological cast.

In Ireland an army surgeon, J. Vaughan Thompson, studied a number of strange creatures that had usually been considered adult animals; he demonstrated that they were really larval stages. These included the zoea of crabs and the nauplius and cypris of barnacles. While Johannes Müller is usually credited with "inventing" the plankton net in the 1840's, Thompson was using such a net as early as 1828 (Hardy, 1953). Although Thompson published very little, his work was of the highest quality: "It has been said of him that 'no great naturalist has written so little and that so good.' " (Singer, 1950).

While many of the investigations of this period were concerned with zoology *per se*,

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those of Edward Forbes produced some of the first ecological generalizations to receive wide notice in science. The most famous of these was his recognition of distribution by bathymetric zones: (1) littoral ("The tract between tidemarks"); (2) the laminarian zones; (3) the coralline zones ("to some thirty fathoms or more"); (4) the deep-sea coral zone ("toward an abyss where life is either extinguished, or exhibits but a few sparks to mark its lingering presence.") (Forbes and Godwin-Austen, 1859). In earlier papers, notably his lecture before the Geological Society in 1844, Forbes suggested that there was a "probable zero of life" at 300 fathoms. It was this mistake that did so much to stimulate the investigation of the depths of the ocean, and Forbes was in a real sense the instigator of the events that led to the CHALLENGER Expedition.

Forbes was also one of the earliest systematic biogeographers and recognized a series of provinces in the European seas—*viz.*, Arctic, Boreal, Celtic, Lusitanian, Mediterranean, and Black Sea. Although he considered these provinces to have originated as the result of dispersal of species complexes from "centers of creation," he had a lively appreciation of the ecological factors governing such dispersion, and we may consider his *Natural History of the European Seas* (completed after his untimely death by Robert Godwin-Austen) the first treatise on marine ecology. Most of his important ideas, however, were expressed in papers presented at meetings, and it was apparently in the discussions that followed them that his influence was most felt. It would be interesting to have a record of the discussion which followed his report on the invertebrates of the Aegean Sea to the 1843 meeting of the British Association. In this report he presented his findings as to distribution by depth, accompanied by the first recognition of population dynamics (as pointed out by Allee *et al.*):

> As each region shallows or deepens, its animal inhabitants must vary in specific associations, for the depression which may cause one species to dwindle away and die will cause another to multiply. The animals, themselves, too, by their over-multiplication, appear to be the cause of their own specific destruction. As the influence of the nature of sea bottom determines in a great measure the species present on that bottom, the multiplication of individuals dependent on the rapid reproduction of successive generations of Mollusca will of itself change the ground and render it unfit for the continuation of life in that locality until a new layer of sedimentary matter, uncharged with living organic contents, deposited on the bed formed by the exuviae of exhausted species, forms a fresh soil for similar or other animals to thrive, attain their maximum, and from the same cause die off.

Forbes then goes on to describe the probable fossil record which might be expected if the Aegean Sea were to be elevated or filled with sediment (1844, pp. 176–178); in doing this he outlined for the first time the methodology of paleoecology. There was in all Forbes' work and thought a strong geological cast, and he is in a real sense the founder of paleoecology:

> To Forbes is due the credit of having been the first to treat these questions in a broad philosophical sense, and to point out that the only means of acquiring a true knowledge of the *rationale* of the distribution of the present fauna, is to make ourselves acquainted with its history, to connect the present with the past . . . Forbes, as a pioneer in this line of research, was scarcely in a position to appreciate the full value of his work. (Wyville Thomson, 1873, p. 6).

A recent appraisal of Forbes' contribution, with an account of his field methods, is given by Ritchie (1956).

The decade 1840–1850 was marked by an active interest in marine biology on the

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continent as well as in England. In the United States, interest during this period was more in the physical aspects of the sea, and the pre-eminent marine scientist was Matthew Fontaine Maury, whose *Physical Geography of the Seas* (1855) marked the beginning of physical oceanography. Diving as a method of ecological investigation was introduced by H. Milne Edwards and A. de Quatrefages about 1844 off the coast of Sicily, but it has only come into serious use since the invention of free-diving apparatus (Drach, 1952). The first seaside summer station was instituted by P. J. van Beneden at Ostend in 1843, and summer classes in marine zoology appear to have been the innovation of Carl Vogt in 1844. It was not until 1859 that the first permanent marine station, at Concarneau, was founded (Kofoid, 1910).[1] During this period the lively interest of literate laymen provided a market for such semi-popular works as Vogt's *Ozean und Mittelmeer* (1848), Quatrefage's *Souvenirs d'un Naturaliste* (1854, translated into English, 1857), and the various superbly illustrated volumes by Philip Henry Gosse, including *A Naturalist's Rambles on the Devonshire Coast* (1853) and *Tenby* (1856). The fever of seashore study reached strange heights in Victorian England, when a well-ordered holiday was incomplete without exercises in the identification of seaweeds and zoophytes, and Gosse conducted classes at the seaside for "a party of ladies and gentlemen . . . and very novel and agreeable the amusement was unanimously voted." (E. Gosse, 1890).[2] It appears that this fad may have been received by some in a spirit of desperate resignation, if we are to judge from the amusing account by Marsden (1947).

The lines of investigation suggested by the work of Forbes and Milne Edwards were carried further by J. R. Lorenz in a remarkable and neglected work, *Physicalische Verhältnisse und Vertheilung der Organismen im Quarnerischen Golfe* (Vienna, 1863). This author discussed in detail the temperature regime, with curves for the entire year at surface and various depths to 30 fathoms, the tidal levels and currents, wave action, prevailing winds, geological formations and salinity in relation to the distribution of plants and animals in the Gulf of Quarnero. He recognized various communities, indicating the characteristic species of the facies, and provided graphs for his physical data (which are absent from many modern papers in this field). It is in all respects a master work, but is still ignored although his usages of the terms supra- and sublittoral are now in general use.[3] Gislén (1930) attributes part of this neglect to the author's early death, which occurred before Lorenz could distribute his book. Whatever the cause for this neglect, it must be said that his achievement was years ahead of its time and indeed is still beyond many later efforts.

The next great decade in the history of marine biology, and of marine ecology in particular, is that of 1870–1880, the time of the CHALLENGER Expedition. It is the decade which saw the beginning of applied ecology under government auspices. The United States Fish Commission, with Spencer F. Baird as secretary, and the Commission zur Wissenschaftlichen Untersuchungen der Deutschen Meere, including

[1] For an excellent summary of this subject, see C. M. Yonge, "Development of marine biological laboratories" Science Progress, no. 173, pp. 1–15, Jan. 1956.

[2] "Since the British mind was all alive and trembling with that zoological fervor excited by the appearance of the hippopotamus in Regent's Park, no animal has touched it to such fine issues and such exuberant enthusiasm as the lovely Sea-Anemone." G. H. Lewes, *Seaside studies* . . . (1858, p. 115).

[3] Lorenz spelled these "Supra-litoral" and "sub-litoral"; the single "t" is etymologically correct, but the spelling "littoral" is now so widely used that it would be tilting at windmills to attempt to restore the older spelling.

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Karl Möbius and V. Hensen, both began their activities in 1871. A year later Dohrn founded the Zoological Station at Naples, but in all its long history it has been devoted primarily to embryological and physiological researches.

While the United Stated and Germany started their investigations of fisheries problems in the same year, the groundwork of the German commission had been laid by Karl Möbius several years before, with his *Fauna der Kieler Bucht* (Meyer and Möbius, 1865). This work is viewed by Nordenskiold (1928, p. 559) as the start of "the modern system and methodics of oecology." Möbius and Victor Hensen, the founder of plankton research, were both members of the Commission. In the first report of the work of the Commission, Möbius (1873, p. 139) introduced three terms which are now universally used in ecology: eurythermal, stenothermal, and euryhaline. The early reports of the German commission inaugurated such lines of research as the distribution of organisms in relation to salinity and quantitative analysis of the plankton, which are still being carried out at Kiel. While the problem of assaying the quantities of plankton in a given volume of water is still unsolved, the methods introduced by Hensen in his monograph (1887), especially the vertical haul with standardized net, are still widely used. It was in this monograph, incidentally, that the term plankton was first used. Hensen continued his work with a special expedition in the Atlantic Ocean devoted exclusively to the investigation of plankton, the famous "Plankton-Expedition" of 1889. Haeckel, who had been introduced to the plankton by Johannes Müller, attacked Hensen's conclusions, but his criticism was vitiated by reliance on "general impressions" and by his idea of zoorema or animal streams, and Hensen (1891) ably defended himself.[4] Kofoid's (1897) criticisms were somewhat beside the point, and it remained for Lohmann, another "Kiel Planktologist" (Johnstone, 1908), to make the next great advance in plankton study with the use of the centrifuge.

In discussing the early history of the German and American commissions, it should not be forgotten that the British may claim priority with the Royal Commission to Investigate Fisheries Problems, which met in 1863. This commission, which included T. H. Huxley, was not a permanent research organization, however, and did little more than offer recommendations in its report in 1866.

The United States Fish Commission began its activities under the guidance of Spencer Fullerton Baird, whose broad interests and appreciation of the complexity of fisheries problems rivaled those of Möbius, although they seem to have begun their careers as applied ecologists independently. In drawing up the program for the Fish Commission, Baird wrote:

> The inquiry, therefore, ultimately resolved itself into an investigation of the chemical and physical character of the water, and of the natural history of its inhabitants, whether animal or vegetable. It was considered expedient to omit nothing, however trivial or obscure, that might tend to throw light on the subject of inquiry . . . (Baird, 1873, p. xiii).

The first annual report of the United States Fish Commission (1873) is a bulky volume in which is embedded, under the authorship of A. E. Verrill, the classic work

[4] It was in this critique of Hensen that Haeckel (1890, transl., 1893) was at his best (or worst) as a fabricator of terms. A few of the many introduced in this paper have survived, notably benthos, nekton, and neritic.

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in American marine ecology, the *Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region.* Allee *et al.* express the opinion that this elaborate report, written in collaboration with S. I. Smith and others, and discussing the occurrences of animals in assemblages and according to substrates, "did not receive the recognition or have the influence among ecologists that it merited." Because it was not the fashion in those days to make detailed acknowledgment of other researches, especially when not directly quoted, it is hard to support or to deny this statement. We do know that Möbius read Verrill's work since he mentions it in his famous monograph on the oyster, and the later work of Möbius was frequently called to the attention of American workers through the publication of translations in the Reports and Bulletins of the Commission. Verrill came closer than Forbes to grasping the idea of the community, but it is Möbius who defined it in unmistakable terms and gave it the name biocoenosis in his book, *Die Auster und die Austernwirthschaft* (1877), which was translated and published in the Report of the U. S. Fish Commission for 1880 (1883).

What we must remember in assessing the comparative influence of these men is that in the United States, where the marine fauna was still incompletely known, Verrill's influence as a teacher was directed to training systematists, and that this phase was followed almost immediately by the era of cell-lineage studies, during which the only proper subject for a doctorate was a study of the early cleavage stages of some invertebrate. In Germany, at least under such men as Möbius and Hensen, students were introduced to the problems of economic zoology in the sea, and from the early work of Möbius in the Gulf of Kiel and on the Helgoland oyster banks there is a direct line of research to C. G. J. Peterson. It is true that in the United States the first seaside studies were inaugurated by Louis Agassiz at Penikese in 1873. This forerunner of the Woods Hole Laboratory was originally the idea of Nathaniel Southgate Shaler, the Harvard geologist and paleontologist, but his part in its history seems to have been forgotten.[5] With the establishment of the Woods Hole Marine Biological Laboratory in 1886 and the building of the permanent station of the Fish Commission in 1885, Woods Hole became a center for seaside studies and soon established a tradition which did little to foster ecological studies. It is true that Verrill's work was supplemented by the faunal survey of Sumner, Osburn, Cole, and Davis (1913), but actually little was added, other than a detailed catalogue, to Verrill's original presentation. The arrival of men like Allee and Shelford on the scene in the early 1920's revived to some extent the original ecological approach of Verrill, but it was not until 1952 that a formal course in ecology was established at Woods Hole.

With the departure of the CHALLENGER from Portsmouth on December 21, 1872, on her four-year cruise around the world, the modern science of oceanography was begun. As a science it was a "possibility" to be fully realized within the short span of two generations (Merriman, 1948); little of the CHALLENGER's results, however,

[5] Shaler's name is not even mentioned in Lillie's (1944) history of the W.H.M.B.L.; however, he does cite the New York Tribune for July 9, 1873. At the end of the account of the opening day at Penikese this statement is found: . . . "Prof. N. S. Shaler of Harvard, who was the first proposer of this scheme, and who is at present in Europe . . . "

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was what might be considered ecology, although much of the basic data secured advanced our understanding of the oceans as an environment for life. From the viewpoint of the history of ecology, the most significant result of the CHALLENGER Expedition was the training of John Murray, whose influence on all phases of marine research prevailed throughout a long and active scientific career. This career was capped by the publication of *The Depths of the Ocean* (Murray and Hjort, 1912) which remains, after 40 years, one of the most essential references on the ecology of the seas. The CHALLENGER Expedition inspired a host of imitators, and much of the effort of governments and universities in the field of marine biology in the decades 1880–1890 was expended in sending out oceanographic expeditions and in writing reports on the collections. Yet as early as 1883 a young student in Denmark, who began his investigations with a conventional catalogue of the booty of a collecting cruise, displayed a sharp interest in the ecological factors governing the distribution of bottom animals.

This was, of course, C. G. J. Petersen, who in 1889 became the first director of the Danish Biological Station and conducted the investigations into the valuation of the sea which were published in a series of papers from 1911 to 1918. Before the publication of Petersen's first report (with Boysen-Jensen) in 1911, a few preliminary efforts at quantitative estimating of the productivity of the sea were made, notably by that remarkable self-made oceanographer James Johnstone (1908) and Fr. Dahl (1893). Nevertheless, it was Petersen who perfected the method, invented the instruments (notably the famous "Petersen grab"), and placed quantitative marine ecology on a sound footing. He also introduced fish tagging as a method of estimating populations. It was generally held, up to the time of the publication of *The Valuation of the Sea*, that plankton constituted the principal food of bottom animals, but Petersen advanced the hypothesis that detritus, especially the organic remains of *Zostera*, made up the principal food resource for the bottom fauna in the shallow Danish waters (Blegvad, 1945, 1951). This contradiction of the older view and the detailed work on the assemblages of bottom organisms, with its recognition of characteristic communities, was a sensation at the time and stimulated similar work in many other

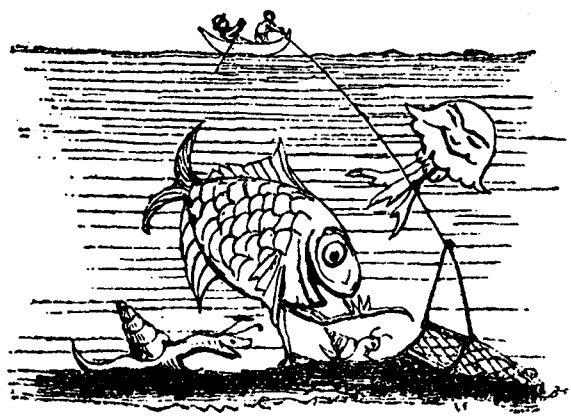

FIGURE 1.—*Edward Forbes' criticism of the dredge, as quoted by Petersen in* Valuation of the Sea

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parts of the world. Petersen himself considered his method an extension of Hensen's investigations.[6]

Although Petersen was the first to designate bottom communities on the basis of the most characteristic or abundant organisms present on a given type of bottom, his debt to the Danish plant ecologist Warming is obvious. The plant ecologists have always been ahead of the animal ecologists in their methods of recognizing and delineating communities for the obvious reason that plants will not move away and thus lend themselves more satisfactorily to statistical treatment of this sort. Sedentary marine animals are equally satisfactory in this respect; hence, it is inevitable that most of the work with communities in the sea has been done with plants and the fixed animals on hard substrates or with the relatively sedentary bottom forms.

A few words should be said at this point concerning the relation of such studies, as those of Petersen and his colleagues, to systematic zoology. Without a good knowledge of the flora and fauna of the region, it is impossible to make a detailed study of the populations. Steuer (1926) suggested that the work in Denmark could not have been done at Naples because the fauna of the Mediterranean is so much richer and still incompletely known. He might also have pointed out that the splended tradition of systematic zoology at the University of Copenhagen aided these researches (as Petersen himself implies in his introduction to his initial paper, 1911), and that without a staff of systematists it is impossible to study even an impoverished fauna. This seems to be one of the principal reasons why such studies as Petersen's have not yet been attempted in North America.[7] However impractical they may seem to some fisheries biologists and even to some ecologists, studies in systematic zoology and botany are a necessary preliminary to critical work in ecology. Many of the great students of ecology have also been highly competent systematic zoologists, including Forbes, Milne Edwards, Verrill, Möbius, and Herdman, and many others, including Petersen, were trained as systematic zoologists.

At about the same time that Petersen became director of the Danish Marine Station, the Marine Biological Association of the United Kingdom, which was organized in 1884, opened its laboratory at Plymouth. Although the laboratory began, at its outset, investigations of fisheries problems, its research program has been guided by individuals and universities, with the result that problems of marine ecology and physiology have received attention. Indeed, it would be possible to compile a satisfactory textbook of marine ecology from the back issues of the Journal of the Marine Biological Association alone. The Marine Biological Association was inspired in part by the example of the Zoological Station at Naples and in part by the United States exhibit at the International Fisheries Exhibition in London in 1883. T. H. Huxley

[6] While the importance of detritus in the economy of the sea has never been seriously questioned since Petersen's work, the idea that the breakdown of *Zostera* was necessarily the principal food resource in the shallow waters of Denmark has been upset by the eel-grass disease epidemic of the 1930's which removed the eel grass, at least as a serious component of the economy, without affecting the organic production of the waters as a whole (Poulsen, 1951; *see also* Burkenroad, 1951, p. 196 [note] in which this is discussed on theoretical grounds).

[7] It is also in part because the United States Bureau of Fisheries was too often placed in the hands of politicians and fish culturists and was never able to carry out the example set in the golden seventies by Verrill and Möbius. A more fundamental reason is that the Fish Commission clung to Baird's original idea that fluctuations in fish populations were the result of fishing pressure, and conducted its investigations accordingly. Is there any connection, incidentally, between the publication of a translation of Haeckel's Plankton Studies in 1893 and the failure of the Bureau of Fisheries to conduct any serious plankton work until Bigelow's investigations in the Gulf of Maine in 1912?

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presided at the original meeting in 1884. It was Sir E. Ray Lankester, however, who, as the first secretary, did most to start the Association and guide it through its formative stages. Early in its career, the Plymouth Laboratory became associated with practical fisheries investigations, when the Association was asked by H. M. Treasury to undertake the English share of the work of the International Council for the Exploration of the Sea.[8]

At the present time the program of the Plymouth Laboratory is concerned with the problems posed by these questions:

> The first is how much living matter can the sea produce, what are the variations and causes of variation in productivity, and how do the organisms obtain the materials necessary for life? The second is how do marine animals in general live, how do they fit their various individual environments, and what alterations in the conditions of their environment can they appreciate? (Russell, 1948).

It would be difficult to find a better summary of the aims of modern marine ecology than these questions, although a more explicit statement as to the interactions of the organisms themselves might be added.

A sketch of the historical development of fisheries research, even as brief as this, would be incomplete without some mention of the active school of fisheries researchers at Liverpool under the direction of W. A. Herdman, the intellectual heir of Edward Forbes, and the phenomenally long career of W. C. McIntosh at St. Andrews. Herdman founded the laboratory at Port Erin, Isle of Man, and compiled the first history of oceanography (1923). Many fisheries researchers in Britain acknowledge their indebtedness to his inspiration. Not the least of these was James Johnstone, whose *Conditions of Life in the Sea* (1908) was the text for many prominent English fisheries biologists of the present generation. McIntosh is best remembered as director of the station at St. Andrew's and as a discerning and sometimes disconcerting critic of fisheries research and theories. In Russia marine ecological investigations were placed on a sound basis by S. A. Zernov, whose *Contribution to the Knowledge of the Life of the Black Sea* (1913) was prepared with a thorough knowledge of the work of Petersen, Johnstone, and McIntosh, among others. Zernov later wrote an excellent textbook, *General Hydrobiology* (1931), which was reissued in a revised, posthumous edition (1949). The quantitative methods introduced by Petersen have been extensively used in Russia by Zenkevich, whose "*Fauna and Biological Productivity of the Seas*" (1947) is a summary of this work.[9] Significant work with bottom communities has also been conducted by Vatova in the upper Adriatic, especially in the Lagoon of Venice.

The study of "self conscious ecology" (to use the phrase of Allee *et al.*) developed in the meanwhile in the rather specialized field of zonation on the shore. Many studies of individual behavior and relationships of animals were made, most of which might be more properly considered natural history or autecology, rather than the compre-

[8] The International Council for the Exploration of the Sea was organized in 1899 as a co-operative effort of the governments of northern Europe and the British Isles. Among the moving spirits responsible for this organization may be named Sir John Murray, Johan Hjort, and C. J. G. Petersen. While it has restricted its investigations primarily to the North Sea and the northern Atlantic between Scandanavia and Greenland, it is nevertheless the outstanding research organization concerned with problems of pure and applied oceanography and fisheries problems.

[9] Unfortunately we have not been as enterprising as the Russians in translation; there are Russian editions of Johnstone, Murray's *The Ocean*, and Russell and Yonge's *The Seas*, but no standard Russian work in hydrobiology has been translated into any other language.

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hensive synecology characteristic of most of the fisheries research. Such studies of the "environmental physiology" of individual organisms are an essential part of the work of ecologists and are especially needed in application to paleoecology, however little they may contribute to our understanding of populations. Among the noteworthy contributions in this field of environmental physiology we may mention Krogh's *Osmotic regulation in aquatic animals* (1939), Pelseneer's *Essai d'éthologie zoologique d'après l'étude des Mollusques* (1935), a summary of the life-long studies of a master malacologist, and the MacGinities' (1949) account of their natural history researches. It might be mentioned that many studies of "marine sociology" or "bionomics" have been as drily descriptive as a report on the anatomy of some animal and are of little more than academic interest.

An exception to this judgment is the detailed work of Gislén (1929; 1930), who studied the rocky subtidal environment of the Gullmar Fjord. With the use of diving gear and counting frames, Gislén catalogued the various hard-bottom associations and computed their biomasses and production of organic matter. In doing this he combined the methods of Petersen and of the students of intertidal zonation with the most intensive use of diving gear up to that time. His work, with its detailed attention to hydrographic as well as ecological factors, provides a model for future studies with the self-contained diving equipment now coming into wide use.

Up to the 1930's studies of shore populations, intertidal zonation, or littoral bionomics were the particular favorite of French investigators, following the venerable tradition of Audouin and Milne Edwards. The leading workers in this field have been P. M. de Beauchamp, E. Fischer-Piette, and Th. Monod, among zoologists, and the algalogist J. Feldmann. Around 1930, however, investigators on almost every temperate coast in the world turned their attention to the seashore, and the result has been a veritable deluge of papers on the general subject of intertidal zonation or seashore bionomics. The most important contributors to this literature have been T. A. and Anne Stephenson and their colleagues, who conducted a 10-year survey (1931-1941) of the South African intertidal (Stephenson, 1947), and have since turned their attention to North America. Recent studies in this field, too numerous to mention here, are reviewed in Chapter 18.

Another approach to the study of communities of hard substrates has been through the experimental device of test squares or blocks, first used by Fr. Dahl (1893) in the lower Elbe. Much of this work, concerned with the time and rate of settling of fouling organisms, or the settling of oyster larvae, has had an economic motivation, but some studies of this nature have been carried out over a period of several years and have yielded valuable information about the development of communities and the variations of populations. Among the most noteworthy of these is the study by Coe (1932; Coe and Allen, 1937) from 1926 to 1935 at the Scripps Institution of Oceanography at La Jolla.

It was about the same time that studies in intertidal zonation became so popular that the original lines of inquiry followed by Edward Forbes were taken up again, and paleoecology began to be developed primarily as a branch of paleontology. The leaders in this movement were T. Wayland Vaughan, who became interested in the interpretation of past environments through his work on corals, and the German

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paleontologists O. Abel and Rudolf Richter. As director of the Scripps Institution of Oceanography from 1923 to 1936, and through attendance at various meetings and committees, and travels to many countries (Vaughan and others, 1937) Vaughan reiterated his text:

> We need to know for geologic purposes the ecology of all the important groups of marine organisms; and the ecology should not be considered merely in an empirical way but it should be based on the deepest ascertainable mechanical and bio-chemical foundation (Vaughan, 1924, p. 331).

It was primarily as a result of Vaughan's activity that the Committee on Marine Ecology was set up, and this treatise indeed owes its existence to him. As a student of coral reefs, Vaughan carried on the traditions of his American predecessors, James D. Dana, Alexander Agassiz, and A. G. Mayer, devoting his studies especially to the Antillean-Caribbean region. Vaughan was in fact one of the few workers who combined studies of living and fossil organisms. Studies of coral or tropical reefs have been intimately associated with geology from the beginning, since Darwin first recognized the relation of coral formations to changes of level between the land and sea, but surprisingly little of the literature on coral reefs contributes more than description of the environment, and it has been only since the work of the Great Barrier Reef Expedition of 1928–1929 that much attention has been given to the ecology of the reef mass as a whole.

In developing his advocacy of paleoecology, Vaughan leaned heavily on the classic work of Johannes Walther (1893–1894), which seems to have been ignored by ecologists in general in spite of the esteem in which it may be held by geologists. In his presidential address to The Geological Society of America, Vaughan (1940) outlined the rationale and methods for paleoecological studies, using as specimen examples a number of recently published papers which he described in some detail. It was in this paper, somewhat unfortunately titled, that Vaughan introduced a scheme of temperature zonation (pp. 444–445) which has been widely used by paleontologists.

In the meanwhile, paleoecology had developed in Germany under the leadership of O. Abel, with the establishment in 1928 of the journal Paleobiologica. The direct method of studying an existing marine environment with the view of interpreting fossil conditions was adopted by Rudolf Richter of the Senckenberg Museum. His studies of the shallow flats near Hamburg, begun in 1920, led to the establishment of the institute "Senckenberg-am-Meer" in 1928 and the publication of a long series of papers in Senckenbergiana. This work has been described, in a general way, by Bucher (1938). While our discussion is restricted to developments in *marine* paleoecology, it must be mentioned that the study of fossil floras has been a fruitful field for paleoecologists, and that much of the recent literature which might be classified as "paleoecology" is in fact the paleoecology of terrestrial floras (Clements and Shelford, 1939). These studies bear directly upon attempts to reconstruct the climatic zones of the past and must be considered by marine paleoecologists. The work of Chaney on fossil floras and their bearing on continental drift (1940) and of Axelrod on West American Tertiary floras (1950; 1952) are cases in point.

The development of marine biogeography, which draws heavily upon paleontology and is properly a branch of ecology in its broadest sense, is discussed in Chapter 13.

Another line of inquiry which has long interested ecologists is the study of estu-

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aries. Forbes (again) recognized the significance of salinity changes and sedimentation in estuaries, especially as related to fossil assemblages (Forbes, 1844, pp. 153–154), but the intensive studies of estuaries has been a comparatively recent development. Dahl's work on the Elbe and the interest of Möbius in distribution as related to salinity have been mentioned in other contexts. One of the pioneer works combining observation of distribution and experimentation with the organisms concerned is that of Ferronière (1901). Much of the work with oyster biology, especially in North America, has been a branch of estuarine ecology, and significant work has been done in England since the turn of the century by various investigators associated with the Plymouth Laboratory. One of the classic investigations was conducted in the delta of the Ganges and Chilka Lake by Annandale (1922), but the most extensive work with estuaries and brackish waters has been done in Holland and Germany and on the borders of the Black Sea. Among the best-known students should be mentioned H. C. Redeke, who provided the original classification of brackish waters (1922), Adolf Remane at Kiel, P. Korringa in Holland (1952) and G. Antipa in Romania, who worked on the delta of the Danube. In the last few years surveys of estuaries from both hydrographic and ecological aspects have been conducted in Australia, South Africa, and North America. In the United States classes in estuarine ecology have been introduced, and an Institute devoted to the problems of Chesapeake Bay has been established. The paleoecological applications of estuarine investigations have been suggested by Gunter (1947).

The continued need of fisheries researchers for an understanding of the basic economy of the marine environment and the interest of workers originally trained in limnology in problems of larger scope than the "microcosm" of a lake have been combined in a line of research which might best be characterized as "dynamic ecology." The studies in marine productivity at the Plymouth Laboratory by H. W. Harvey (*see especially* 1950), and A. C. Hardy and their colleagues, the plankton and productivity research of E. Steeman Nielsen (1952) in Denmark (and aboard the GALATHEA), and of G. E. Hutchinson at Yale and George Clarke, Gordon A. Riley and Bostwick Ketchum at Woods Hole on plankton cycles indicate the direction which much marine ecological work will probably take in the next few years. A general statement of the problem is given by Clarke (1946), and Ketchum (1951) has provided a summary of plankton researches. For two reviews of fisheries investigations *see* Graham (1954) and Herrington (1954). An especially interesting phase of productivity research is the experimental fertilization of restricted regions of the sea. The largest experiment of this type was carried out in Scotland, by adding superphosphate to Kyle Scotnish (Gross *et al.*, 1950). This was primarily an experimental study of nutrient cycles "rather than economic problems of marine pisciculture."

The researches in productivity and nutrient cycles are leading to an intricate synthesis of many previously separated lines of inquiry, and the symbolic language of mathematical expressions is often necessary to express the relationships involved. An idea of the ramifications of these inquiries is given by Conway (1943), pages 360–380 of Hutchinson's monograph (1950) on the guano deposits of western South America, a problem intimately connected with the cycles of productivity in the sea, and the work of Riley (1947a; 1947b) on plankton cycles. It is interesting to note in

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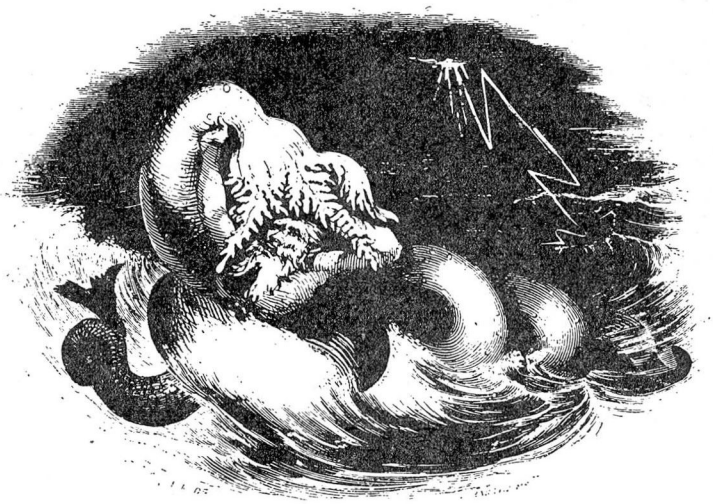

FIGURE 2.—*Poseidon in the clutches of a holothurian, or, the ecologist's dilemma*
From E. Forbes' *British starfishes*

this connection that the hypothesis put forward by Pütter (1909) to the effect that dissolved organic matter in the sea constituted an important component of the food of plankton organisms is being re-examined after the denial of its validity by Petersen and his colleagues, and that serious attention is now given to dissolved organic substances, especially in colloidal form, in the sea although their significance as a direct food source remains uncertain (Keys *et al.*, 1935; Fox, 1952). The demonstration by MacGinitie (1945) of mucous feeding nets in certain worms capable of straining out larger protein molecules and mucous sheets in lamellibranchs which trap material in colloidal suspension suggests the manner in which some organisms at least may utilize this material.

In summary, we may say that the present trend in marine ecology is toward a synthesis of the knowledge of the old-time naturalist, of the student of natural assemblages as apparently static end points, of the economic biologist concerned with fisheries problems, and of the geochemist concerned with the cycles of erosion and deposition in geologic time. Such a synthesis, which must treat the oceans of the world and their margins as one complex, interrelated environment, will be the logical fulfillment of the work of such pioneers as Forbes, Möbius, and Petersen. There are many who believe that such an understanding of the oceanic environment is essential to the continued survival of man, and we have seen how much of the research in marine ecology has had an economic motivation. It is not our purpose to contribute to such optimistic hopes, either for synthesis or man's survival, but to summarize as concisely as possible the present knowledge of marine ecology as a necessary step toward these ends.

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Chapter 2

Classification of Marine Environments*

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The classification and terminology presented in Figure 1 are results of several years of discussion by the Committee. Every attempt was made to develop a scheme acceptable to as many workers as possible and which would not upset well-established usages. Our first attempt was compiled on the basis of a questionnaire which included an original diagram by Siemon W. Muller (which has been expanded as Fig. 2). There were more than 20 replies to this questionnaire, and the preliminary classification was published in Annual Report No. 9 of the Committee (Ladd *et al.*, 1949). A second version, attempting to answer later criticisms and suggestions, appeared in Annual Report No. 11 (Ladd *et al.*, 1951). These preliminary versions have already found their way into textbooks and special papers, although some of the earlier terms were subsequently abandoned, as indicated in the following discussion.[1]

As our knowledge of the sea and its life develops, the terminology employed to describe the environment and its life increases in complexity. The efforts of many workers, often in apparently unrelated fields, to apply old terms or invent new ones for specific situations have resulted in duplications, overlapping, and conflicting meanings. The term littoral, for example, has been used to mean the region between high-tide and low-tide levels (the "space between tidemarks" in the words of Forbes and Hanley, 1853, who seem to have been the first to define the word in this sense), the region between the shore and somewhere between 20–50 fathoms, or the entire continental shelf. As early as the 1860's Lorenz (1863) proposed supra-littoral for the term above extreme high water, and sub-littoral for the region between 2 and 14 fathoms. Since that time variations have been rung upon this basic term littoral, so that we have epilittoral, praelittoral, supratidal, or subterrestrial, all more or less the same as supra-littoral, and adtidal, infralittoral, subtidal, and elitoral for the lower end of the series; the region in between has had to be called "eulittoral" to separate it from the others. It should be understood that we are not referring here to the realities or limits of these subdivisions or the problems of zonation on the shore (*see* Chapter 18), but to the manner in which the terms have been applied.

While we may agree that littoral is the oldest and most universally understood term for that region, it is unfortunate that it has such vague limits. As the term for

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[1] The diagram from Annual Report No. 11, for example, was used in modified form by S. P. Ellison (Jour. Sed. Petrol., vol. 21, 1951, p. 216), in Odum's *Fundamentals of Ecology*, and in Clarke's *Elements of Ecology*, and in Puri's study of the Miocene of Florida (*Fla. Geol. Surv., Geol. Bull. 36, p. 43, 1953*).

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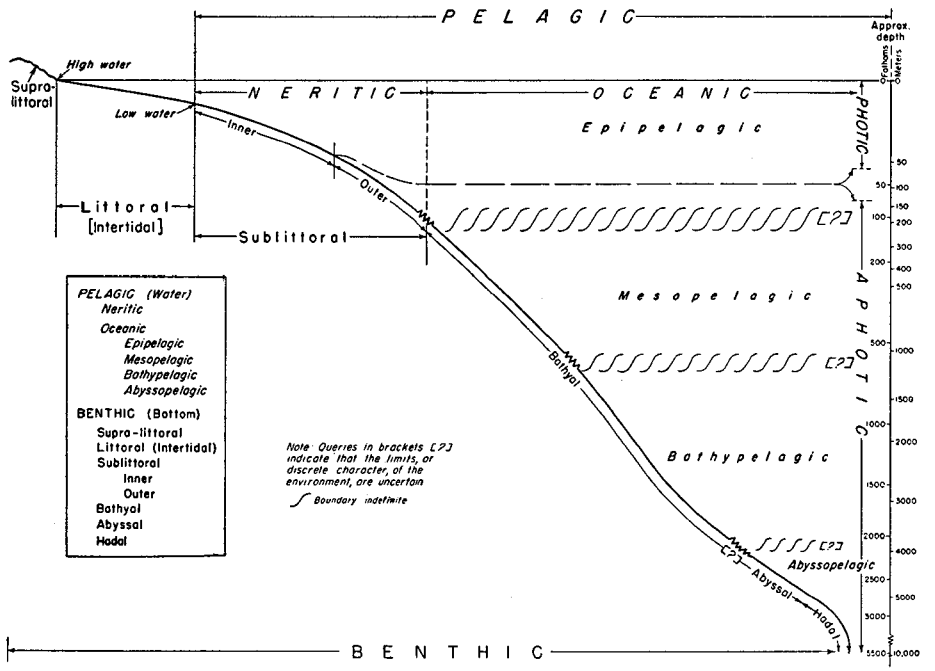

FIGURE 1.—*Classification of marine environments*

the environment at the edge of the sea, whether limited by the tides or extending vaguely downward, it is used in virtually every language, and one might as well try to introduce a new word for ocean as attempt to abandon littoral. In English, "intertidal" (or in French, "intercotidale") is conveniently self-limiting in meaning, but the term requires translation to be conveyed in other languages. It also requires tides, which are lacking or inconspicuous on many shores. It is also protested that such a term as supratidal, when used for the region above high tide when there is a tide, is improper because it extends the term beyond its natural limits—*i.e.*, how can there properly be a supratidal zone when such a zone is *above* the tide? Logically, the same objection might be made against supralittoral when littoral is restricted in its meaning to "intertidal." People who are troubled by such inconsistencies may consider using the terms proposed by Du Rietz (1940; 1947)—*i.e.*, geoamphibiontic, hydroamphibiontic—, although these terms were devised for a more specialized purpose. While we prefer to restrict "littoral" to intertidal limits or seasonal changes in level, it is still used occasionally in its wider meanings, which should be obvious from the context. Terms based on characteristic plants or animals are unsatisfactory for more than local usage because of the uneven distribution of the organisms concerned —*e.g.*, a "Laminarian" zone often occurs where there are no *Laminaria*.

One of the difficulties about the use of "littoral" is that there has been a vacuum, insofar as acceptable terminology is concerned, for the shallow bottom and its life, between the low-water line and the edge of the continental shelf. The life of this region

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has been variously referred to as "sublittoral benthos", "neritic benthos", or simply as shallow bottom or coastal flora and fauna. A classification of environments must find a place for the conditions not represented by the shallow muddy-sandy bottoms of the temperate and boreal regions of the northern hemisphere for which such a term as "sublittoral" has been adequate. The term for the aquatic environment overlying this region, the water over the continental shelves, is "neritic," proposed by Haeckel to complement "oceanic", the envionment of the "blue water."

A divergence of views concerning the use of the term "neritic" has been evident in recent years. In the sense defined by Haeckel it has been employed by biologists, but paleontologists, working with the remains of the benthic organisms of shallow seas, have applied the term to the environment of the bottom itself. By verbal extension of this concept of the meaning of the term, it has been applied to the intertidal or littoral (*sensu stricto*) as "upper neritic" (Ladd *et al.*, 1951). While such a usage is implicit in the French "zone néritique" of the Société de Biogéographie's 1940 symposium volume (Legendre, 1940), it is still broader in implication than the suggested divisions of the neritic which oblige us to regard the important region between water and the maximum depth of large attached algae or of reef-coral growth as "middle neritic." The objection here is not to the recognition of subdivisions of the bottom biota, but to the implicit subdivision of the water masses of the shelf which is the logical consequence of this usage. When a difference in the plankton population has been recognized, for example, the terms "inner" and "outer neritic" have been used to describe them. Thus, "inner neritic plankton" would overlie a "middle neritic" bottom fauna. Therefore, it seems best to adhere to Haeckel's usage for neritic and use other terms for the bottom environment. As early as 1877 the Swedish botanist Kjellman divided this region into sublittoral and elittoral (Gislén, 1930), but Appelöf, in one of the most influential works of the early twentieth century (Murray and Hjort, 1912), shifted the sublittoral down to Kjellman's elittoral, and the confusion has been growing continually worse (Fig. 2).

Gislén (1930) proposed the term *sanidal* (of or pertaining to the shelf), but this term has not been generally used by other workers. Several authors, especially Pruvot, have used the term *coastal* for this outer region of the bottom beyond the algae. In a text which has enjoyed wide influence in North America (Hesse, Allee, and Schmidt, 1937), the intertidal and adjacent bottom, down to the attached algae limit, was referred to as "eulittoral", and the term "sublittoral" was employed in the sense of Appelöf. This scheme was adopted by Sverdrup, Johnson, and Fleming (1942), with slight modifications. In the 1951 edition of Hesse, Allee, and Schmidt, the classification used in the oceans was adopted.

It is plain from Figure 2 that the continued use of littoral in its classic sense as pertaining to the marginal zone of the sea, whether delimited by tide levels, seasonal water levels, or effects of wind and waves, will cause the least confusion. Prefixes like "eu" take the edge off this fine old term and should be rejected; if the region being discussed is not littoral, it is supralittoral or infralittoral. In discussing a region where tidal differences are pronounced, "intertidal"is a convenient term. As for the benthic environment of the continental shelf, it is probably too late to discourage the further

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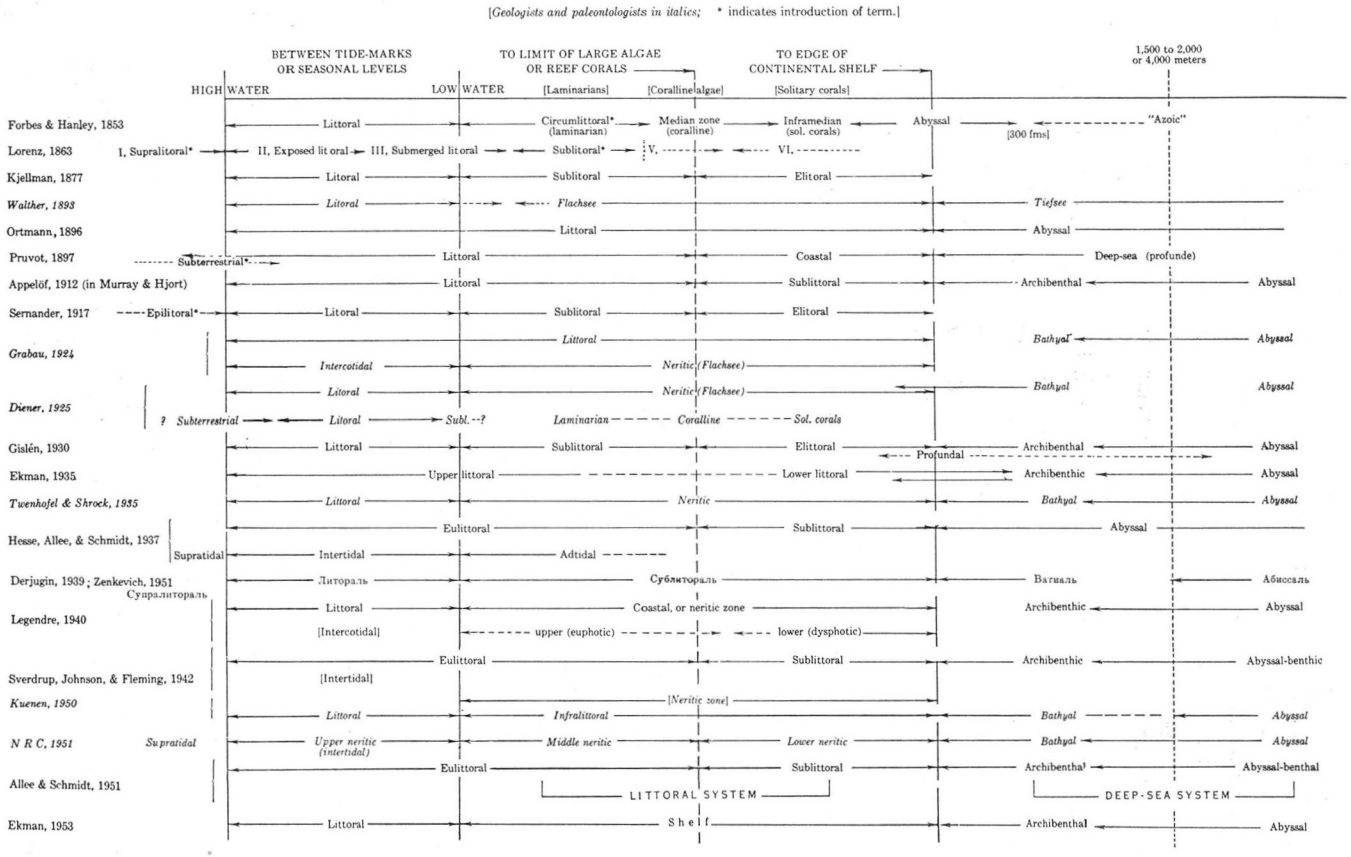

FIGURE 2.—*Terminology of major benthic divisions of the sea*

Based on a compilation by Siemon W. Muller.

use of "neritic", but certainly this term should be used in consistency with the conditions in the overlying water masses. In his English edition, Ekman (1953) advocates and uses the term "shelf".

There has been less argument—and less confusion—about the high seas and the deeper parts of the ocean, perhaps because our information to date is too scanty to tempt the coiners of terms. Archibenthal (or archibenthic), continental slope, bathyal, and archibathyal have frequently been applied to the environment of the continental slope down to about 1000–2000 meters, but their usage has not gone much beyond the diagrams in textbooks. We suspect some difference between the environment of the intermediate bottoms and the great abyssal depths, but we do not know where the transition is. The subdivision of the waters above the bottom, the great pelagic region, is more satisfactorily established, because of the greater body of work dealing with planktonic and nektonic organisms. (Plankton and nekton, it should be mentioned, are descriptive terms for types of organisms, and it is unnecessary to use such a term as "nektoplanktonic" to describe the *environment*). Such terms as pelagic—of or pertaining to environment inhabited by plankton and nekton, often considered synonymous with the "high seas" (*i.e.*, oceanic), and its various combinations—are universally understood. The term epipelagic has long been in use as indicating the *oceanic environment* far from shore, and in view of this usage it seems best to reject the term epilittoral widely used by Scandinavian botanists for the supralittoral since here the prefix "epi" has exactly the opposite meaning that it has in "epipelagic."

In Figure 1 the major environmental divisions are indicated in the conventional manner. Because the limits of the various regions vary with latitude, underlying geologic structure, and various environmental factors such as temperature and light penetration, it seems best to indicate the depths in a somewhat flexible manner. Some idea of the proportionate representation of the various regions is better conveyed by indicating them on a hypsographic curve of the ocean bottom (Fig. 3). From this it can be seen that the regions which have caused most of the argument over terminology are comparatively insignificant in area and volume. However, they are most significant from the biological standpoint, and it must not be forgotten that little is represented in the fossil record beyond the continental shelf, and that consequently the neritic zone and continental shelf are the most important environments in terms of the geological record and, therefore, from the viewpoint of paleoecology as well.

Recent investigations in the deep sea, as discussed in Chapter 22, indicate that further refinement in the classification of deep-sea environments is necessary. The abyssal region, roughly between 2000 and 3000 meters, may be better defined as the region in which the temperature is never above 4°C, and extends downward to about 6000 meters. The distinct characteristics of the fauna of the deep trenches suggest that we are dealing with another environmental region, for which Bruun has proposed the term "hadal" (from Hades); Zenkevich uses the term "super-oceanic deeps".

The region below 10°C is termed the "psychrosphere", as opposed to the warmer upper regions, the "thermosphere", by Bruun. This seems to be a somewhat better choice of terms than "stratosphere" and "troposphere" which are used by German physical oceanographers. An example of this usage will be found in the Chapter on the Black

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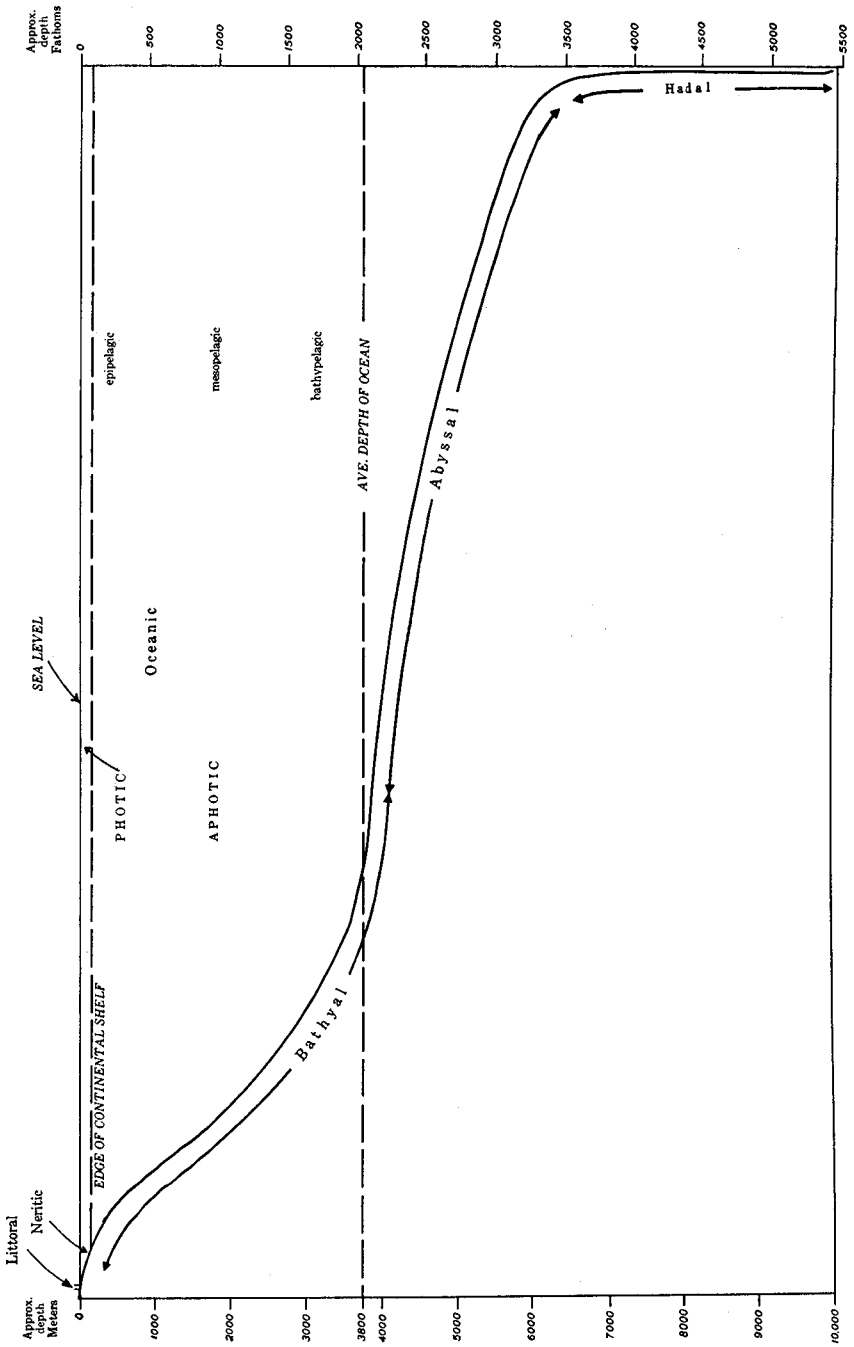

FIGURE 3.—*Classification of marine environments on a hypsographic curve*

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Sea (Chapter 25), where the discussion is based on oceanographic work in which these terms are employed. Although drawn by analogy from meteorology, the terms are inverted in application to the water masses, so that the bottom of the upper layer, or troposphere, lies on top of the lower layer, or stratosphere. Most American oceanographers avoid this terminology, and it seems even less necessary in an ecological context. For some reason ecologists have not as yet paid as much attention to temperature as a factor in the major divisions of the ocean, although it is of primary concern to biogeography (Chapter 13), but have concerned themselves more with the factor of illumination, to the extent that photic and aphotic are familiar words. The regions of illumination do not, however, coincide with temperature, and the photic zone is only a small part of the thermosphere. As with littoral, we see no reason to weaken the basic term of the series by adding the prefix, so that the division of the sea on the basis of the illumination is into "photic" and "aphotic," and if the intermediate is required, "disphotic", zones.

The extension of the term abyss to the edge of the continental shelf, a definition apparently introduced by Ortmann (Fig. 2) and reiterated by Hesse, is still retained by some European workers, with some inevitable confusion. For example, we find a discussion of a meso-abyssal fauna at 60–500 meters on the Algerian coast (Dieuzeide, 1954) and a statement in the recent text by Bodenheimer (1955) that the living representatives of ancient forms, such as *Lingula*, *Spirula*, and *Chimaera* find their last refuge in the abyssal zone—*i.e.* at depths greater than 200–500 meters (although this is true only for *Spirula* in this definition of abyssal, and true for none of them if we define abyssal as the region below 2000–3000 meters).

Such conflicts in terminology are even more pronounced in the classification of waters by salinity. We find in some schemes of classification that sea water, of 35 ‰, is not necessarily "marine"; some European hydrobiologists who work with the lowered salinities of the Baltic consider anything down to about 18 or 20 ‰ "marine", while among workers in the same region there is even more lack of agreement concerning the other subdivisions (Hiltermann, 1949) (Fig. 4).

Although seldom precisely defined, the terms "brackish" and "estuarine" are clearly separable by usage. While "brackish" itself may be a vague term which has been applied to water which is not quite fresh as well as to highly concentrated brine, it carries with it a connotation of relatively stable conditions, or at any rate a seasonal stability which is not included in the meaning of "estuarine". Estuarine waters are subject to tidal and seasonal variations (Chapter 23).

The widely used brackish-water spectrum scheme of European workers is based on the biological characteristics rather than the hydrographic properties of the waters concerned, although chlorinity is the secondary base for the classification. Since the biota is in effect a resultant of prevailing conditions, this scheme does provide a rough key to hydrographic conditions. As originally proposed by Redeke (1922), this classification was related to chlorinity rather than to the total salinity, since the salinity determinations are derived from chlorinity content according to Knudsen's formula, and because the proportions of the ions are more variable in coastal and river waters than in the sea. For practical purposes, however, the salinities are now used (Table 1).

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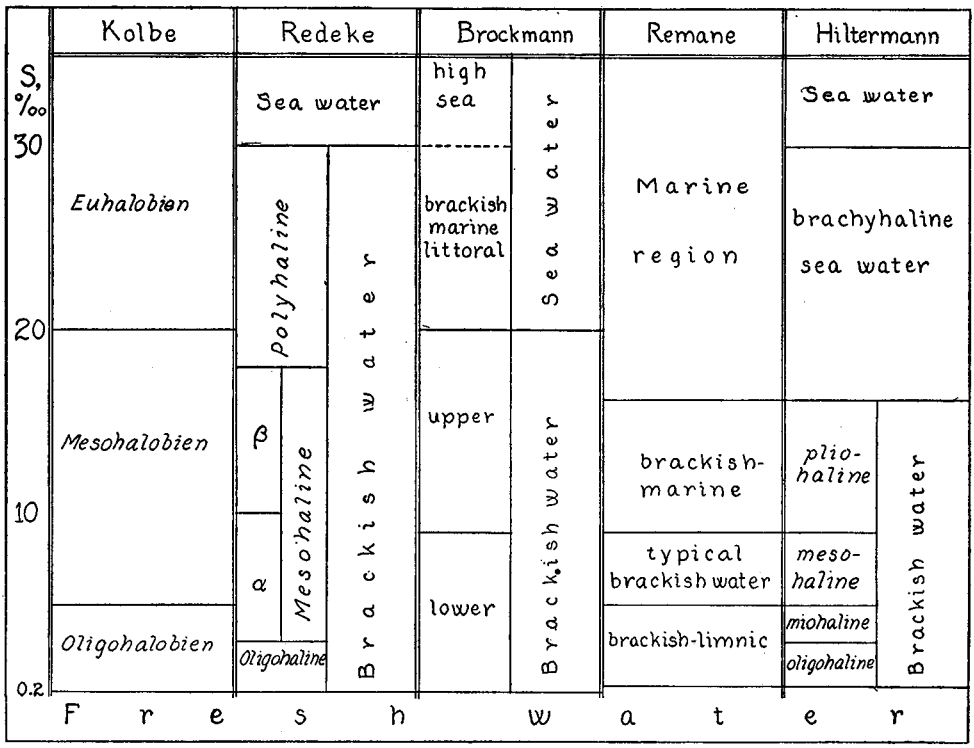

FIGURE 4.—*Terminology of European brackish waters*

After Rottgardt (1952)

Remane (1934; 1940) proposed a somewhat different system, using such terms as "limnetic-brackish mixed area" and "marine brackish mixed area", and extending the limits for marine water down to about 16.5 ‰ salinity. This latter modification, as Dahl (1948) points out, seems to be based on Remane's experience with conditions in the Gulf of Kiel.

TABLE 1.—*Salinities*

Redeke (1922; 1933) Cl, ‰		Välikangas (1933) S, ‰
	Fresh water	
Less than 0.1	("Infrahaline")	Less than (0.2) 0.5
	Brackish water	
0.1–1.0	Oligohaline	(0.2)0.5–(2.0)3.0
	Mesohaline: alpha (Redeke);	
1.0–5.5	meiomesohaline (Välikangas) beta (Redeke)	(2.0)3.0–8.0(10.0)
5.5–10.0	pleiomesohaline (Välikangas)	8.0(10.0)–16.5
10.0–17.0	Polyhaline	16.5–30.0
	Marine water	
More than 17.0	("Ultrahaline")	More than 30.0

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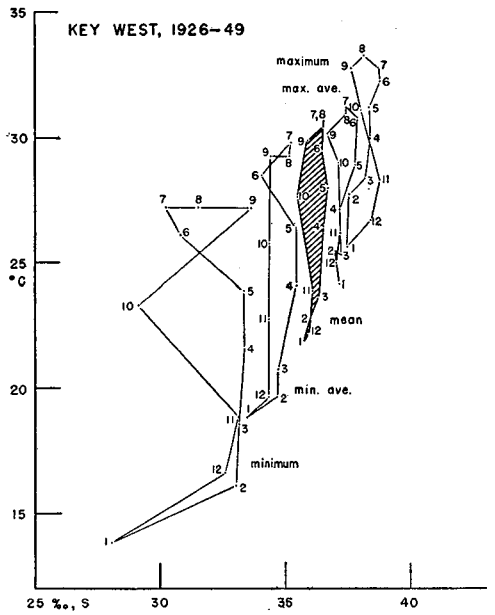

FIGURE 5.—*Hydrographic climate polygons for Key West, Florida*
(Hedgpeth, *in* Ladd *et al.*, 1951)

An additional environment, for which the term "metahaline" was proposed (Hedgpeth *in* Ladd *et al.*, 1951), is found in several parts of the world where shallow lagoons are connected with the sea, but subjected to excessive evaporation and inadequate fresh-water inflow. "Hypersaline" (sursalée) and "ultrahaline" have also been commonly used for such an environment.

In such variable environments as estuaries and brackish waters it seems better to present the features of the environment in some graphic form, as done by terrestrial ecologists for climate, instead of using terms which can apply to only a single factor in the environment. Temperature and salinity, for example, have been represented graphically according to their monthly means (Fig. 5). When several such "hydrographic climates" are plotted on the same graph, comparison of different regions will be simplified. (See Hedgpeth *in* Ladd *et al.*, 1951; Hedgpeth, 1953, for examples.)

It had been hoped to include in this discussion of classification a section on the shore lines, on a world-wide basis similar to that by Valentin (1952). At this time (1955), the conflicting views of various geomorphologists make this inadvisable, and the recent scheme proposed by Zenkovich (1954) is yet to be critically appraised by western students. For most ecological work, a simple description of the shore as "sand", "mud", or the like is adequate; refinements may be required for special work, but in such cases the services of a sedimentologist are also necessary.

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——Ibid: no. 11, 1950–51, 82 pp., 1951.

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MANUSCRIPT COMPLETED MAY 31, 1955

ADDENDUM

A committee of the *Commission Internationale pour l'exploration de la Mer Méditerranée* has adopted a benthic classification which compares approximately with that of Figure 1, p. 19, as follows:

Supralittoral	Supralittoral
Littoral	Mesolittosal
Inner sublittoral	Infralittoral
Outer sublittoral	Circalittoral
Bathyal	Epibathyal
	Mesobathyal
Abyssal	Infrabathyal
Hadal	Hadal

Although mesolittoral seems an unecessary neologism, the proposed usage of infralittoral and circalittoral will probably be preferred by many to the inner and outer sublittoral of our scheme. Details of this classification will be found in:

PÉRÈS, J. Le problème de l'étagement des formations benthiques: Rec. Trav. Station marine d'Endoume, Fasc. 21 (Bull. 12), pp. 4–21, 1957.

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Geol. Soc. America
p. 29–52, 7 figs.

Memoir 67, Vol. 1, 1957
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Chapter 3

Concepts of Marine Ecology*

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Every theory of the course of events in nature is necessarily based on some process of simplification and is to some extent therefore a fairy tale.

Sir Napier Shaw:
Manual of Meteorology

The terminology of the major environmental regions of the sea, considered in Chapter 2, is relatively simple; a comparable classification of the major ecological divisions is much more difficult. This is because ecological terminology is often based on subtle and at times incompletely defined concepts, and because many of the concepts of ecology have been developed with reference to terrestrial examples and conditions which are not always homologues of conditions in the sea. For a concise statement of the general concepts of ecology, *see* Dice (1955) and the short text by E. P. Odum (1953).

While it should be obvious that the greatest difference between land and sea as environments is that between air and water, the implications of this difference are not always considered, beyond recognition that the greater density of water (775 times that of air) makes it possible for aquatic organisms to float and do without rigid skeletal support, and that osmotic work is negligible for the many isotonic marine organisms. Water, especially sea water, carries particles about in a manner impossible in air, and, because of the essential continuity of ocean basins, there is in time a much more nearly complete mixture of substances carried about in the water. Theoretically, there is no real barrier to the complete mixing of particles carried about in the sea. Such mixing may require several thousand years for the world ocean and perhaps only a few hundred years in a given ocean basin, and, while this may be slower than aerial mixing, it may also be comparatively more nearly complete, at least for particles of especial value to organisms. Nevertheless, there are differences in various parts of the ocean, primarily because of temperature and current structure, and we do find major patterns of both water (*see* Chapter 5) and organisms (Chapter 13) although the boundaries associated with these patterns shift back and forth in space and time. Because of the great volume of the oceans, the quantity of particulate matter carried in suspension is immense (Chapter 14), and this quantity makes possible the enormous variety and numbers of organisms adapted to feed upon such material. (*See* Jørgensen, 1955, for a review of the quantitative aspects of filter-

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I am indebted to many friends and colleagues for advice and assistance in the preparation of this chapter; more often than not I have heeded their advice but have nevertheless persisted in my own opinions.

Parts of this chapter are taken from drafts by Gordon Gunter (Flux equilibrium and bottom community structure) and Maxwell S. Doty (Succession and climax).

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feeding invertebrates; also Turpaeva, 1953; Yonge, 1954a; 1954b; 1954c.) Such filter- or suspension-feeding organisms make up most of the epifauna and infauna of the sea bottoms (Chapter 17). Their numbers are greatly reduced in fresh water, and they are of course absent from the land. Another conspicuous difference between the organisms of land and sea is the extensive utilization (as would be expected of organisms in fluid medium) of actively motile dispersal stages, especially during the larval life, by sedentary and sessile animals in the sea. Some of the most critical problems of marine ecology involve the nutrition, dispersal, and eventual fate of the hosts of marine invertebrate larvae (Chapter 17).

Although the potentialities for mixing and diffusion and the consequent interdependencies are greater in the sea than on the land, this does not mean that the sea is a monotonously uniform environment, without well-defined regions. The impression gained from the example of the concentration of conservative elements in sea water, the common ions whose proportions are so constant that their gross concentration may be determined on the basis of chlorinity alone, is misleading when applied to other factors of biological significance. There are wide variations, both seasonal and from ocean to ocean, in the concentrations of nutrient salts (Chapter 11), particulate matter and metabolic products (Chapter 14), and dissolved gases, especially oxygen (Chapter 9). Such variations are reflected in the populations of fishes, in the outbreaks of red tides (Chapter 29), and in the fluctuations of littoral populations (Chapter 28). Some of these pronounced fluctuations in populations tend to recur in the same regions, an indication perhaps of a wider oscillation of factors, but no clear cyclic tendency has yet been demonstrated.

THE ECOSYSTEM

Thus we must remember at the outset that the sea is an aqueous medium in which, compared to the terrestrial biosphere, relationships and similarities in various regions and parts of the world are more significant than divergences and differences. No community of organisms in the sea is completely independent, and some are so intimately related, such as the great community of mid-water organisms to the near-surface plankton, that it is impossible to separate them. This is not to say that well-defined communities do not exist in the sea, for they obviously do, but that among many major marine communities the interdependencies are more pronounced than on land. Thus we must deal with interrelated systems rather than discrete communities in order to understand ecological processes in the sea. Community studies are of course an essential part of ecological study, but they are not the whole answer. The study of communities might be likened to the anatomy of ecology, whereas that of ecosystems, with their attendant complications of populations and energy transfer, would be considered the physiology of ecology. In Figure 1 we have, to continue this analogy, the ecological anatomy of the ecosystem of the Oresund, from which the temporal and energetic aspects have been omitted. Within such a complex of communities and their physical setting (the biotope-biocoensis of continental European ecologists), there are many cycles of various kinds, involving nutrition (Chapter 11), respiration (Chapter 9), and the skeletal requirements of organisms (Chapter 10). One of the most important of these cycles, or circular causal systems, is that of Carbon (Fig. 2).

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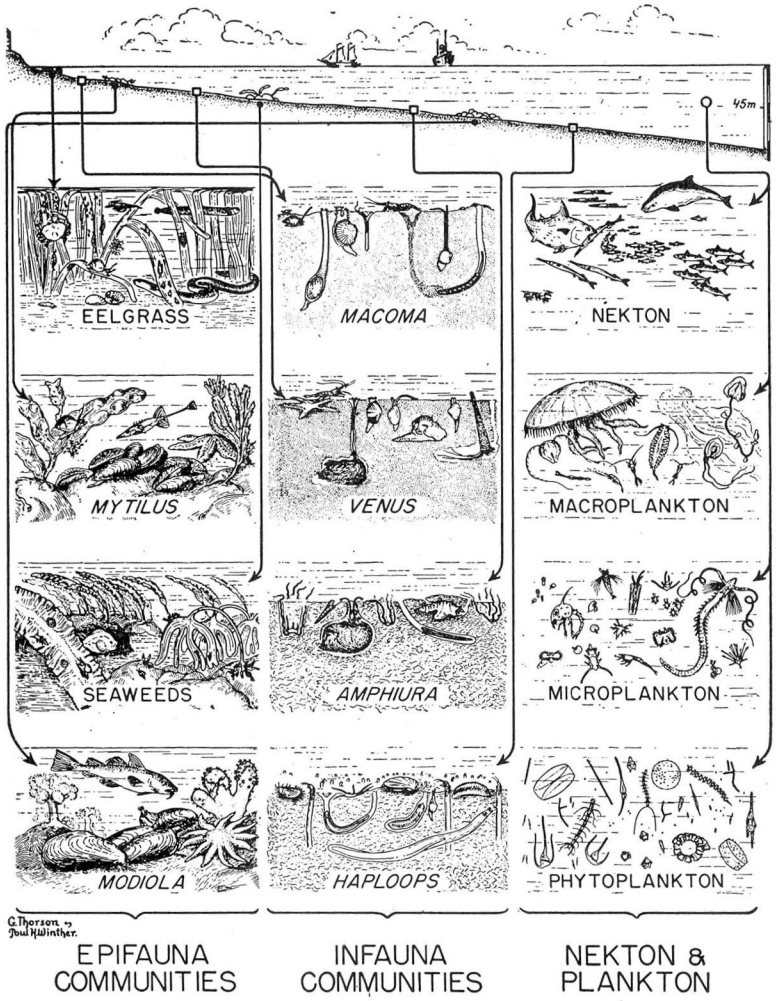

FIGURE 1.—*Diagrammatic section of the Danish Sound from the coast of Sealand toward Kullen*

Showing the various communities involved. (By Gunnar Thorson and Poul H. Winther; courtesy G. Thorson)

Such biogeochemical cycles leave their traces in the sediments, and eventually paleoecologists may obtain some idea of the magnitude of an extinct ecosystem through the biogeochemical approach. (*See* Volume 2, Chapter 24.) The complications of an ecosystem, with its cycles within cycles, is further emphasized when we consider the possible pathways of matter and energy in a comparatively simple ecosystem (Fig. 3).

The paleoecologist is drastically limited in his treatment of the marine environment because often he must deal with the remains of a single community from such a complex. Nevertheless a good paleoecologist, like a good paleontologist, should be able to reconstruct something from the few remains available to him, while the ecologist often loses himself in the forest of details before him. Such reconstruction, to be

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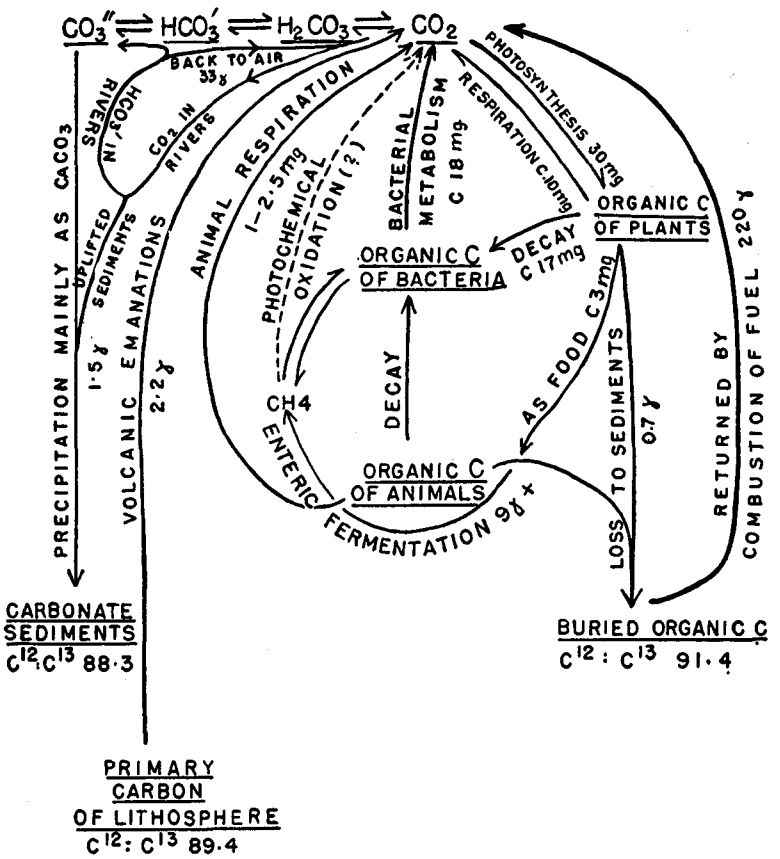

FIGURE 2.—*Carbon cycle* (*quantities as* $cm^2 \times year^{-1}$)

After Hutchinson (1948); (for more recent values, *see* Hutchinson, 1954, and Chapter 10 of this volume).

meaningful to an ecologist, must, however, attempt more than generalizations about temperature, depth, and substrate, which are physical aspects that may be inferred from a post-morten assemblage and may not necessarily be the conditions that governed the occurrence of the organisms concerned when they were alive. Such data alone, even when referable to an existing ecological complex, cannot be considered enough to tell us what is going on in nature's house, any more than scattered bits of information about the fuel bills and room arrangement can tell us what is really going on in the house next door.

The ecologist then, is interested in the sum of things, and his concept of nature is that of an ecological system or ecosystem:

"... The more fundamental conception is ... the whole *system* (in the sense of physics), including not only the organism complex, but also the complex of physical factors in the widest sense.... It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. These *ecosystems*, as we may call them, are of the most varied kinds and sizes They form one category of the multitudinous physical systems of the universe, which

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range from the universe down to the atom... Some of the systems are more isolated in nature, more autonomous, than others. They all show organization, which is the inevitable result of the interactions and consequent adjustments of their components. If organization of the possible elements of a system does not result, no system forms or an incipient system breaks up. There is, in fact, a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest. It is in this way that the dynamic equilibrium . . . is attained." (Tansley, 1935, p. 299–300; for further elaboration, *see* Evans, 1956)

Although the ecosystem concept is now generally current in ecology, it has recently been criticized as "too all embracing and subtle" (Andrewartha and Birch, 1954, p. 14), at least if ecology is to be understood as the distribution and abundance of animals in nature. Such a limitation of ecology is inadequate for the study of conditions in the sea, where conditions are, in fact, "all embracing and subtle." In so far as a general theory of life (as opposed to a special theory of ecology) is concerned, the ecosystem concept would appear essential. The general theory of open systems attempted by Von Bertallanfy (1950) is essentially based on ecology, although certain elaborations by Von Bertallanfy (1952) seem more philosophical than scientific. It might also be observed that many of the speculations about the origin of life are in essence ecosystem theories (Oparin, 1953; New Biology, No. 16, 1954; *see also* Chapter 4, Vol. 2); as Mainx (1955, p. 25) says, "every biological statement strictly speaking, not only relates to the organism but also takes in a part of the environment as well."

As our understanding of the complexities of natural systems increases, we find it progressively more difficult to separate clearly the "external" factors (except that of the prime energy source,

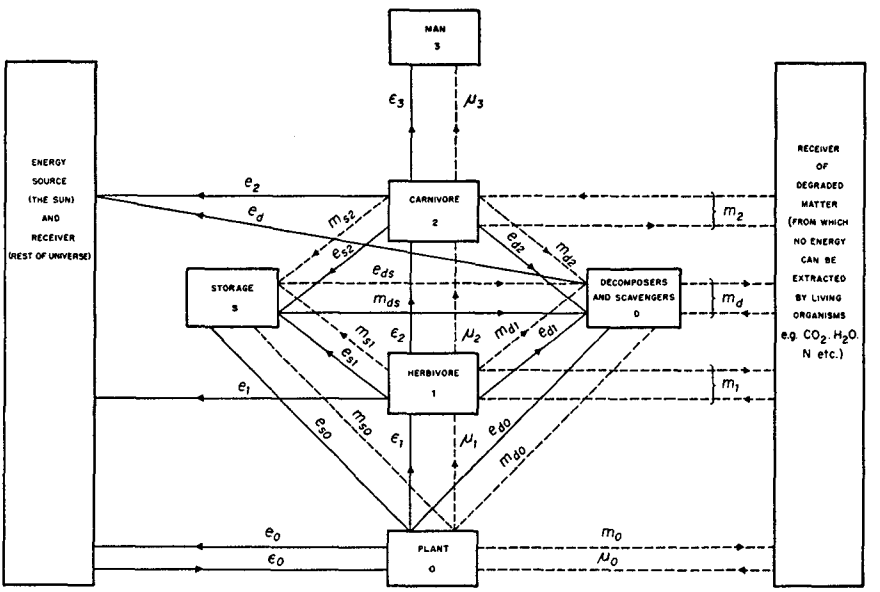

FIGURE 3.—*Diagram showing the relationships between the cycles of matter and energy in a simple biological system*

From MacFadyen (1948)

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solar energy), which we summarize in the somewhat metaphysical term "environment," from the "internal" factors of the organic complex itself. While the community concept remains a major aspect of ecology, the tendency seems to be to regard it as one of the phases of the ecosystem, a sort of living substrate, as it were, upon which the ecosystem operates, and to regard an established or "climax" community as an indication of a system in dynamic equilibrium. The formulation of the concept of a living system as an energy-converting engine capable of attaining a "moving equilibrium" with the environment was made by Lotka in his "*Elements of Physical Biology* (1925), a work now considered a classic of modern ecology. Lotka was careful to distinguish between the physico-chemical phenomena of equilibrium and steady state (in which the source, or input, is equal to the sink, or output) and the moving equilibria of biological systems. A similar concept, that of "flux equilibrium," which has not had the disadvantage of being widely misused, was stated by Lund (1928; 1931). An apparently similar concept was advanced by Von Bertallanfy, who coined the term *Fliessgleichgewicht* (flow equilibrium) in 1942, but adopted the term "steady state," which he considered "well defined" in his English writings (Von Bertallanfy, 1952, p. 125). The self-regulation of physiological processes, which is a prime corollary of such concepts as that of flux equilibrium, was long ago philosophically applied in the context of evolution (Holmes, 1948). It was termed homeostasis by Cannon (1932), and the word has now become fashionable in genetics and other disciplines and was recently discussed by Emerson (1954) as a factor of social and ethical evolution.

According to these various concepts, we can consider a living system, whether an individual, a species, or a population, or an ecological community as being capable, under the conditions of flux equilibrium and self-regulation, of several potentialities. It may grow or increase in volume, so that the amount of energy income is increased, or it may utilize energy more efficiently whether or not the income fluctuates. In the latter case there may be an increase in the complexity of the system (at this point it should be clear why such a term as flux equilibrium is better than steady state). If, on the other hand, the energy fails from causes outside the system, or from non-adaptive self-regulation within, the system falters and slowly dies out. Odum and Pinkerton (1955) have suggested that open systems "perform at an optimum efficiency for maximum power output, which is always less than the maximum efficiency," and apply their proposition to photosynthesis, communities, and civilizations, using "steady state" in the sense evidently understood by Von Bertallanfy, but not by physical scientists. Lotka anticipated the dangers of such reasoning, and it does seem that analogies between biological systems and the second law of thermodynamics are, in the present state of our knowledge, only approximate. "Out limited mental powers . . . are incompetent to deal directly with unexpurgated nature in all its complexity" (Lotka, 1925, p. 301).

TROPHIC RELATIONSHIPS

For problems of practical ecological analysis the ecosystem must be abstracted or simplified. The most useful simplification is that of trophic or feeding levels, which stems from the Eltonian pyramid of numbers. Elton's original observation was that in a given environment there is a "relative decrease in numbers at each stage of the food chain," which results from the fact "(a) that smaller animals are preyed upon usually by larger animals, and (b) that small animals can increase faster than large ones, and so are able to support the latter" (Elton, 1927, p. 69–70). Thus the rate of reproduction at the different levels of the pyramid is an essential part of this concept, and the Eltonian pyramid should not be confused with a pyramid of biomass or "standing crop." A standing-crop pyramid, in terms of mass, may in fact be inverse, as illustrated by the homely analogy of the contents of a kitchen pantry as compared with the consumers in the household. In Figure 4 the inverse relationships between numbers and mass, as observed in a square meter of bottom near Plymouth, are indicated. It is true, of course, that each level of this pyramid is not necessarily dependent upon the production of the level immediately below it, but it would be hard to find such an example in nature. The simplified scheme of energy flow or transfer

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through the ecosystem from the producing level through the various consumer—or trophic—levels from herbivores to carnivores was originally set forth by Lindeman (1942). When the problem is stated in such terms, our major concern is with "productivity," "production" and "standing crop," and the "efficiencies" of the various trophic levels. In recent usage, especially by botanists, "productivity" has been restricted to "primary productivity," understood as the rate of fixation of carbon by photosynthetic organisms, and "production" is understood as the net amount of protoplasm after losses from death and metabolism. The amount of living matter at a given moment is the standing crop, or biomass. Some authors have used "production" when they meant "productivity" and have considered "biomass" as a measure of energy. These matters are discussed in more detail in Chapter 17; further discussions will be found in the papers by Ivlev (1945) and MacFadyen (1948) as well as in that by Zenkevich (1951).

The most difficult problem in modern ecology is that of defining and measuring efficiency. It seems to be a popular idea that nature, especially in the sea, is as wasteful as prolific, an impression probably gained from the apparently lavish overproduction of the great schools of fishes and pods of whales and the spectacular mass mortalities of fishes and invertebrates associated with "red tides." There also seems to be a general impression that the efficiency of this process is low, that something like only 10 per cent of the organic matter accumulated by one trophic level or group is transferred to the next. This 10 per cent is obviously derived from Petersen's (1918, p. 22), discussion of the Kattegatt, in which he postulated that only 10 per cent of the matter of one link in the food chain is incorporated into the matter of the next link. Petersen was simply using the 10 per cent figure to emphasize his point that, from the viewpoint of economics (a social science), predatory fishes were "far from economical to produce," and the small word *if* that preceded his discussion seems to have been overlooked. A recent example of such extrapolation is the estimate by Popovici and Angelescu (1954, p. 159) that it requires 780,000 kilos of euphausiids to produce 78,000 kilos of blue whale.

The first step in the process, that of fixation of carbon by plants, is not very efficient in terms of the total amount of incident solar energy, since about 50 per cent of the energy is in parts of the spectrum not absorbed by plants. According to Rabinowitch (1945, p. 50): "the average conversion yield [of photosynthesis] in direct sunlight is of the order of 3% of the *absorbed* energy, or 2% of the incident visible light, but in weak light in the presence of ample carbon dioxide it may rise to as much as 30%." Such high experimental values as 30 per cent are not encountered in nature. When compared on a unit-volume basis, the photosynthetic rates of aquatic plants (both fresh water and marine) are not greatly different from terrestrial plants (Verduin, 1952).

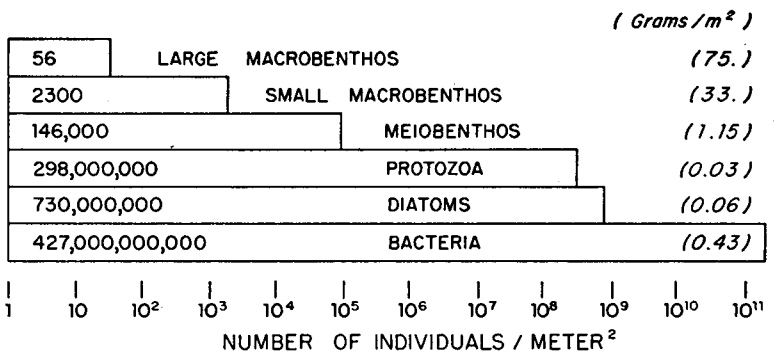

FIGURE 4.—*Comparative pyramids of number and mass per unit area of bottom mud*

Mass in terms of wet weight. Compiled from Mare (1942)

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The problem is complicated by differential absorption of differential utilization of various wave lengths of usable light, and the determination of the exact quantities of usable light which penetrates sea water (Chapter 6; *See* also volume 1, number 2 of Limnology and Oceanography (1956), devoted to problems of primary productivity.) Whatever the quantity of plant matter that may be required to produce one unit of herbivore tissue (the ratio seems to be about 20 to 1 for better beef cattle), it does not necessarily follow that the next step should be in the same ratio. Nor does it follow that the conversion of plant to animal tissue should have the same ratio in marine and terrestrial ecosystems. In the economy of the sea, macroscopic plants are relatively insignificant (although standing crops and production per comparable unit may be 100 times greater; Blinks, 1955, whereas on land the opposite is true, and we find no great herds of large herbivores in the sea comparable to terrestrial grazers and browsers, except for such fishes as the anchovy which is the intermediate link in the chain from phytoplankton to guano birds. With the exception of manatees the larger gregarious animals of the sea, especially mammals, are carnivores, and it would appear that such gregarious marine carnivores mature at comparatively older ages and live somewhat longer than terrestrial herd animals. In general, it would seem that there is at least one, and usually several more links in the food chains of aquatic, especially marine ecosystems, and the first step may be more efficient, in terms of herbivore tissue accumulated, than usually estimated; Harvey (1950) considers the efficiency of herbivorous copepods to be 70 per cent.

The food chains of the sea are further complicated by the presence of various "feed-back" links represented by the detritus and suspension feeders, organisms that feed both on primary plant material and broken-down organic material from other trophic levels, as well as by the changing food habits of many abundant organisms, such as herring, at various periods of life (Fig. 5). The figures compiled by Jørgensen (1955) suggest growth efficiencies of 60–72 per cent for young stages of filter feeders, and that this efficiency drops to about 10 per cent in mature individuals. In terms of energy input versus energy output, however, an inverse scheme of efficiencies can be inferred, and there is confusion in ecological literature between growth and energy efficiency. If we are interested in the efficiency of an organism in terms of "species" or as some sort of ecological integer, we must derive some figure from these varying efficiencies, which requires a rather thorough knowledge of the requirements of an organism at all periods of its existence.

These various considerations of efficiency, when applied to communities or larger ecological systems, lead us to the conclusion that a mature balanced community is "inefficient" in terms of growth, but that it may be considered "efficient" in terms of transferring energy without the frictional lag of adding substance to the system. These contradictory ideas of efficiency were realized by Lindeman, who suggested they might be reconciled by considering that activity at higher trophic levels or in more mature communities is increased—*i.e.*, the rate of consumption is greater. Allee *et al.* (1949, p. 520) propose a further generalization: "within a given community, the biological efficiencies increase as the rates of production, or productivities, increase." It is not clear what this means, and they do remark that "confirmation is lacking for marine and terrestrial communities."

At this time it is like setting up a straw man to ask whether an ecological system in the sea is more or less "efficient" than a terrestrial system since the different situations must be examined in their own terms. For that matter, there is little agreement as to the comparative magnitude of primary production in the sea and on the land. On the basis of computations by Riley, Rabinowitch (1951) estimated the

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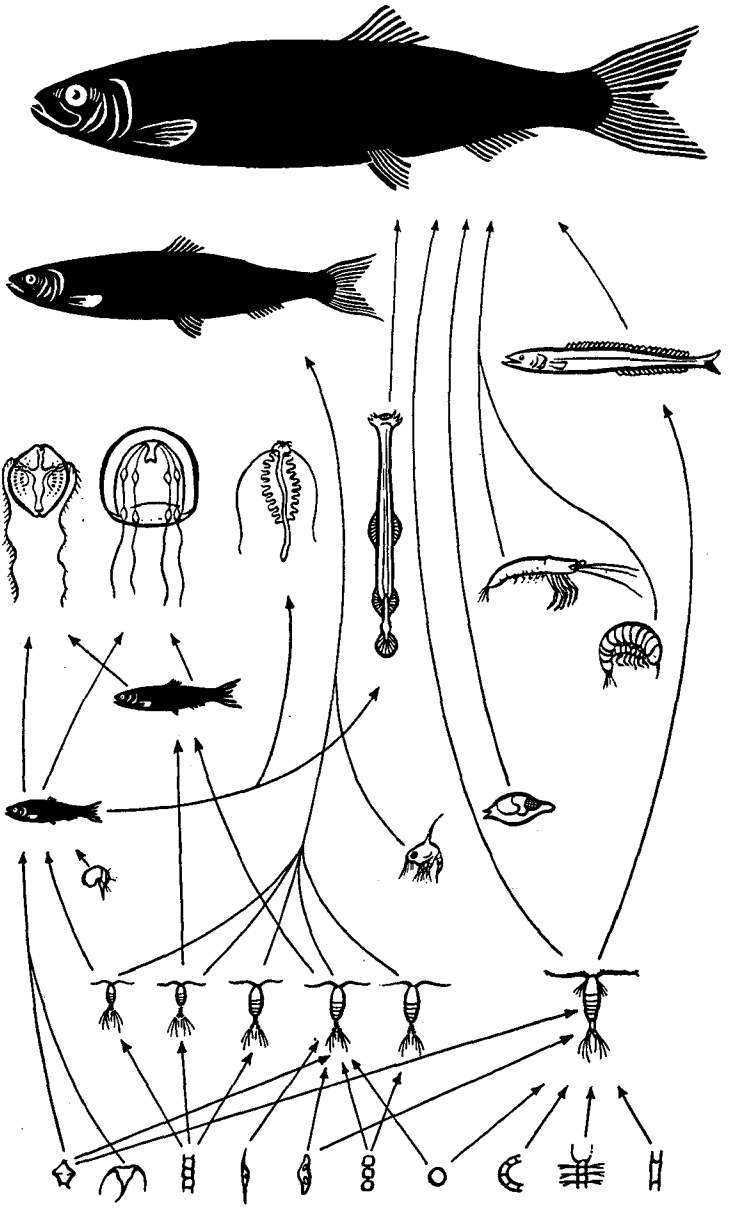

FIGURE 5.—*Food chain or web of the herring at various periods of life*

Compiled from data of Hardy (1924). From Buchsbaum (1954) courtesy R. Buchsbaum.

annual fixation of carbon in the sea at 15.5×10^{10} tons, as compared with 1.9×10^{10} tons on land. This estimate has been vehemently attacked by Steeman Nielsen (1952), who estimates the annual fixation in the sea at 1.5×10^{10} tons. Another recent estimate, by Loomis (1949, p. 2), places the figure at 9×10^{10} tons. All these

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estimates involve attempts to calculate the rate of carbon fixation over the entire surface of the ocean on the basis of comparatively few observations, and they must be considered, at the present state of knowledge, simply as approximations. It remains to be seen whether Steeman Nielsen is correct in concluding from such data that "For man, therefore, the sea will hardly ever have the same importance as the land as a source of nutrition."

TABLE 1.—*Mean quantity throughout the year of plants and animals below unit area in the sea off Plymouth*

Average depth 70 m (Harvey, 1950)

Wet weight of tissue containing 80 per cent of water per acre (lb)	Type of organism	Dry weight of organic matter, g/m²				
		Quantity below a square meter (g)	Daily production per square meter (g)	Daily loss by respiration %	Food assimilated daily (g)	
					Lost by respiration	Built into new tissue
?180	Phytoplankton	0.4	0.4–0.5	—	—	—
70	Zooplankton	1.5	0.15	4	0.06 vegetable tissue	0.15 vegetable tissue
80	Pelagic fish	1.8	(0.0016)*	1¼	0.025 animal tissue	—
—	Bacteria	0.04	—	30	0.013 dissolved organic matter	—
50	Demersal fish	1–1.25	(0.001)*	1¼	0.015 animal tissue	—
800	Epi- and in-fauna	17	(0.03)†	1¼–2	0.2–0.3	—
—	Bacteria	0.1	—	30	0.03	—
					Total...0.34 to 0.44	

* Based on a natural mortality of 30% per annum, because they were eaten.

† Based on a natural mortality of 60% per annum, beausce they were eaten.

There have been few attempts to set up a balance sheet for any part of the sea. In the comparatively well known waters near Plymouth, Harvey (1950) made a notable attempt to estimate the total biomass and its rate of turnover.[1] Although this study was based on data accumulated over several years as well as on surveys of the water column for this specific purpose, he was unable to fill in many details, and his summary tables, repeated here as Tables 1 and 2, show many gaps. He estimated herbivore efficiency at 70 per cent, as compared with an efficiency of 10–11 per cent for carnivores. These percentages refer to assimilated food. Assimilation of plant matter by marine herbivores is far from complete, and there is a steady rain of fecal matter, including partly assimilated plant material, which supplies part of the requirements of many of the bottom organisms. While the carnivores may be less efficient, they also consume less. Harvey suggested that "the total daily loss by respiration of the whole animal community (0.34–0.44 of organic matter) is slightly less

[1] *See,* however, the recent appraisal of Long Island Sound by Riley *et al., The Oceanography of Long Island Sound 1952–1954,* Vol. XV of Bull. Bingh. Oceanogr. Coll., 1956; although it concerns a restricted region it is an admirable example of the type of studies needed in marine ecology.

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TABLE 2.—*Balance sheet of animal protoplasm off Plymouth*
(Harvey, 1950)

	Percentage loss of biomass per annum "Annual Mortality"	Percentage increase daily by weight (g)	Percentage loss daily by respiration (r)	Percentage of food assimilated, which is built into new tissue $\left(\frac{100\ g}{g+r}\right)$
Zooplankton herbivores	—	10	4	70
Fish, community of all ages	30 50	0.08 0.14	1.25–1.5 —	5–6 8½–10
Bottom fauna; most of the biomass are well-grown individuals	60	0.16	2	11
Full-grown fish, bivalves or worms, increasing in tissue weight not more than 20% per annum	—	<0.05	1–1.25	5

than the deduced daily production of organic matter." The yield per 100 g of vegetable matter assimilated is, according to Harvey, roughly as follows:

70 g of herbivorous short-lived zooplankton

11 g of herbivorous well-grown long-lived bivalves or worms

4–7 g (6–7 per cent of 70 g) of pelagic fish feeding on herbivorous zooplankton

1 g (6–10 per cent of 11 g) of demersal fish feeding on well-grown bivalves

0.3 g of carnivore feeding on carnivore, as fish on fish; or more if both are small and short-lived.

The data and procedures necessary to turn such a study into a more strictly quantitative analysis are indicated in a study by Cushing (1955), of the relation between diatom production and herring. The desiderata include: (1) successive estimates of the number of plankton organisms in the same water mass, (2) a simultaneous estimate of the number of pelagic fish, (3) the quantity of plant food consumed per day by herbivores, and (4) some measure of phosphorus regeneration in the region concerned.

Such a cautious attempt to strike a marine balance sheet is in strong contrast to that produced by Odum and Odum (1955) for a coral reef at Eniwetok after 6 weeks of field work. Working on a transect parallel to the wind across a windward reef, Odum and Odum estimated populations by the quadrat method and measured organic matter and oxygen simultaneously at various stations along their transect. As a result of admittedly crude and preliminary methods, they arrived at a balance of 4 per cent between gains and losses across the reef and remarked, "In view of the rough nature of some of the estimates it is not certain whether this is a significant difference or whether the community is in perfect steady state with losses matching gains."

This *tour de force* will probably excite comment for some years, and it will be of particular interest to have the experiment repeated several times as well as to test some of the assumptions on which the measurements were made. They have, for example, assumed that "the living part of a coral is more plant than animal," and that the animal part of the coral is essentially herbivorous, an assumption considered

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debatable (Hand, 1956). Their estimate of a turnover of biomass of 12.5 times per year raises again the question of periodicity in the tropics (the work was done during the months of June and July) and indicates that similar measurements at other seasons would be desirable. While the coral reef has long been assumed to be in balance with the environment simply on the basis of gross observation, it is a question whether the balance determined by this investigation is the correct one, especially since the results are given somewhat sweeping implications, "Here is an ecosystem which has had millions of years to evolve an effective composition, which is built for a low efficiency. This may be support for the hypothesis (Odum and Pinkerton, 1955) that there is an optimum but relatively low efficiency that produces the most effective trophic structure whose survival is based on a high primary productivity" (p. 318).

As imperfect as our understanding of the trophic structure of the sea may be, such efforts to strike a balance sheet are steps in the right direction and may be expected to become one of the principal procedures in marine ecology. Some middle ground between such a counsel of perfection as that of Elton and Miller, "The ultimate and proper aim of an ecological survey, however difficult its achievement may seem at the present level of our knowledge, is to ascertain and measure the population and dynamic relationships of all the species living in a place over some period of time" (Elton and Miller, 1954) and the gross measurement of "trophodynamic mush" from a plankton net must be found. We must always bear in mind that the character of our data, and to a large extent the conclusions we draw from such data, are determined by our sampling methods. These are reviewed in Chapter 4 (*see* also the post script to this Chapter.)

THE COMMUNITY

Since the original formulation of the community concept by Moebius, who called an oyster bank a "biocoenosis", the study of communities has been principally in the hands of terrestrial botanists and ecologists, and some of the concepts developed for terrestrial situations are not generally applicable to the sea. The term community is a useful general word for the organisms occurring together in a particular place (environment or biotope) and presumed to have some relations with each other. Biocoenosis is usually understood to imply more demonstrable interdependence and interrelationship. Although the term thanatocoenosis suggests, by its etymology, a dead or extinct community or biocoenosis, it is often used in paleontology to apply to a death assemblage, without implying any ecological relationships. The usage, however, is not consistent, and Craig (1953) has suggested abandonment of the term in favor of "fossil assemblage."

A community is further understood to consist of populations rather than individuals of the species involved, although the biotope of a small community may be an individual organism, such as a kelp plant (Fig. 6). While the environment or habitat in which a species occurs, such as a fucus plant, is often thought of as the "niche" of that species, the term niche has a more comprehensive meaning in ecology, as the role or function of the species in the community or ecosystem. It is this concept of the niche which is implied in the idea that within a given biotope two species do not

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occupy the same niche (or, two species with the same requirements cannot live together). This generalization, known as Gause's hypothesis, has been criticized as based on an idealized model which does not exist in nature (Andrewartha and Birch, 1954, p. 407–412), and another model has been devised to illustrate the reverse—*i.e.*, that two species having the same requirements can live together (Skellam, 1951). Some of the difficulties are semantic: as Gilbert, Reynoldson, and Hobart (1952) emphasize, the various ways in which Gause's hypothesis (which does not appear to have been explicitly stated by Gause) have been stated embody subjective language, and much of the evidence cited from nature in behalf of the hypothesis is negative—*i.e.*, that ecologically similar animals are not found living together, or that animals occupying the same place or niche that appear to be similar actually have minutely different requirements, which is not the same as saying that ecologically similar, or identical animals cannot or do not live together. An obvious implication of the hypothesis of niche specificity is that there should not be two identical niches in the same community. This aspect is discussed by Hutchinson (1953), who suggests that apparent violations of Gause's hypothesis indicate nonequilibrium conditions. On the other hand, the ecological function (as energy converters) of many organisms, especially marine invertebrates, differs at various periods of their life, so in one sense an organism may occupy more than one niche or even move from one community (the plankton) to another (the benthos).

The character of the community may in a general way indicate the nature and variability of the environment as well as tell us something about the developmental

FIGURE 6.—*Microfauna of the brown alga* Fucus vesiculosus

Courtesy G. Thorson, drawing by Poul Winther

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stage of the community, as Thienemann (1954) has suggested in his three "basic biocoenotic principles": (1) the variety of species in a community is greater under more diverse conditions; (2) the variety of species is reduced, but the individual numbers are increased in a community as the environmental conditions depart from the normal or optimum for most of the species concerned; and (3) the variety of species, balance, and stability of the community are greater as the conditions in a given environment become more stable and continuous.[2] That is, in a mature, well-balanced community, under comparatively stable conditions, there are more niches. The environment or "milieu" is not necessarily monotonous and unchanging under "stable" conditions since there is usually a fluctuation or oscillation within ranges tolerated by the majority of species in a community which results in corresponding internal adjustments. Tentative evidence that such situations may persist for significantly long periods has been adduced from a study of stream and pond communities in a Permian river delta (Olson, 1952) and has been suggested for the estuarine environment (Chapter 23). In the case of the Permian communities it has been suggested that the community remained relatively stable as long as the available ecological niches were occupied, but an environmental change which eliminated one or a few species, leaving unoccupied niches, and upsetting the internal balance of the community, led to rapid change or extinction of the community. Unoccupied niches in a community are, as suspected by many ecologists, a sign therefore of an environment or biotope (in the sense of being the matrix of the bioceonosis) that is either out of balance or newly constituted.

On the other hand, the greater diversity of niches and organisms occupying them is a well-observed phenomenon of transition zones or borderlands between major communities. Such transition regions are known as ecotones, and the greater variety of species in them is known as the "edge effect," a well-established concept in game management (Leopold, 1933, p. 131–132). River-delta regions and estuaries, while themselves enduring biotopes, may also be understood as ecotones, and a diverse community may indicate either a long-established community in a comparatively uniform environment or a result of the increased number of niches in the transition between communities (which are themselves reflections of environments).

Much of our knowledge of communities in the sea has been derived through the study of populations of commercially important organisms rather than through academic studies of community structure, and population dynamics is now one of the major fields of ecology. A formidable literature has grown since the pioneer work of Baranov (1918) and Volterra (1926) with fisheries problems and the experiments with laboratory problems by Gause (1935). Among the more significant recent contributions should be mentioned the review paper by Nicholson (1954), the books by Andrewartha and Birch (1954) and Lack (1954) and papers by Ricker (1946; 1954), Beverton (1953), Baerends 1947, translation (1950), and Burkenroad (1951), dealing with marine populations. All of this may seem at first glance to have little bearing on the problems of paleoecology, but Boucot (1953), using the life-expectancy tables of Deevey (1947), has indicated how knowledge of mortality and survival

[2] Je variabiler die Lebensbedingungen einer Lebenstätte, um so grösser die Artenzahl der zugehörenden Lebensgemeinschaft.

Ja mehr sich die Lebensbedingungen eines Biotops vom Normalen und für die meisten Organismen Optimalen entfernen, um so artenärmer wird die Biozönose, um so charakterischer wird sie, in um so grössern Individuenreichtum treten die Einzelnen Arten auf.

Je kontinuierlicher sich die Milieubedingungen an einem Standort entwickelten haben, je länger er gleichartige Umweltbedingungen aufgewiesen hat, um so artenreicher ist seine Lebensgemeinschaft, um so ausgegleichener und um so stabiler ist sie.

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rates may be used to separate assemblages from communities in a Devonian formation. This is a promising beginning, and such idealized life assemblages may become a common tool for paleoecologic analysis. When combined with data on reproductive patterns (*see* Cole, 1954, for an analysis of the consequences of varying brood size and age at reproduction), such an approach may yield information on the ecological status of a fossil community. A recent example of this type of analysis will be found in the paper by Olson (1957).

The realization that a community of organisms in nature might go through an orderly sequence of changes came fairly early in the development of community studies, and by the first decade of this century the concept of succession was well established (Allee *et al.*, 1949, p. 47). The elaboration of the concept, in which the developmental stages (seres) are considered to lead to a comparatively stable community, the climax, as "the final response to climate" is due principally to plant ecologists and is set forth in the text by Clements and Shelford (1939). The largest climax community, as for example the grasslands or deciduous forest region, is considered to be a biome.

A number of attempts have been made to apply the concept of the biome to the sea. Shelford's attempt to divide the sea into various biomes (*in* Clements and Shelford, 1939, p. 353) has been criticized as "artificial" and "untenable" by Allee *et al.* (1949, *see* p. 449 and 459), but they come to no satisfactory conclusions themselves, suggesting instead that the oceans should be regarded "essentially as a single major community, and the whole of marine ecological associations constitutes essentially not only a single major community and a single biome, but a single biome-type" (p. 596). Jones (1950) in his review of bottom communities revived the marine biomes of Shelford, and Marshall (1953) proposed that the rocky-shore community be called the "Balanoid biome-type." The New Zealand school of shore ecologists advocates application of a whole suite of terms from terrestrial-community ecology to the sea shore on the assumption that the rocky shore is a biome, to be considered as a physiographic climax, "since it is dependent upon the tide rather than upon the climate" (Beveridge and Chapman, 1950).

The difficulty with such attempts to equate marine and terrestrial climaxes is that the same words and concepts are being applied to different phenomena. Application of the term biome to the sea depends, as is suggested by the foregoing, on the recognition of a successional sequence in the sea leading to a stable or climax situation. Shelford's first conclusion was that true or "biotic" succession, fulfilling his criteria of dependence on later forms upon earlier forms and a dropping out of earlier forms, did not occur in the sea, but that there was only a "direct development" of climaxes, "aspection" (changes from season to season), and "annuation" (changes from year to year). On the basis of work done by Hewatt (1935) on the repopulation of an intertidal *Mytilus* bed, Shelford was convinced that true succession did occur; he extended his concept, with its hierarchy of terminology, to the sea.

The equilibrium condition observed on a rocky coast, or on a set of test plates in a fouling study, is attained in a relatively short period of time as compared with similar phenomena on land. As Redfield and Deevey (1952) say, it is "a climax which is characteristic of the particular substratum and locality." In their review of the problem of succession in fouling communities, these authors observe that most of the work which has demonstrated such succession has been done on the Pacific coast

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of North America where seasonal variations are less pronounced. Similar work, demonstrating seral progression at Banyuls on the French Mediterranean coast, has since been published by Huvé (1953); this is also a region without pronounced seasonal changes.

The sequence on fouling plates may be completed in a few months or a year. Hewatt found that the original community on rocks was not completely reconstituted after 2½ years, when the observations were abandoned. Ralph and Hurley (1952) estimated that the attainment of a climax association of mussels on piling required 3 years in the somewhat similar temperature regime of New Zealand. The colonization of rock surfaces is much slower in Tasmania, where population of established communities is relatively low (Guiler, 1954).

A number of studies of the establishment of fouling communities has indicated that micro-organisms are the first to settle on new or denuded surfaces, and it has been suggested that the formation of a slime film of diatoms or bacteria is a necessary first step in the process. In this event, according to Redfield and Deevey (1952), a true biotic succession would be demonstrated. Other researchers, however, have found that a slime film is not essential to initiate the process (Fig. 7). It is not clearly brought out by Redfield and Deevey that a large part of such slime films consist of particulate organic matter or peloglea (*see* Chapter 14), or that settlement on fresh panels alongside older panels with well-developed films may be influenced by the populations of larger fouling organisms already developed on the older panels.

The short time scale for such sequences means not only that the various subdivisions or seral stages are transitory, if they can be recognized at all, but also that the changes in biota and environment may be of a different order from that on land. According to the theoretical or perfectionist concept of climax, the biota becomes stable in response to a stable environment. Of course this theoretical ideal is not

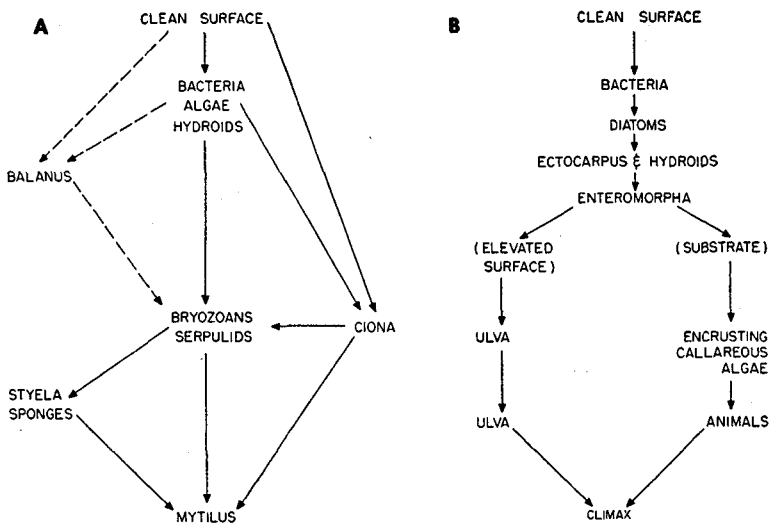

FIGURE 7.—*Successional sequences observed in studies of marine fouling*

(*A*) after Scheer (1956); (*B*) after Huvé (1953)

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useful in practice because the environment does not cease changing. When the changes in the environment are of a different order from the periodic changes in the biota there appears to be a phasic difference. If the environment should cease to change or if the changes were slower, this phasic difference would be reduced, and a climax could be said to be approached. When the phase difference remains constant or within a consistent range of variation, then the biota can be considered to be in dynamic equilibrium with the environment. This seems to be a more useful way of regarding climax, especially in the sea, and in this context the application of the terrestrial scheme to the shore as suggested by Beveridge and Chapman (1950), or in a tidal inlet (Dexter, 1947), is particularly unfortunate.

Coral reefs are probably the oldest living communities in the sea, perhaps older than any extant terrestrial biomes. A formation such as the Great Barrier Reef or a Pacific atoll (*see* Chapter 20) is as good a regional climax as an evergreen forest, but it does seem inappropriate to call an atoll, or a whole group of scattered atolls, a biome. In some respects, coral reefs are similar to oyster reefs of nearshore or estuarine regions. Like corals, oysters build up physical structures which provide an environment for other organisms and may eventually become islands. Oyster reefs in the depositional environment of estuaries build themselves out of existence in a relatively short time or are covered by silt and become re-established in somewhat different parts of the bay. Unfortunately the gastronomic appeal of oysters has attracted the destructive activity of man, and it is now impossible to separate natural and human causes in the history of oyster reefs. The oyster banks of the German bight, the type of the biocoenosis, have been virtually obliterated by overfishing. The failure of these beds to re-establish themselves after fishing has been suspended seems to be due to wholesale removal of cultch and reduction of spawning stock below the minimum necessary for repopulation (Korringa, 1952). For the marginal beds of Helgoland, Caspers (1950b) suggested a sort of alternating sere between the oysters and a clam, *Nucula*. Here the conditions may be more similar to those of level bottom than they are to those governing the development of estaurine reefs on the Atlantic coast of America. Such estaurine reefs are the temperate analogues of the mangrove associations, and both may be true seres in that they terminate in terrestrial "mesophytic" formations.

The aggregations of organisms on the bottom, whether they are considered to be organized communities in the ecological sense or statistical artifacts of overlapping populations, are formed of relatively short-lived components. Most of the common organisms considered to be indicators of bottom aggregations have maximum life spans of not much more than 5–6 years, and the effective life span of the populations is somewhat less (Chapter 17). In general, however, the life spans of shallow-bottom organisms are probably somewhat longer than those of intertidal communities, which include many annual and semi-annual plants and animals. As our discussion of the formation of fouling communities suggests, the equilibrium form of such communities is determined more by the physical factors of the environment than by the organisms of the community. This may be even more applicable to level-bottom communities, as indicated by the recent work on larval settling. Both the intertidal and shallow-sea regions abound in aggregations of organisms that include many closely related species and ecologically similar forms that at first glance might be thought to be competitors for the same niches. Either such competition has been overestimated by observers, or the life spans of the organisms and the time span of the populations are so short that there is insufficient time for such interactions to influence the character of the association. Thus the soft-bottom community would be determined primarily by the physical factors of bottom composition and local hydrography, and the real com-

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petition would be among the larvae seeking physical space on which to settle and metamorphose. As a result, there may be pronounced local variations from place to place and a contrasting general similarity over a large area. In some areas the conditions may be such that little uniformity can be attained by the organisms, and the traditional view of a relatively uniform bottom community dominated by a comparatively small number of conspicuous species must be abandoned in favor of an apparently patternless or "reticulated" distribution of a large variety of species in a "patchiness of occurrence which is unpredictable, and at present unexplainable" (Hartman, 1955).

The explanation is not to be sought in the character of the bottom community itself, but by studying the ecosystems involved. This implies more than observing that the Kattegat and the San Pedro Basin are different places. It requires recognition that the aggregation of bottom animals is one of the living substrates of the ecosystem, that this aggregation cannot be considered a self-contained community but only part of a community. This was fully realized by Petersen, who tabulated bottom aggregations as an index to the community. The omission of motile animals was regretted by Shelford, who nevertheless continued the characterization of communities on the basis of the bottom organisms. The bottom is primarily a food-gathering area, at least below the depths at which plants may live. Not only is it abundantly populated, at least in many parts of the shallow sea, by animals that live within it or on its surface, but there are many animals that wander about its surface with varying degrees of motility. Among the latter are schools of bottom-feeding fishes and crustaceans. There are also organisms whose diurnal migrations bring them near the bottom during part of the day, and many of these either feed or are fed upon. A rational ecological synthesis of the bottom community cannot be made without considering this important part of the community, as well as the physical factors of the region concerned.

The major plankton complexes of the sea, whether they be considered features associated with certain temperature conditions or of water masses, are equally difficult to split off from the rest of the marine ecosystem. It is obvious that the vast realm of bathypelagic life, occupying the region below the limit of light penetration and the bottom of the sea, cannot be considered independent in any sense from the surface plankton communities. This is not alone because they depend on the food that rains down to them from this upper layer, but because many of the organisms migrate almost to the surface nightly, and others, like the sperm whales, apparently descend to considerable depths to feed. Then there is the possibility that communities of deep-sea bottom organisms may depend in large degree upon some major windfall such as the carcass of a whale, or the accumulation of terrestrial plant debris in trenches and ocean basins (Heezen, Ewing, and Menzies, 1955), and this may explain the apparent patchiness of deep-sea life on the bottom (Chapter 22). Only intensive investigation will provide us with the information necessary to recognize the degree of interdependency between these communities or, on the other hand, the degree to which they may be considered independent. Speculations about the "physiology" and "succession" of plankton communities, based on the supposed exclusion of zooplankton by phytoplankton or vice versa on the basis of external metabolites or "ectrocrine" substances (Lucas, 1955), while of theoretical interest, are equally

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tentative (*see* Friedrich, 1952a; 1952b; 1954). We may be dealing here with the phenomenon of optimum numbers, now known as Allee's principle (Odum, 1953, p. 157–161). It is apparent that aggregations of a species have different properties ecologically from those of individuals, and, if there is "exclusion" of one aggregation by another, its effect on the composition and regime of neighboring pelagic communities must also be investigated. The character of the plankton community of the north Pacific, for example, may well depend on biological events in the community of the Pacific equatorial waters, just as the herring and plaice stocks of the North Sea may depend on the physical changes in the Gulf Stream. Certainly such possible dependencies emphasize the difficulties in any attempt to recognize discrete climax formations or biomes in the pelagic biosphere.

A NOTE ON TERMINOLOGY

The subtlety and complexity of circumstances in nature have provoked in ecologists a terminology which demonstrates again the difficulties of language as a means of communicating ideas. While there have been many complaints about the jargon of ecology, such complaints, like those about jargon in other disciplines, are sometimes beside the point. It is easy to deride jargon as an ugly effluvium of the language, and it is true that there are many unfortunate expressions in the technical writing of ecology. Picking out such atrocities is rather like shooting sitting ducks, and their persistence in any specialized literature suggests that the numerous writings on the subject of jargon and gobbledegook which are embellished with delightfully horrible examples are consulted only by professional editors, who find a certain masochistic pleasure in comparing notes. By a less offensive name, jargon is necessary in technical writing; the objection is not to the use of specialized terminology (at least in moderation), but to such loose application of it that justifies the criticism that the writer of it has abdicated his reasoning power in favor of mere words.

The chief difficulty with ecological terminology is not that there is a terminology but that many of the terms have conflicting definitions. The vagueness of the terms "environment" and "habitat" inspired Andrewartha and Birch to avoid them altogether and to adopt such circumlocutions as "the sort of place in which 'x' may live." Perhaps this is going a bit too far; many of the common words of ecology would lose their usefulness if too rigidly defined, and such elaborate evasion adds materially to the length of the discussion. As Arkell (1956, p. 466) says, "Some terms . . . have been used in the past with many different meanings and will remain more useful if not formalized by strict definitions. It would be a mistake to leave no unrestricted words of this kind in the common pool of language."

As there is no definition of species which satisfies everyone, so also is there no definition of community upon which everyone will agree, but no one would seriously propose to abandon either term, even when subjecting community analysis to statistical procedures and the language of information theory (Margalef, 1956a; 1956b). Association, in the sense of referring to the characteristic plants or animals usually found together in a community, is also a useful term. Many of the other terms used in ecology seem to have private meanings for the authors that use them and may sometimes vary from paper to paper. Such variable or ambiguous usages are not peculiar to English, and lectures on terminology and concepts are a part of the ecological literature of other languages. (*See*, for example, Günther, 1950; Caspers, 1950a; Petit, 1954, p. 583–587.)

The hope has been expressed (Craig, 1953) that this work would establish a simple terminology for marine ecology and paleoecology that would reconcile the conflicting terms from paleontology and stratigraphy that are being introduced in paleoecology. While this expressed faith in our authority is flattering, we doubt that any recommendations by anyone will be universally acceptable. The experience of our committee in compiling the terminology adopted in Chapter 2 is enough to convince us that discretion remains the better part of valor.

We have tried to set an example by using as few special terms as possible, and have tried particularly to avoid unnecessary prefixes. For example, ecology is by definition a biological science, the study of interactions between organisms and environment in *the living world*, so bio-ecology is redundant. Some paleontologists like to add 'neo" to words, so we have neoecology, also an unnecessary

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and redundant term. Whoever wishes to use an elaborate terminology must define the words and should remember that there are still many unreconstructed people to whom ecology is an unnecessary synonym for natural history.

POST SCRIPT: STATISTICS

The most serious gap in this *Treatise* is an adequate treatment of statistical methods in ecology; unfortunately it was not possible to find a competent author in time to prepare such a chapter. Some statistical procedures most useful in ecology are described by Siegel (1956). The old saw that statistics are the ultimate degree of prevarication is too often true in ecology because a sample, however obtained, is treated as sacred, and data are subjected to statistical procedures which add their own bias. A naive faith in standard deviation or correlation *per se* as proving something, and a failure to realize that many of the data of ecology are nonparametric and hence not amenable to parametric tests, have made many of the statistical analyses in ecological literature of uncertain value. Too many ecologists, especially fisheries workers, employ statistical procedures without any clear idea of what they mean and, what is worse, often apply them to data which are of doubtful biological validity. For example, the idea that the size of a large fish school may be estimated by the tagging and recapture method without reference to the schooling behavior of the fish is inexcusably bad biology and a squandering of public funds. Adequate statistical procedures are tedious and time consuming, and it would be well to spend a comparable amount of time at the outset in working out an adequate sampling technique.

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Chapter 4

Obtaining Ecological Data in the Sea*

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INTRODUCTION

In this chapter we are concerned primarily with the methods of observing and obtaining marine organisms as the most essential part of ecological investigations. The section on Sampling the Benthos has been prepared by Gunnar Thorson, that on Dredges and Trawls by Gordon Gunter. There are several comprehensive works, in addition to their appropriate chapters in standard texts, dealing with instruments and their uses, the most recent of which are Welch's Limnological Methods (1948), the Russian volume on Oceanographic instruments by Snezhinskii (1951), and the National Research Council Symposium volume on Oceanographic Instrumentation (Isaacs and Iselin, 1954). *See also* the symposium at the 1953 British Association meeting (Barnes *et al.*, 1953). Since the techniques of observation on the shore are essentially those of terrestrial ecology, there is little need to mention them here. (*See*, for example, Hewatt, 1937; Dexter, 1943.)

We do not intend to minimize the importance of physical and chemical data in ecological investigations, of course, but it must never be forgotten that an ecological investigation is essentially an investigation of organisms *in situ*, and physical and chemical information without specific reference to organisms is the stuff of meteorology and hydrography, not ecology.

The primary data of any ecological investigation, therefore, are the species of organisms concerned. These data may be represented by actual specimens retained in a collection, measurements of specimens which are returned to the environment or processed in some way (as in a fisheries), observation of specimens without more than passing note ("sight records"), or photographs. It should be obvious therefore that the first procedure in an ecological investigation is, or should be, essentially an exercise in systematics, the identification of species, and understanding *inter alia* the relation of these species to other groups in both the evolutionary and physiological senses. It is, of course, sometimes necessary to conduct an ecological investigation in a remote region without knowing the species involved; careful workers, however, will make every effort to get their species identified before publishing their results.

The ideal instrument for collecting ecological data, whether from the bottom or the ambient medium, should be simple, with as few moving parts as possible, designed to collect quantitatively and without damaging the specimens beyond hope of determination. It should be operable by a person without specialized training, producing

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reliable data without constant supervision. There is no such instrument, and probably there never will be such an instrument. Indeed, with such things as underwater television, the bathyscaphe, and quantitative plankton recorders, our instruments are becoming more complicated than ever. However, for most routine gear, "Kelvin's laws of oceanographic instrumentation," as summarized by Eckart (*in* Isaacs and Iselin, p. 161–162), are appropriate: (1) there is ample driving power in the sea; (2) the instrument should not be dependent on lapped bearings or other precision parts for its operation.

Many of the instruments described in the following pages may be obtained from the firms listed by Pratt *et al.* (1949) and Pratt (1953); others are obtainable from firms dealing in fishing supplies, and a few must be manufactured to order or improvised.

METHODS OF OBSERVATION

Our unaided ability to peer into the sea is very slight, at best only a few feet in a clear, calm lagoon. While there have been some promising advances in providing us with some temporary adaptation to life in the water, the limitations of these devices are many, and our chief methods of observation in the sea are still indirect. We are much better off than our grandfathers, who had to rely upon fanciful drawings of life in the sea, compiled by some land-bound artist from the chance collections of a dredge, but still we do not see all that we would like to see.

DIVING SPHERES

A generation ago William Beebe (1934), descending half a mile into the sea in his bathysphere, was one of the heroes of the day. Today his record has fallen like that of a sporting event, as some daring Frenchmen have descended five times as deep (some 13,000 feet) in their bathyscaphe (Cousteau, 1954; Houot, 1954, Houot and Willm, 1954; Monod, 1954). The new bathyscaphe is as intricate as a submarine, which it resembles, with immense batteries, motors, ballast tanks of gasoline and birdshot, but still only one small window and cramped quarters for a crew of two. Now that the strange vessel seems a success, the demands for a cruise to the depths are so heavy that passengers must be chosen by lot. Clearly few of us can hope to take a voyage in one of these reverse balloons, so we must still rely upon the verbal descriptions and photographs by the explorers. Already there are suggestions that we may know even less about the mid depths of the sea than we thought we did, for there are amazing reports of sharks 5 and 6 feet long, squid that discharge white ink, and great villages of burrows on the bottom out of which nothing emerges. Such observations will inevitably stimulate the development of effective fishing gear, but here again the expense of developing such apparatus will be so great that few can hope to use it intensively.

Another device, intermediate in expense and complexity as well as in performance, is the Japanese diving chamber or "Kuroshio" (Inoue *et al.*, 1953). This apparatus, suspended from a cable, is designed to descend to about 200 meters and has been used for continuous observations to that depth. It is provided with a fishing net, water- and sediment-sampling devices, and the usual observation windows.

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"SCAPHANDRE AUTONOME" OR AQUALUNG

For observations in the shallow sea, to depths of about 40 fathoms (240 feet) by the most skilled individuals, the recently invented self-contained diving apparatus is now so widely used that it is to be considered a standard piece of equipment. There are several instruction manuals (*see* especially Tailliez *et al.*, 1949; Schenck and Kendall, 1950) and a host of popular books describing the delights of underwater exploration (Cousteau and Dumas, 1953; Rebikoff, 1952). While the aqualung is a convenient means of exploring the shallow sea, superior to the light diving helmet and the conventional diving suit, it is still a shallow-water apparatus. It has many uses as an exploring tool (Drach, 1952; Bascom and Revelle, 1953), but it is misleading to imply that using this apparatus is as safe as driving an automobile; for one thing, a diver should not explore unknown regions without a companion to rescue him from difficulties, which means that not one but two outfits should be available.

Too often it seems that the person with the best qualifications for diving is not the most competent observer, or is not interested in doing the work that needs to be done. Nevertheless, the aqualung or SCUBA (Self-Contained Underwater Breathing Apparatus), as Bascom and Revelle (1953) call it, will be the major instrument for increasing our knowledge of that narrow band of the sea between the low-tide line and the region where boats and diving spheres must take over. As yet the actual contributions to ecological literature based on free-diving observations have not been more than preliminary papers (Drach, 1952, and earlier notes; Forster, 1954), but, when the right combination of observer and diver is found, such contributions as that made by Gislén (1929–1930) with the use of the standard diving suit can be expected from the aqualung. It is somewhat surprising to realize how few serious explorations have been made with diving equipment since the pioneer explorations of Milne Edwards and Quatrefages in the 1840's. (For a general history of diving, *see* De Latil and Rivoire, 1954, transl., 1956).

UNDERWATER TELEVISION

The use of television underwater was introduced by the British Admiralty for military purposes, in particular the location of wrecked submarines (Stamp, 1953), and the applications of television to marine biology are under investigation (Barnes 1952; 1953). When perfected, underwater television will make possible the observation of active organisms in their natural environment, especially beyond the reach of free divers, and we may look forward to seeing, at some future time, views of life in the great deeps, projected in our living rooms. But this is still a few years away, at least. At present the use of television is limited by the expense of watertight housing for the camera, the length of the cable (a very expensive item), and the substantial amount of equipment required on the vessel. A still unsolved problem of operation is that of aiming the camera. Even when perfected, there will still remain the tantalizing problem of uncatchable animals swimming by that tempted the original bathysphere explorers into describing, in taxonomic terms, "the fish that got away."

UNDERWATER PHOTOGRAPHY

The use of cameras beneath the sea was first attempted in 1893 with some success by L. Boutan at Roscoff, but the primary limitation at that time was a suitable light

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source. Boutan considered that the best system on theoretical grounds would be one in which sea water was inside as well as outside the camera, and attempted to use such a camera. This was not so successful as enclosing the entire camera in a watertight box, which is in essence the method used today. Immersion cameras, filled perhaps with distilled water and some inert oil to equal the refractive index of sea water and with special lenses, may well be the next development in underwater photography. Today underwater photography, both with still and motion cameras, is a popular hobby with skin divers and aqualung enthusiasts, and there are many outfits available, as well as a manual for their use (Schenck and Kendall, 1954). The critical problem for such underwater photography is, as first discovered, the light source, and, with the exception of flash outfits usable only in shallow water, an adequate light source entails expensive equipment beyond the means of a small laboratory or most individuals. Nevertheless, shallow-water photography has now reached the stage where the camera is almost as useful to the marine ecologist as to his terrestrial colleague.

In deeper water the camera has been a major source of information, both to geologists and ecologists, although all such photographs have been taken blindly, either by a trigger which operates the camera as the apparatus touches the bottom, or by remote control from the deck of the vessel. Such deep-water cameras were first designed and used by Ewing *et al.* (1946a) at the Woods Hole Oceanographic Institution in 1940, and similar devices, with various improvements, have been widely used elsewhere (Von Bonde *et al.*, 1951; Owen, 1954). The most elaborate apparatus was the Benthograph developed at the Allan Hancock Foundation, in which the camera, Strobe light system, and batteries were enclosed in a diving sphere (Emery, 1952); this apparatus produced many remarkable photographs before it was snagged and lost off the California coast.

So far, deep-sea photography has been done only with still cameras and black and white film, taking only one exposure or several in series; the Benthograph could take 325 exposures at 30-second intervals. Motion-picture cameras have not been adapted for deep water since the "shooting in the dark" aspect would entail too much waste of film, and a light supply adequate for color is yet to be devised.

METHODS OF COLLECTING

SAMPLING THE PLANKTON

Basically the plankton net is a cone of fine meshed material mounted on a ring, terminating in a bottle or metal cylinder. The usual material for the net is the silk bolting cloth used for flour milling; while this is now being replaced by longer-lived nylon (with crimped fibers that hold knots better than ordinary nylon), nets of nylon are difficult to keep clean because they become dry almost before the sample can be removed. As a result, material from the previous tow may adhere to the net and clog the meshes.

The original plankton nets were qualitative collectors, but very early in the history of plankton investigations efforts were made to design nets or to operate them in such a way as to produce reliable, comparable samples. The first quantitative nets, designed by V. Hensen in the 1880's, were essentially standardized nets used accord-

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ing to specified procedures to produce samples in a desired column of water. The original assumption was that the plankton was evenly distributed throughout the water column, and, although this is no longer considered true, the vertical, measured haul is one of the standard methods of quantitative plankton analysis. At present many plankton investigations are conducted with standardized nets hauled vertically, horizontally, or diagonally for specified periods; usually the nets are equipped with a metering device that records the distance travelled or volume of water passed through the net.

The disadvantage of such nets is that most of them fish throughout the water column, and the total sample is collected in the bottle without indication of the distribution of the organisms in the water. A net with a magazine of storage nets on a revolving mechanism, activated by a propeller, has been designed by Motoda (1953); this apparatus is designed to take successive samples at different depths as it is hauled to the surface. Plankton nets are fragile and cannot be towed except at slow speeds, and large nets may be clogged with medusae or salps. If the mesh is fine enough to trap very small animals and phytoplankton, the tendency to clog is increased, and the speed at which the net may be towed must be even less than for a larger meshed net. In the efforts to overcome these disadvantages and produce a device both reasonably inexpensive and reliable, two samplers have been developed that are now widely used.

The first is the Hardy continuous plankton recorder (Fig. 1), first used nearly 30 years ago, and described in detail by Hardy (1939). The Hardy recorder is a tanklike object with a small aperture of about 1¼ inches, leading into a tunnel. A band of gauze travels across the end of the tunnel and is covered by a second band as it leaves the tunnel; both bands, with the plankton between them, are reeled into a tank of preservative. The band is usually marked off into divisions, and when the instrument is towed between known points the approximate location of the various parts of the record may be determined. This instrument is sturdily made and is regularly towed by commercial ships in the North Sea at speeds of 8–16 knots. The instrument is returned to the laboratory for unloading and reloading. It has been in regular use since 1931, and more than 40,000 miles of samples have been taken by it. The principal disadvantages of the instrument are that it operates only at one depth (when towed for several hundred miles this means that it cannot compensate for the diurnal migration of plankton) and squashes the organisms into lumps unsuitable for critical systematic purposes. A whole crew of examiners, however, has been trained to identify the important species in their mashed condition, and there is now a vast accumulation of data for the North Sea. So far, the Hardy continuous plankton recorder is the only instrument that gives a reasonably satisfactory synoptic picture.

The Clarke-Bumpus sampler (Fig. 2), first manufactured about 1940 and since widely used in limnological as well as oceanographic investigations, is a small cone-shaped net of conventional design attached to a metering apparatus and a closing device (Clarke and Bumpus, 1950). The apparatus is attached to a frame which is secured to a light cable and may be opened and closed by messengers. Several nets may be attached to the same wire in tandem, thus making it possible to secure a series of samples at various depths. This sampler, originally designed for the study of

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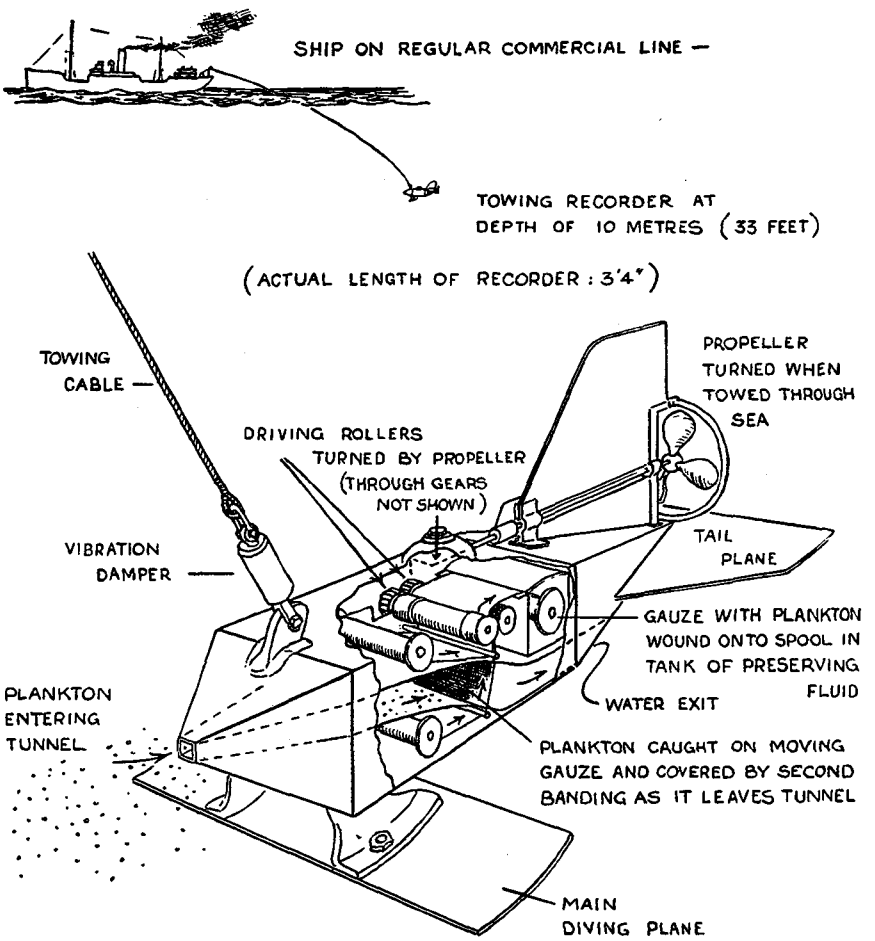

FIGURE 1.—*Hardy continuous plankton recorder*

Courtesy K. M. Rae and the Scottish Marine Biological Association

zooplankton, Crustacea in particular, has been successfully used in studies of the larger phytoplankton as well. A number of studies of the Clarke-Bumpus sampler, comparing its performance with that of other nets, have been made, indicating that it is a reasonably satisfactory instrument although it may not record the distribution of plankton along the distance but only the total for that distance. The ability to record the distance, or volume sampled, is one of the principal advantages of the Hardy recorder; at this time no studies are available which compare the performance of these two samplers under comparable conditions. The machinery of the Clarke-Bumpus sampler is more susceptible to clogging by larger organisms than is that of the Hardy sampler. The small size of the Clarke-Bumpus net, considered by some to be a disadvantage, at least in marine studies, apparently has no significantly different catching properties as compared with larger nets (Winsor and Clarke, 1940), but

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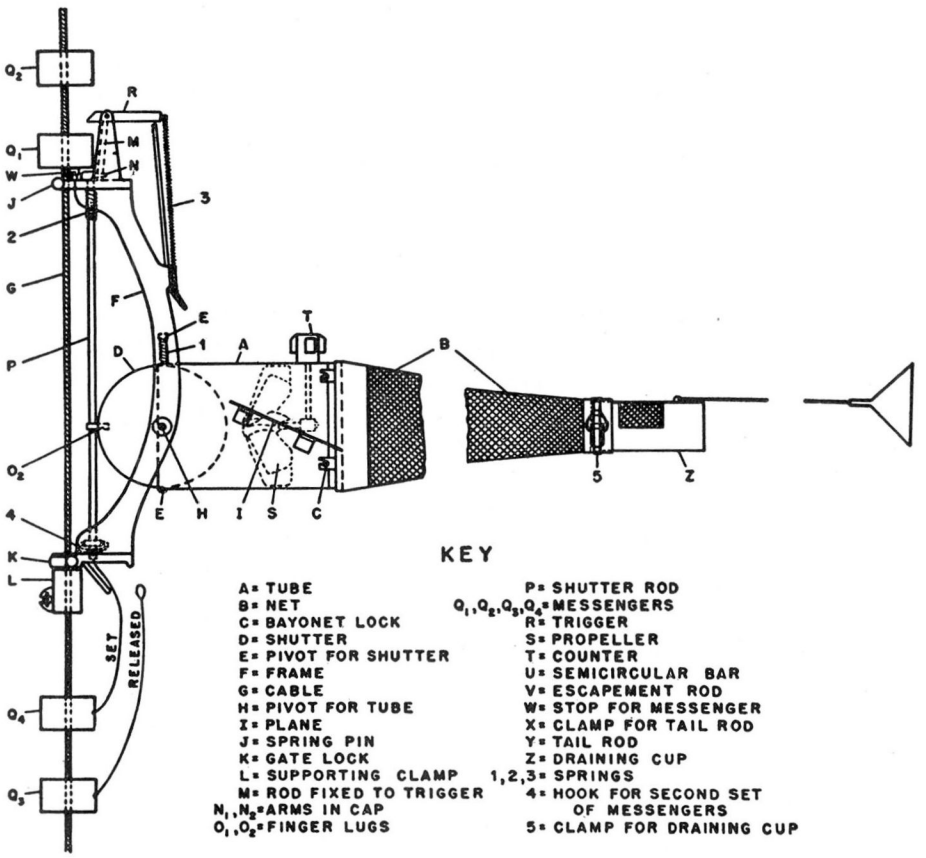
there have been occasions where the small net has become clogged, producing reverse readings because of backwash.

Certain operational difficulties, not mentioned in the literature, are well known to those who have used the Clarke-Bumpus sampler. The instrument is not easy to attach to the cable, and this operation requires two men. While it is stated that a number of samplers may be attached to a single line, the maximum number in practice is two since the release mechanism is not always activated by the messengers. The bearings and metering devices of the manufactured models are not adequate for reliable service in sea water and need frequent servicing and replacement.

Another manner of quantitative sampling is to pump a measured volume of water (Gibbons and Fraser, 1937), but this method has limited application, since larger plankton organisms may avoid the intake of all but a very powerful pump, and the



Idealized side view of sampler with shutter in open position, the first messenger having tripped the trigger for the first time. The first messenger of the second set below the instrument has been cast off. A brass cup with draining window is shown clamped to tail of net with a drag attached.

FIGURE 2.—*Clarke-Bumpus plankton sampler*

From Clarke and Bumpus, 1950.

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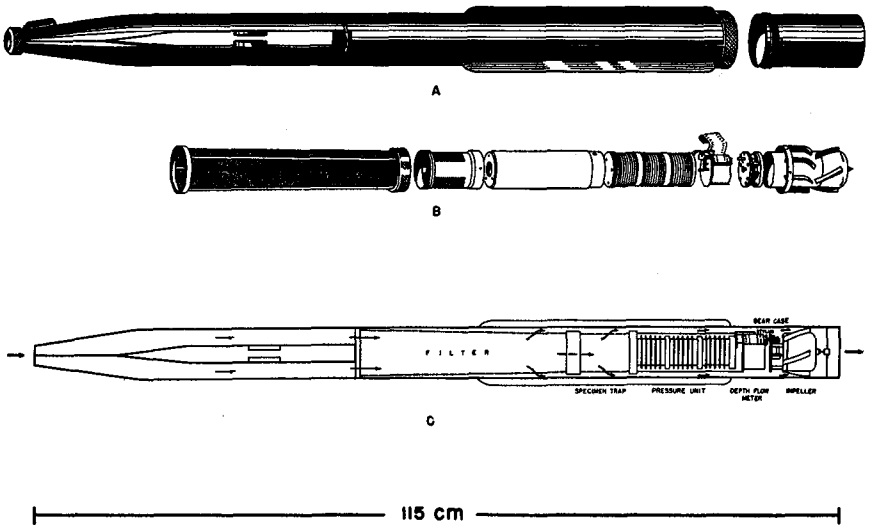

FIGURE 3.—*High-speed plankton net*
From Ahlstrom *et al.* (in press)

sampling column is even more limited than with a standard vertical net (Wiborg, 1948).

All standard nets, recorders, and samplers accumulate collections or masses of plankton which must be measured and identified at shore laboratories. To meet the need for some device that will give an immediate indication of the quality or quantity of plankton while at sea, a number of "indicators" have been devised. These are essentially cylinders with a disc or small bag of silk netting or metal screen, and are designed to be towed at relatively high speeds for a short distance. Several types were designed some years ago by Hardy (Glover, 1953) and were used by fishermen to obtain an impression of the richness of the waters, and the standardized discs or bags are then placed in preservative for later study in the laboratory.

Another family of high-speed samplers is more intricate in design, in that all of them include some sort of metering device to record the distance traversed or volume of water passed through the net. One of the most elaborate of these high-speed indicators is the High Speed Plankton Sampler developed at the Scripps Institution of Oceanography (Fig. 3). This is designed to travel at speeds sufficient to punch a neat hole in an unfortunate fish (as it has done) and is equipped with a pressure unit to record depth as well as a metering device. Less complicated samplers, without the pressure gauge, are being used in the Gulf of Mexico (Arnold and Gehringer, 1952). One is actually a half-meter net of monel metal screen with two current meters; although rather large and awkward, this high-speed sampler has caught organisms up to 5–7 cm. in length not usually caught in conventional nets.

The most intricate of high-speed samplers has been designed by Motoda (1953). This is similar to his vertical successive sampler, consisting of 10 cylinders or tubes which revolve into position, as well as metering devices for depth and distance. With

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this instrument, equipped with gear trains adjustable to two speeds, it is possible to take successive samples on a rapid traverse and thus obtain some idea of the variation in plankton abundance along the traverse of the net. The machinery appears to be even more complex and certainly less durable than that of the Hardy indicator.

As with any other type of collecting gear, no one type of plankton net, whether qualitative or quantitative, is suitable for all types of plankton. This was pointed out by Lohmann in 1903, and, as Glover (1953) says, Lohmann's dictum still holds. Plankton traps and pumps, however, seem to be more useful in limnological work, while one spectacular modification of the plankton net can have little use in fresh water except possibly in the very deepest lakes. This is the ingenious parachute net (Wheeler, 1941), which fishes as it descends to the bottom, where it is released by a tripping mechanism or by the solution of a block of salt.

SAMPLING THE BENTHOS

By Gunnar Thorson

Zoologist, Zoological Museum, University of Copenhagen, Denmark

Quantitative sampling of the macrofauna.—When introducing the quantitative technique in marine benthos ecology Petersen (1913, p. 23) clearly pointed out that even on level-bottom flats no single instrument is able to procure a complete representation of the whole fauna of a locality. It is therefore most essential to select the right combination of instruments (both quantitative and qualitative), as few as possible, and complementary to one another, so as to give the most reliable picture of the composition of the fauna. If we intend to obtain a quantitative impression of a fauna, the sampling technique is still more critical, since the values from a relatively small series of samples must be multiplied to indicate the number of specimens and animal weight per square meter, and these figures must again be generalized, often for huge areas of the level bottom.

For quantitative samplers of macrobenthos the general rule for all marine field devices is especially applicable: the more solid and simple their construction, the better. As we must deal only with small series of test samples, representing huge areas of level bottom, the size and handiness of the sampler in proportion to the size of the samples it procures are to be emphasized since a larger series of samples will give us more comprehensive material.

The $\frac{1}{10}$ square meter Petersen grab (Fig. 4), the classical apparatus for quantitative benthos ecology, meets these demands (For description *see* Petersen, 1911, pp. 48–50). This iron grab, which weighs about 45 kg, is dropped in the open position to the bottom, and the shock releases the catch so that the grab is closed as the strain is applied. The grab bites $\frac{1}{10}$ of a square meter out of the bottom surface, the jaws biting deeper the heavier the grab and the softer the bottom. The sample is washed through a set of three sieves with coarse, medium and small ($1\frac{3}{4}$ sq. mm) meshes respectively. All macrofauna retained in the sieves are picked up, identified, counted, and weighed. For a large series of samples, washing is best done mechanically. The sieves may be installed in a rocking device and the water applied from overhead

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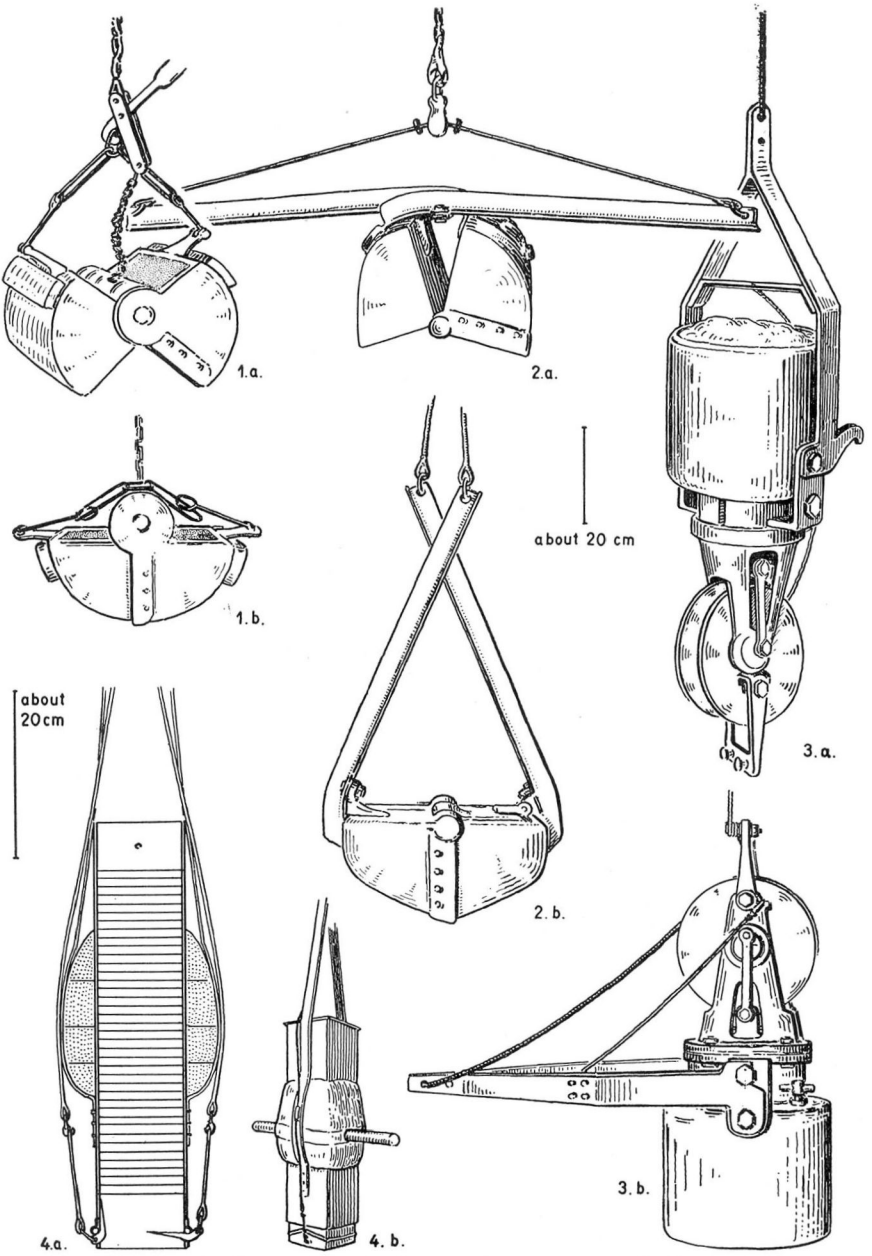

FIGURE 4.—*Types of quantitative grabs for level-bottom animal research*

(1a) the Petersen grab open, ready to hit the bottom; (1b) the same, closed with the sample inside; (2a) the van Veen grab open, ready to hit the bottom; (2b) the same, closed; (3b) the Knudsen grab ready to plunge; (3a) the same coming up upside down with the sample in the cylinder (the scale above, right refers to Figs. 1, 2, and 3); (4a) (with the scale below, left) "close-up" in longitudinal section of the Enequist bottom sampler; (4b) the same, seen from outside. *Note*: In the van Veen the cable should be a single loop, through rollers at the ends of the arms, for a stronger bite. Drawn by Poul H. Winther for G. Thorson.

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through a series of shower heads adjusted to give a fine, gentle spray that will not injure the more delicate worms, etc. This method has been used extensively by Hartman (1955).

The problems of the 1/10 sq. m. Petersen grab may be summarized as follows (*see* also Heuts, 1946, Marlier, 1953, and Ursin, 1954):

(1) Animals that can move rapidly escape the grab and are normally not caught (Steven, 1930; MacGinitie, 1939). This defect of the grab may be overcome only by using supplementary apparatus (trawl, dredge, or camera) in the same locality.

(2) On hard sand and shell bottoms deeply burrowing animals are never taken, and even in certain muddy bottoms there is a chance that they are taken occasionally only and to a most varying degree which cannot give us an idea of their true abundance (Johansen, 1927; Steven, 1930; MacGinitie, 1939; *cf. also* Lee, 1944). This point, regarded by MacGinitie in particular as the most serious disadvantage of the Petersen grab, must, however, be considered in connection with the following facts: (a) the tidal flats where MacGinitie works seem to be much richer in deeply burrowing animals than most other level-bottom areas (the number of deeply burrowing animals from the North Atlantic procured with all types of instruments is significantly smaller; *cf.* Molander 1928); (b) "the deeper the water, the shallower the burrowers go" (MacGinitie, 1939; *see also* Petersen, 1913, p. 24), and (c) the softer the bottom the smaller the number of burrowing forms (MacGinitie, 1939). This means that those bottom types on which deeply burrowing animals escape the 1/10 sq. m on a large scale are the same in which the grab is unable to work regularly for other reasons (*see* point 3). In other words: in those substrata (mixed and muddy bottoms) in which this grab can successfully work, there will be few animals burrowing so deeply that they escape the grab (Molander, 1928).

(3) On hard sand and shell bottoms, and in certain types of tough clay, the jaws will not bite deep and often will not close completely, so that the grab will bring up a small and fragmentary sample or none at all. Comparisons with more effective apparatus on similar types of bottom show that the Petersen grab will take only one-third to one-fifth of the animal numbers actually present (Johansen, 1927; Knudsen, 1927; Hagmeier and Kändler, 1925; Hagmeier, 1930; Smith, 1932; Thamdrup, 1938; Holme, 1949; 1953). The efficiency of the grab on such hard bottoms may be considerably improved by adding lead or iron plates to increase its empty weight from 45 kg to 75–100 kg (Hagmeier and Kändler, 1925, p. 27; Hagmeier, 1930), but nevertheless we must realize that this grab will not give a true quantitative picture of the macrofauna in hard sand-bottom or shell-gravel substrata; here another series of instruments must be used.

(4) When lowered on a taut wire the grab will normally hit the bottom in the right way. If the ship is drifting, the grab will, however, often be hauled to an oblique position by the taut wire before closing its jaws. If so, only a fraction of a true quantitative bottom sample will be brought up. This is further complicated when the ship is rolling (Davis, 1925, for the 1/5 sq. m Petersen grab). To avoid this, force must be applied so that the grab will close as soon as possible after hitting the bottom. At shallower depths (down to 100 m at least), this can be done by hand force, the winch afterwards hauling the grab to the surface. Even without drifting—*i.e.*, when working regularly—the grab may push some bottom material to the side when closing, thus taking up a smaller quantity of bottom material than calculated (Orton, 1925, with suggestions for preventing this loss). Davis (1925, p. 49), aware of Orton's objection, found the loss in this way very small.

(5) When the instrument hits the bottom the resulting water current in front of the instrument will often push tiny animals away from the surface (Ekman, 1933, p. 314; Lindroth, 1935, p. 350), and when the jaws bite together the natural stratification of the bottom sample inside the grab is disturbed and the animals will not be found in their right position (Molander, 1928; Hjort and Ruud, 1938, p. 146). The rough and simple construction does not allow the grab to close completely, and the finest part of the bottom material will, therefore, be partially washed out. In this way several of the smaller animals may also be lost (Johansen, 1927; Hunt, 1927). These points make the Petersen grab less suitable for microfauna studies, for which other sampling devices are needed.

In spite of these objections the 1/10 sq. m Petersen grab is still regarded as the most

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practical and handy instrument for quantitative sampling of level-bottom macrofauna by several investigators (Hagmeier and Kändler, 1925; Zenkevich, 1927; Hagmeier, 1930; Vatova, 1934; 1935 1936; 1949; Yonge, 1948), though it is admitted that more reliable apparatus is needed for future investigations. This grab has been used by Thorson for thousands of samples from East Greenland to the Persian Gulf with a very high percentage of successful samples from all soft and mixed bottoms down to at least 150 m, and Petersen (1915, p. 19) found that it functioned well to at least 700 m on the soft bottoms of the Skagerrack. Vibe (1950, pp. 42–43; *cf. also* Thorson, 1946) describes a special technique for Arctic regions in which the Petersen grab is operated through holes in the sea ice, hauled to the surface by the eskimo dogs and the samples stowed together as frozen cuboid blocks on the dog sledge and taken to the laboratory.

For deeper water and harder bottoms Petersen constructed the $\frac{1}{5}$ sq. m bottom grab, differing only in size from his small grab. The apparatus, too large to be operated from a small motorboat, but well fitted for a stable cutter or a small steamer, has the benefit of being much heavier—*i.e.*, biting deeper in the bottom—and of taking a sample of double the area of the small grab. It must, however, be operated with the greatest care since it may be dangerous to the crew, especially when the ship is rolling (Davis, 1923; Thorson's observations). During the Danish GALATHEA Expedition, 1950–1952, this grab was used 41 times to procure bottom samples from depths between 2000 and 10,120m. Twenty-eight of these samples—*i.e.*, 68 per cent—proved to be successful, containing for most hauls from 15 to about 40 liters of bottom material per grab. Four of these samples were from depths exceeding 10,000 m, and three of them were successful. The greatest content of bottom material was found when the weight of the grab had been increased by adding some extra iron plates (courtesy Dr. A. Bruun). The $\frac{1}{5}$ sq. m Petersen grab seems to be the best all-round grab for quantitative sampling hitherto constructed, as it has worked in the most varied types of sediment and at all depths.

To obtain reliable quantitative samples from hard sandy bottoms and from shell-gravel substrata, however, another series of instruments is needed.

The $\frac{1}{10}$ sq. m van Veen grab has the same size and weight (45 kg) and the same construction of the jaws as the small Petersen grab. Each jaw is, however, connected with a long lever, so that the jaws work like a nut cracker. The jaws therefore bite strongly into the bottom and will obtain about three times as much material on hard sand bottom and three times as many animals per unit as the Petersen grab of a similar size (Thamdrup, 1938). The van Veen grab may also be constructed in the $\frac{1}{5}$ sq. m size.

The van Veen grab is less handy than the more compact Petersen grabs. Its two long levers are awkward, especially in rough weather, and the objections given in points 1, 2, 3, and 4 for the Petersen grabs will also apply, at least partially, for the van Veen grab. During the GALATHEA Expedition it was further found that this grab was unfit for work at great ocean depths as the standing waves or swell at the surface or deeper down will act upon the levers so as to close the grab long before it hits the bottom. For work on hard level bottoms down to some hundred meters this grab, however, has proved most useful and very effective; on such bottom it is an

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excellent supplement to the Petersen grabs. During recent years it has been used with good results by Jones (1952) off the coast of Cumberland and by Ursin (1952) and Birkett (1953) on the Dogger Bank. (*See* also Marlier, 1953, and Ursin, 1954.)

Lee (1944) constructed a very large grab (jaw-biting principle) taking a sample of 0.56 sq. m. Until now this grab seems to have been used only by its constructor and only in one area of the seas (Martha's Vineyard). It seems to be very effective on hard level bottoms and to dig to a considerable depth. Because of its heavy weight and large size it can be operated only from a rather large ship.

The $\frac{1}{20}$ sq. m Holme sampler, weighing about 45 kg, is also constructed for hard level bottoms (Holme, 1949). In use it is often weighted to 110 kg. This sampler is a semicylindrical scoop mounted on a frame. By unwinding cable from a drum after the sampler has hit the bottom, this scoop, starting upside down, is rotated through 180° on a horizontal axis, thus shoveling in the substratum. The loss of material caused by the jaw-closing principle in the Petersen and van Veen grabs is avoided, and an overhead scoop functioning as a cover during hauling protects the sample from being washed out. The scoop digs about 8 cm (sometimes up to 15 cm) below bottom surface at its deepest, and the efficiency of this sampler on hard level bottoms seems to be nearly the same as that of the van Veen grab, but each haul will yield a sample of only half the bottom area procured by the van Veen grab. In 1953 Holme described and figured a new model with two counter-rotating scoops comprising together $\frac{1}{10}$ sq. m bottom area, weight 115 kg, which seems to yield good samples and to function well. The methods of collecting and the validity of the samples are discussed in detail in his paper.

Another recently invented sampler of this general type is the $\frac{1}{10}$ sq. m Smith spring-loaded bottom sampler, designed for use in rough weather and on hard sand bottoms (Fig. 5). It consists of a pair of semicylindrical jaws which dig to about 7 cm, operated by heavy springs; the mechanism is so designed that it will not release unless the instrument sits squarely on the bottom. This sampler seems to be even more efficient than the van Veen sampler and will function in weather when the van Veen cannot be used (Smith and McIntyre, 1954; verbal information by Dr. A. R. Longhurst).

The $\frac{1}{10}$ sq. m Knudsen sampler (Knudsen, 1927), especially constructed for hard level bottoms, is based on quite different principles. An iron cylinder, 30 cm high and 36 cm in diameter and open below, is closed at the top by an iron cover on which a water pump is fixed. When the sampler hits the bottom, a lever will fall, making the wire ready for hauling. As soon as the winch has tightened the wire, this will rotate a drum acting upon the water pump which will suck the cylinder completely into the sea bottom with a force of 2000 kg or more. Having rotated the drum to cause this effect, the taut wire comes free of the drum and acts on the lever again, which now hauls the cylinder off the bottom with its content of 30 liters of bottom material. As soon as the cylinder is free of the bottom it capsizes and is hauled to the surface upside down. This is the most effective of all quantitative macrofauna samplers yet constructed. While the Petersen, van Veen, Lee, and Holme samplers take samples of the shape of half a cylinder, *i.e.* dig deeper in the middle of the sampling area than along its edges (Ekman, 1933, p. 314) and bring up samples with their natural strati-

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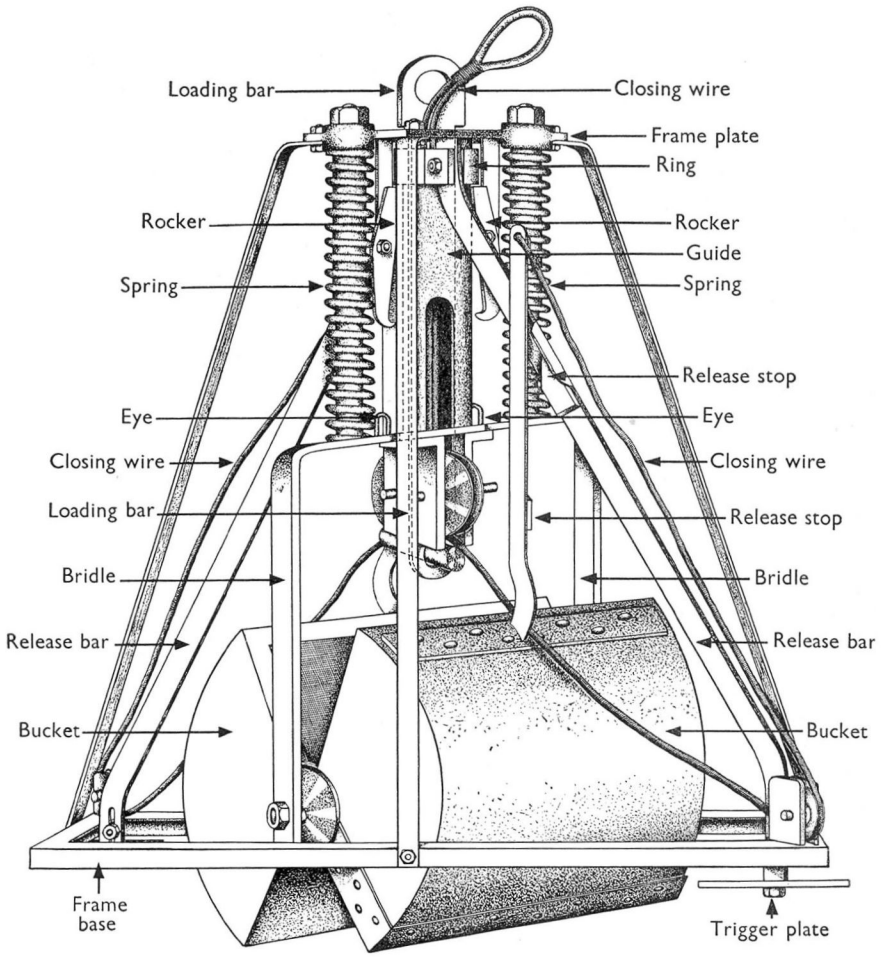

FIGURE 5.—*Smith spring-loaded bottom sampler*

From Smith and McIntyre (1953), reproduced by permission of the council of the Marine Biological Association of the United Kingdom.

fication disturbed—the Knudsen sampler, because of its steep walls, will bring up a sample with its natural stratification and of equal depths (30 cm) all over—*i.e.*, including even the deepest burrowers. On hard sandy bottoms this sampler brings up a far greater bulk of bottom material and about 4–5 times as many grams of bottom organisms per square unit as the $\frac{1}{10}$ sq. m and $\frac{1}{5}$ sq. m Petersen grabs, respectively (Johansen, 1927; Zenkevich, 1928, p. 203; *cf. also* Hagmeier, 1930, p. 131). As it is very heavy (exact weight not given), and not at all handy, the Knudsen sampler can be operated only from a large ship with solid gear. If it should happen, and it generally does, that the cylinder is completely filled with bottom material before all the wire has been wound off the drum, the further rotating of this becomes a very hard task, and the cylinder is anchored so hard in the bottom by suction that it is nearly impos-

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sible to haul it up (*see* Knudsen, 1927, p. 4 with suggestions to avoid this calamity). For that same reason the Knudsen sampler is unfit for soft bottoms, while on hard bottoms it will normally function well (Hagmeier, 1930, p. 131; Zenkevich, 1928, p. 203). Objections are: (1) When the ship is drifting the cylinder may hit the bottom surface obliquely and give an inexact sample. (2) The capsizing of the cylinder during hauling makes the natural stratification of the sample partially illusory, since several animals inhabiting sandy surfaces will instinctively move upward when covered by sand, thus changing to an unnatural position (Hagmeier, 1930, p. 131). (3) In rough weather and open sea there is risk of loss of material during hauling (Holme, 1949, p. 324). (4) It also seems difficult to remove the sample from the cylinder without disturbing its natural stratification. If, however, the technique for operating this sampler might be simplified, the Knudsen sampler would no doubt be the most effective instrument available for sampling hard level bottoms. *See* also Ursin (1954) and Marlier (1953).

The $\frac{1}{25}$ sq. m Otto Pettersson sampler (Pettersson, 1928; Molander, 1928; Hjort and Ruud, 1938; and critical remarks by Ekman, 1933, p. 314), constructed for muddy and mixed bottoms, consists of a quadrangular iron tube which is driven down into the soil by the impact of a weight of 20–40 kg sliding along an iron shaft and striking the lid of the apparatus with a shock. As it is being hauled up, a horizontal shutter cuts off the bottom sample below and at the same time closes the tube. The apparatus will reach down to 15 cm and 5 to 7 cm depths in muddy and mixed bottoms, respectively, and will bring up a sample with a rather natural stratification. For studying the vertical distribution of the animals in the bottom substratum this apparatus seems to be most useful. Main objections are: (1) The apparatus will not work well in hard sand or gravel bottom, and even in mixed bottoms will hardly dig deep enough to procure the deepest-burrowing animals. (2) The samples obtained are too small for quantitative macrofauna studies and too large for the microfauna, and the sampler is not very handy. If the tube were reduced to take 1 sq. dm bottom only and the weight striking the lid were increased, the apparatus would no doubt be most valuable as a microfauna sampler, especially when it was changed so as to allow the water current to pass through the tube during lowering (Ekman, 1933, p. 314).

Some quantitative grabs originally constructed for taking bottom samples in fresh water have been used for sampling marine substrata: (1) The Ekman grab taking samples of $\frac{1}{32}$ sq. m (Ekman, 1911, used by Larsen, 1936; and Miyadi, 1940a; 1940b; 1941c), (2) The Birge-Ekman grab taking samples of $\frac{1}{44}$ sq. m (Birge, 1922, used by Yamamoto, 1950), and (3) The Ekman-Lenz Grab taking samples of $\frac{1}{50}$ sq. m (Lenz, 1931; used by Miyadi 1941a; 1941b). These handy grabs, so excellent for fresh-water studies (*see*, however, the critical remarks of Ekman, 1933, pp. 320–328) may be useful to marine ecologists also, especially on soft bottoms in shallow estuarine waters where only a small jolly boat or skiff is available. The $\frac{1}{40}$ sq. m bottom sampler of Lang (1930; 1931; *see also* Ekman, 1933, p. 316), especially constructed for fresh-water lakes with very soft bottoms, may also be used for marine purposes, but only in soft muddy bottom and at shallow depths. For hard level bottoms in similar shallow water the hand-operated (long steel tubular handle) grab of about $\frac{1}{30}$ sq. m bottom unit constructed for sampling river beds seems most useful (Allan, 1952).

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The samples procured by all these grabs are, however, so small that large series are needed to give a true impression of the marine macrofauna, and they therefore are to be recommended only if no marine equipment is at hand.

Borutski (1952) calls attention (with figure) to a Russian bottom sampler constructed and used by Klassen in the delta of Volga as early as 1912; he claims on that basis Russian priority in quantitative methods of bottom investigations. Since Petersen published his first quantitative paper in 1911, and since he started the investigations with his bottom sampler several years earlier, this maintenance of "patriotic priority" seems rather out of place. The instrument may, however, be useful though data on its efficiency and reliability are not available.

The writer knows of no other instruments at present available for taking quantitative samples of the macrofauna of the level sea bottom. Among these samplers the student has to choose those most suitable for his purpose. If a small boat with a small winch only is available, the writer would prefer the extra weighted $\frac{1}{10}$ sq. m Petersen grab for all mixed and soft bottoms, supplemented with the $\frac{1}{10}$ sq. m van Veen grab for hard bottoms. If a fairly large ship with a good winch and solid gear is available, Thorson would replace these two instruments by the $\frac{1}{5}$ sq. m Petersen grab and the $\frac{1}{10}$ sq. m Knudsen sampler respectively.

A true picture of the quantitative composition of the macrofauna of the level bottom of a certain area is, however, dependent not only on the reliability of the grabs used but also on the pattern in which the samples are dispersed throughout the area. If the purpose is to get a quick, provisional orientation on the quantity of macrofauna in an area hitherto not investigated, the best will be to take the samples in transverse sections ("profiles") from the shore toward deeper water (Petersen, 1913, p. 29). Since the composition of the bottom substratum as well as the hydrographic factors are generally more uniform with greater depths, a larger number of samples is needed from shallow than from deeper water in order to yield equally reliable results. Ten samples with the $\frac{1}{10}$ sq. m Petersen (or van Veen where indicated) grab from each of the depths 10, 20, 30 and 50 m, followed by two samples taken with the $\frac{1}{5}$ sq. m Petersen grab from each of the depths 100, 150, 200, 300, 400, 500 m, etc., seem to give a rather reliable quantitative picture of the fauna (Thorson, 1946, p. 9). In narrow fjords where the bottom flats are less uniform the samples must be more numerous and more densely placed than in the open sea (Petersen, 1915, p. 17; Lindroth, 1935, p. 351; Broch, 1927, pp. 29–32). [As indicated by the postscript to Chapter 3, more thought should be given to sampling methods and statistical treatment of the samples obtained. In many types of community study, where it cannot be assumed that the distribution of organisms in the samples are "normal", the application of nonparametric tests to paired series of samples may yield results more susceptible to objective confirmation and repetition than simple comparisons of average composition of a single series of samples. J. W. H.]

If, however, a thorough quantitative investigation is to be carried out in a well-known area to study the fluctuations from year to year or to calculate its total productivity, it seems reasonable to use the Wollaston method (*cf.* Davis, 1923, pp. 6–7, or Fisher's "coefficient of dispersion", Holme, 1950) which gives a truer idea of the average quantities and allows statistical treatment afterward. *See* also Hutchinson (1953).

Normally sections of bottom samples in shallower depths will arrive on deck in such rapid succession that it will be impossible to sieve and examine them all at once. If so, each sample should be placed with its label, but without sieving and cleaning, in a tub in a shaded place and treatment postponed until the whole section of samples has been taken. The animals will thrive much better in their natural bottom substrata than in glass dishes after having been washed (*cf.* Thorson, 1946, pp. 8–11). When sieving the samples through a set of three sieves much care is needed. First of all the finest sieve must always be of the standard size (meshes $1\frac{3}{4}$ sq. mm.). Secondly, too strong a jet of water

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may disturb many delicate animals, especially worms, and washing slowly and carefully requires much patience especially in tough clay substrata. The picking up of animals from the sieve must also be done with much caution and thoroughness (*cf.* Lindroth, 1935, p. 352). Many worms actively crawl through the meshes, and quite large individuals may be lost during a prolonged sieving. To minimize such losses, the contents of the sieve should be washed into a jar as often as possible (Holme, 1953, pp. 20–21). Polychaete tubes must be examined individually, and lamellibranchs must be inspected for dead specimens that have only mud inside their shells, etc.

Recent investigations have demonstrated the close relation between the type of bottom substratum and the animal population inhabiting it (Chapter 17). Therefore, before sieving, a small sample of the substratum should be taken for closer examination or an "underway bottom sampler" (Emery and Champion, 1948) used for this special purpose. An exact code for expressing grain-size distribution of the varying substrata will make a natural link of quantitative bottom sampling in future (for technique *cf.* Davis, 1925, pp. 6–9; Emery and Gould, 1948; *see also* Holme, 1953, p. 3). The apparatus described by Ekman (1947) to examine the toughness of a marine soil also seems to be most useful for future studies.

Even if the animals procured are to be studied more closely in a preserved condition it is most essential to control the living weight (for weighing technique *see* Petersen, 1911; Jensen, 1919; Thorson, 1946, p. 10) at regular intervals, for instance for one of each five samples, before placing the animals in the fixative. This will give an idea of the waste of weight caused by fixation, and this figure must be known if we later intend to find the rate: dry organic weight/living weight, which is the key for calculating productivity. Therefore, it is also of value to choose the same fixative (alcohol or neutralized formalin) for all aminals and samples, since alcohol and formalin weights are very different.

Attention must also be paid to the very promising collaboration between the quantitative bottom-sampling methods described above and the modern technique for photography of the sea floor which during recent years has obtained most remarkable results (*cf.* Clarke, 1941; Ewing *et al.*, 1946a; 1946b; Ewing, 1948; Bonde *et al.*, 1951; Northrop, 1951; Vevers, 1951; 1952). A series of amazing photos has shown that such animals as sea pens, sea urchins, spatangids, sand dollars, starfish, and brittle stars often lie freely exposed on the surface of the bottom, now and then in huge numbers. A comparison of quantitative samples and photos from the same bottom areas will help us to find out what these photos and their visible animals actually stand for. As soon as we know this the sea pens, spatangids, brittle stars, etc., seen in the photos will be serviceable as indicators also of the deeper-burrowing animals, for instance, lamellibranchs and polychaetes, which the quantitative samples have shown to be associated with the "photo animals." Furthermore, as each photo will normally cover a significantly larger area of the sea floor than is obtainable from a few quantitative samples, and since the area photographed is known, such photos may give us valuable information on the uniformity of the bottom—*i.e.*, the quantitative reliability of our scattered samples, and of the quantity of such larger animals that are so sparse that they will not be caught regularly in a few samples.

Although not so used in European investigations, the orange-peel bucket has been employed in the United States as a quantitative bottom sampler (Packard, 1918; Hartman, 1955; Shepard and Moody, 1953, Fig. 8). The orange-peel bucket is designed for digging out pipes, caissons, etc., and its chief advantage is that it is a standard piece of equipment manufactured in several sizes. Its disadvantages as a sampling grab are many, and inherent in its construction. The grab consists of four sectors designed to take a hemispherical bite out of the bottom. The sectors are operated by a large wheel-and-sprocket mechanism within the upper framework. This mechanism may be operated by a second cable or by a slack release mechanism activated by a messenger. Usually a canvas sleeve is placed over the upper works to prevent washing out of the contents when the bucket is being hauled up, but the instrument is designed to permit active drainage from the surface of the sample (when

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closed, the upper part of the jaws are not completely tight, and there is a notch between each sector on the circumference). In hard bottoms or in mud with small stones or heavy bivalves, the jaws seldom close tightly, and much of the sample may be lost. In very soft bottoms the bucket may sink several feet, bringing to the surface a large compressed plug of mud that must be cleaned from the working mechanism (and in which the specimens may become entangled) before the next sample can be obtained. While this digging action of the orange-peel bucket is cited as an advantage in obtaining deeply burrowing mollusks and worms, the disadvantages of a disturbed sample of unpredictable volume mixed in with the mechanism are much greater. It is also difficult to compute the precise area sampled since the jaws when open describe a greater circumference than when closed. In a bucket of 10 inches closed diameter, the open diameter is 11.5 inches, which means that the area is greater by 25.4 inches or 32.4 per cent; not all of this greater area, however, is completely encompassed by the open jaws, and it will vary with the depth of bottom to which the bucket has penetrated. For these reasons the orange-peel bucket can be recommended only as a reconnaissance sampler and should not be used in critical work that is to be compared with the results of other regions.

Quantitative sampling of the microfauna.—The microfauna of the bottom includes not only the minute adult organisms, some of which are extremely numerous, occurring in concentrations of millions per square meter, but the early larval stages of the macrofauna. A complete study of the macrofauna can be achieved only by using the techniques developed for microfauna studies, and of course the microfauna itself must be studied if we are to obtain a complete analysis of the community.

The 100 sq. cm Enequist sampler (Enequist, 1941; Nyholm, 1952), which weighs 35 kg, consists of an external quadrangular metal tube with two handles and a heavy leaden mantle surrounding a quadrangular, 50-cm long, tube of steel fitting closely in it; the two tubes are bolted together. With its heavy weight and sharp edges this instrument will sink deeply into all muddy and mixed bottoms but not into hard sand and gravel bottoms. Two flaps near the lower opening, placed so as to allow the sample to enter the tube smoothly, will close as soon as the sampler is hauled up, thus preventing the sample from escaping. The outer tube is removed, and the undisturbed sample enclosed in the inner tube may be divided into horizontal layers of 1 cm each by pushing plates of duralumin through horizontal slits in the tube wall. Except on hard sand and gravel bottoms, this instrument seems to be easily operated even from a jolly boat, and to be very effective in procuring samples with an undisturbed stratification sufficiently large to assure young stages of bottom invertebrates in adequate numbers. Thorson, having seen it at work at Kristineberg Zoological Station, is of the opinion that this is the best single instrument available at present for obtaining quantitative samples of the microfauna.

The 200 sq. cm Ekman grab for marine bottoms (Ekman, 1933), weight 39 kg, is a heavier and improved model of the older fresh-water grab (Ekman, 1911). In soft bottoms it functions well (Lindroth, 1935, p. 333) and brings up samples the upper part of which have an undisturbed stratification, and with the "half-suspended" surface layer of the bottom with its microfauna intact. The sampler is closed by two small scooplike jaws to prevent loss of the sample, but this construction impedes the

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penetration of the sampler in sandy or even mixed bottoms (Enequist, 1941). Further, as is also the case with the Otto Pettersson sampler, the samples obtained are rather small for macrofauna studies and too large for microfauna studies, but Ekman (1933, p. 320) held out the prospect of constructing a larger grab if experience with this provisional model proves to be successful. In its present construction this apparatus is, however, less versatile, less simple and handy, and more expensive than the Enequist sampler, which seems to be preferable for microfauna purposes.

The Hjort-Ruud (1938) bottom sampler for the mudline (*i.e.*, about 200 m depth) consists of a tube 15.5 cm in diameter—*i.e.*, securing a bottom sample with a surface area about 190 sq. cm. A rubber ball enclosed in a valve above the tube allows a current of water to flow through when the apparatus is lowered and cuts off this current when the instrument is hauled on board, thus sealing the tube with the sample and the natural water mass above it. The sucking force obtained when the valve closes is sufficient to retain a sample of mud of medium toughness with undisturbed stratification until it arrives on deck (tube not closed below). A bundle of glass tubes inside the tube will procure water samples from 2, 10, 15, 20, and 30 cm above the bottom, thus allowing us to study the microclimate there. This latter invention, which is most useful, may no doubt be installed also in the Enequist sampler. According to Professor Ruud (Personal communication to Thorson) only a core of clay of a certain toughness may adhere to the tube until it arrives on deck, and the glass tubes will hardly give a reliable picture of the stratification of the water just below the bottom, since some mixture seems always to take place.

The Krogh-Spärck "chandelier sampler" (Krogh and Spärck, 1936), which like the preceding sampler is constructed according to the sounding-tube principle, consists of a central, torpedo-shaped load bearing six horizontal arms, each of which carries a vertical tube of brass. In each tube a celluloid tube (50 cm long, inner diameter 28 mm) may be inserted, its upper mouth being provided with a rubber valve which permits the water current to pass during lowering. To function, the celluloid tubes must be forced at least 10–15 cm into the substratum. When hauled up the rubber valves will close, and the tubes, still open below, will by combined sucking and adhesion bring the samples on deck. Here the celluloid tubes are immediately stopped and removed, new tubes are inserted, and the instrument is again ready for use. The area of bottom surface covered if all six tubes function well is only 37 sq. cm—*i.e.*, an area large enough to obtain quantitative data for protozoans, ostracods, and small nematodes, but too small to obtain a reasonable number of O-group young of macrofauna. This sampler functions best in mud bottom of medium toughness. In very soft bottom some of the tubes will be empty when they arrive at the water surface, and sandy or gravelly substrata will not be brought up at all (Thorson, personal experience). As the dispersion of one sample on 6 tubes complicates the technique, the simpler devices described above are to be preferred. A modification of this sampler (one celluloid tube with a rubber valve and placed on a shaft) was used by Smidt (1951, p. 5, Fig. 1) for shallow-water studies on microfauna in the Danish Wadden Sea.

A simple bottom sampler of this type, now widely used in quantitative studies of Foraminifera, was designed by Phleger (1951). The Phleger Bottom Sampler is a short weighted tube with a removable lining tube and replaceable cutting edge (in

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the event the instrument should be damaged by striking hard bottom or a rock). The liner consists of clear plastic tubing (cellulose acetate butyrate) with an inside diameter of $1\frac{3}{8}$ inches (*i.e.*, 3.5 cm; so that the area covered is 9.6 cm). The instrument is so designed as to take a short core of the upper sediment layers without disturbing the surface layer. When weighted with 35–40 pounds of molded lead the instrument may be operated from a light winch to depths of 500 m. The instrument has been operated to depths of 4600 m. but requires sediment of some cohesion to bring up a successful core. The advantages of this sampler are its ease of operation; the removable lining, which makes it possible to take a large number of samples in rapid succession and store them for examination; and the undisturbed condition of the surface layer. Although the area covered is small, a number of samples may be taken to compensate for this. In addition to providing quantitative samples in easily handled size, the Phleger Bottom Sampler has produced interesting qualitative results, revealing various microfaunal types (echinoderids, minute hydroids, etc.) not previously known from the regions in question.

The Hunt vacuum sampler (Hunt, 1926), especially suited for hard sand and gravel bottoms, seems to be most valuable on such substrata, where the Enequist sampler cannot be used. The Hunt sampler is provided at its lower end with a "sampling tube" with a bell-shaped mouth (diameter 7.5 cm) which is hermetically sealed by a glass diaphragm from the superposed "trap tube" emerging in a "pressure chamber" above. On reaching the bottom the diaphragm is automatically broken. The pressure of the overlying water column forces a sample of the bottom through the "sampling tube" and "trap tube" into the "pressure chamber," and the trap device prevents the sample from escaping when the apparatus is raised. With increasing pressure—*i.e.*, at a greater water depth—the instrument will sample from a greater depth in the bottom material but never from a wider area (*i.e.*, about 45 sq. cm) than that encircled by the margin of the bell; the sample thus is quantitative as to surface area. Even the finest particles and the smallest organisms are brought up, although the natural stratification is of course disturbed. This sampler works well from 10 to 70 m depth at least and seems to be rather handy. Its weight is not indicated, but it is not very heavy. An enlarged model, able to take 100 sq. cm of bottom area so that the samples would be directly comparable to those obtained by the Enequist sampler, would make this sampler more useful.

A new suction corer, with about $\frac{1}{50}$ sq. m bottom area, is briefly described and figured by Holme (1953, pp. 10–12). The technique seems to be a mixture of that of the Knudsen sampler and the Hunt sampler; suction is produced by hydrostatic pressure instead of by a pump. It seems to penetrate well even in a bottom of muddy sand (to an average of about 16 cm), and the sample comes up with a rather undisturbed stratification. When further details are known, this sampler may prove most valuable.

Summarizing this review on microfauna samplers, the writer recommends the Enequist sampler for all mixed and soft bottoms, supplemented by the Hunt sampler (enlarged to take 100 sq. cm) for sandy and gravelly bottoms. The marine Ekman sampler also seems most useful for soft bottoms, especially when reduced to take 100 sq. cm, while the other instruments mentioned seem to be less versatile and reliable.

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For quantitative sampling of microfauna on sand or mud flats in the tidal zone, the 25 sq. cm "wadden skimmer" of Smidt (1951, p. 5, Fig. 2) seems to be most useful. The reader's attention is also called to the nonquantitative microsampler dredge of Mortensen (1925) which according to Remane (1933) and Thorson's experience yields excellent results, and to the sledge dredge of Beauchamp (1932).

When a quantitative sample of the microfauna is to be obtained, the problem still remains of how to drive out all the tiny animals so as to get a true quantitative impression of its fauna. The old methods of examining each sample, using two needles after having stirred it up in a glass dish, sucking up the animals with a pipette, is extremely time-consuming and even with the greatest thoroughness only a small fraction of the animals actually present might be obtained. For large-scale studies with a small staff this method is hopeless. It is imperative to find methods parallel to those invented by Berlese (1905), Tullgren (1917; *see also* Haarløv, 1947), and Overgaard (1948) for the terrestrial microfauna—*i.e.*, to use mechanical means to drive the animals out of the soil.

Recent experience, though still at an experimental stage, seems rather promising, and these problems will no doubt be solved in the years to come. A combination of three (or more) principles may be used to drive the animals out, viz.: (1) By increasing the air pressure in a glass dish in which the sample is placed to 4 or 5 atmospheres, air is physically forced into the body fluids of the tiny organisms. If, then, the sample is suddenly exposed to normal atmospheric pressure, air bubbles ("bends") will arise inside the organisms, the bouyancy then forcing them toward the surface. (2) Increased buoyancy may be obtained by exposing the sample to water of much higher salinity (for instance a saturated solution of NaCl, $CaCl_2$, or, better, $MgSO_4$) than found in nature (*cf.* Ladell, 1936; Beak 1938, Hemmingsen 1952, p. 387). (3) By sending an interrupted direct current through the water-covered substratum. This current will be stopped by the mud particles—*i.e.*, will run more intensively in the narrow water spaces between these particles than in the free water masses above. The animals, therefore, will leave the substratum and concentrate in the more "calm" water (Dittmar, 1951, for fresh-water muds, hitherto not used for marine substrata).

Many of the organisms obtained by these methods will be dead, but identifiable, and for the purpose of statistical quantitative analyses identifiability is the only requirement. Micro-animals for physiological and experimental purposes may be obtained in the old-fashioned way. For further, nonquantitative methods to drive the microfauna out of bottom samples, *see* Remane (1933).

A list of the firms that manufacture and distribute the instruments is given by Pratt *et al.* (1949). Instruments not mentioned by Pratt may be obtained from the following institutions: The Holme scoop sampler (blueprints available at the Plymouth laboratory), the Hunt sampler (the instrument available at the Plymouth laboratory may be borrowed there and copied), the Ekman marine bottom sampler (may be built in the workshop of the Physical Institute of the University, Uppsala, Sweden or from a working drawing), the Enequist sampler (one instrument available only but may be borrowed from Klubban's Biologiska Station, Fiskebackskil, Sweden), and the Hjort-Ruud bottom sampler (may be built at the Biological laboratory of the University, Frederiksgate 3, Oslo, Norway).

DREDGES AND TRAWLS

By Gordon Gunter

Zoologist, Gulf Coast Research Laboratory, Ocean Springs, Mississippi

Most of our qualitative knowledge of what lives at the bottom of the sea is based on the results of dredging and trawling rather than upon the quantitative bottom samplers. The original "naturalist's dredge" was simply a commercial clam or oyster

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dredge appropriated by the biologist for his own uses, and most of the refinements or improvements in such gear have been made by commercial fisherman. The dredge is essentially a metal frame to which is attached a bag of chain, netting, or heavy canvas. The frame may be triangular, circular, or rectangular, with or without teeth or some sort of cutting edge on the bottom piece. Because of the tendency of such an apparatus to dig into the bottom, thus becoming an anchor and placing a severe strain on the running gear, its size is limited. Dredges are usually only 2–3 feet wide; that of the CHALLENGER was 4½ feet wide. The older dredges, such as that used on the CHALLENGER, were provided with a row of ravelled rope ends or tangles, which often trapped ophiuroids, crinoids, and long-legged arthropods (Fig. 6). For procuring deeply burrowing animals in greater quantities such conical dredges as described and used by Gustafson (1935, pp. 3–5) and Powell (1937), and the deep-cutting dredges used by Powell (1937), Ekman (1947), MacGinitie (1948), Dell (1951), and Forster (1954), have proved to be most useful (*see also* Drach, 1952; Nyholm, 1952).

The trawl is a very old fishing device, consisting in its original form of a large net attached to a beam of heavy timber, 40–50 feet long, which was raised off the bottom

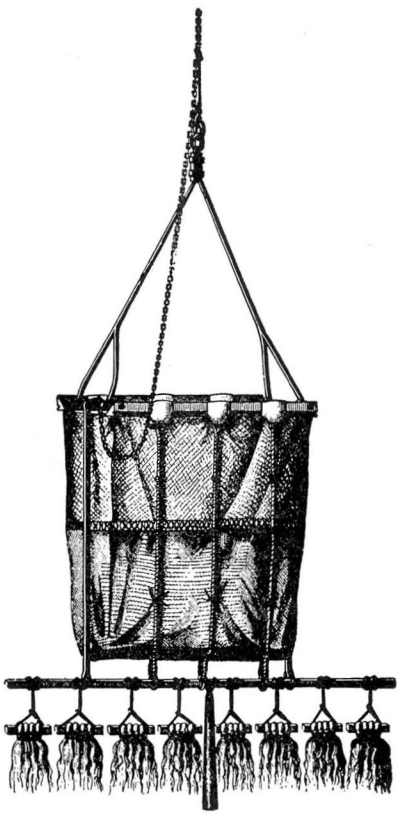

FIGURE 6.—*Dredge, as used by H.M.S.* CHALLENGER
From C. Wyville Thomson (1878)

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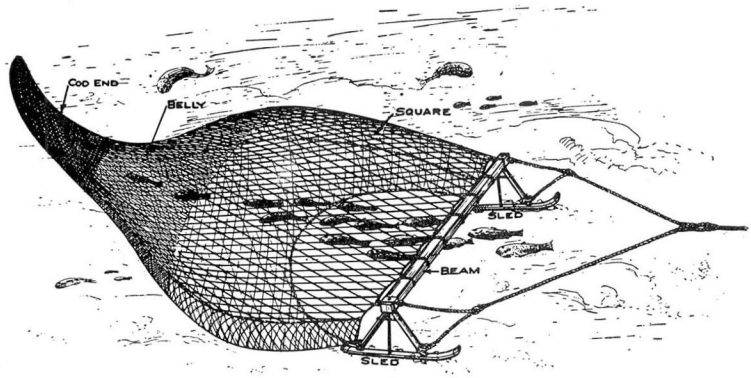

FIGURE 7.—*Beam trawl*

From Symonds (1947); courtesy the New England Trawler Equipment Company

on a pair of skids or runners; hence the name beam trawl (Fig. 7). Such trawls were in common use by the fourteenth century and were replaced by the otter board trawl when steam power made it possible to handle much larger gear at sea. The beam trawl is the model for the instrument subsequently modified for biological collecting, principally by reducing its size (that used by the CHALLENGER had a 15-foot beam) and later by modifying the frame so that the trawl would fish equally well upsidedown or rightside up; this device is usually known as the Agassiz or Sigsbee trawl (Fig. 8) and is still the basic design for trawls used for collecting in very deep water.

The otter trawl is essentially a large baglike net with the foot rope or lead line weighted by sinkers or leads, and the head or cork line provided with floats. It is provided with a pair of boards or "doors" which act like kites under water, spreading out the net as it is pulled along the bottom (Fig. 9). In many of the recent rigs the boards are separated from the net by ground lines or cables. Actual details of such rigging vary from fishery to fishery (Bullis, 1951; Scofield, 1948; Symonds, 1947). The commercial trawl is a large net, operated by two winches or two separate drums. and requires considerable experience and skill to operate, especially in rough weather. In shallow-water trawling for shrimp it is customary to try out the ground with a small trawl, about 12–15 feet wide with comparatively small meshes (less than 2 inches), the try or test net. In such small models the boards work best when attached close to the net. Nets of this size, which may be hauled in by hand in shallow water or operated from a light winch, have been used in ecological investigations and may be obtained from various ship chandlers and cordage concerns catering to shrimp fisheries.

To apply quantitative methods to trawling and dredging, some measuring device should be attached to the gear to record the distance travelled over the bottom. While this is feasible with dredges and the beam trawl, the difficulties of attaching such a device to trawls without rigid frames are obvious.

An example of a dredge with a metering device is the epibenthic dredge designed by R. Bieri and J. Bradshaw (Fig. 10). The metering device, or "bottom walker," operates only when the arms touch the bottom, functioning therefore like a pedom-

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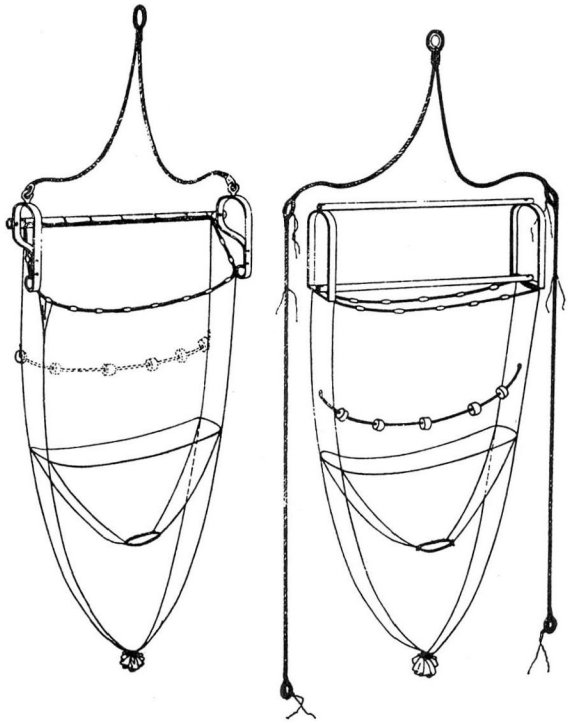

FIGURE 8.—*Beam trawl*

Left, as used on the CHALLENGER; right, as modified by Agassiz and Sigsbee (from Sigsbee, 1880)

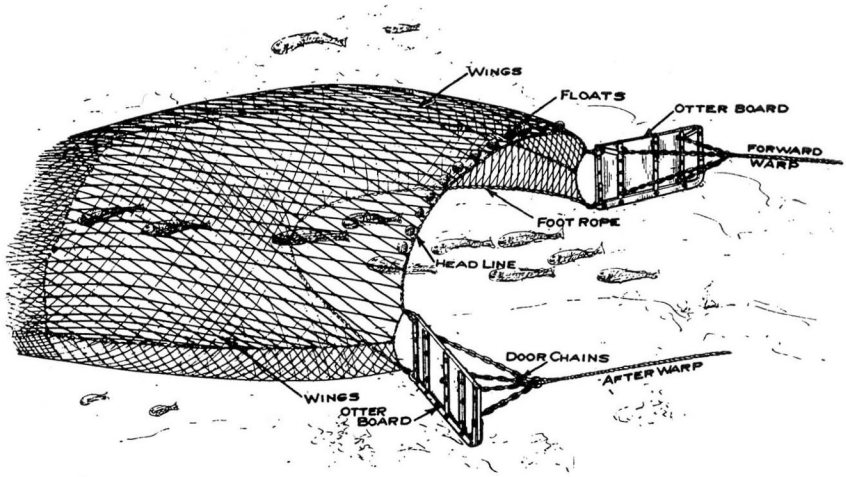

FIGURE 9.—*Otter trawl*

From Symonds (1947); courtesy the New England Trawler Equipment Company

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eter. This dredge has been used in successful hauls to 2000 m and is especially good for collecting demersal or near-bottom organisms not usually taken in plankton nets, and may of course be adapted for larger benthic organisms. A similar device, more elaborately constructed and equipped with closing apparatus, has been developed by Riedl (1955).

Although the information gained from trawling, like that from bottom grabs, is fragmentary at best, trawls are good tools if properly used. In clear waters they are notoriously inefficient for catching motile animals, as has been demonstrated by motion pictures. Yet vast numbers of animals are caught with them, possibly because there is not much light near the bottom. On the Louisiana coast, for example, commercial divers have reported that within 6–8 feet of the bottom at depths of 8 fathoms it is "as black as night." Possibly this explains the efficiency of trawls in these waters. Trawls may also be more efficient at night.

The trawl is often used in fisheries exploration, to determine the potential fishery for bottom fishes and invertebrates, and such explorations have produced important ecological information. Good recent examples of such studies are those carried out in

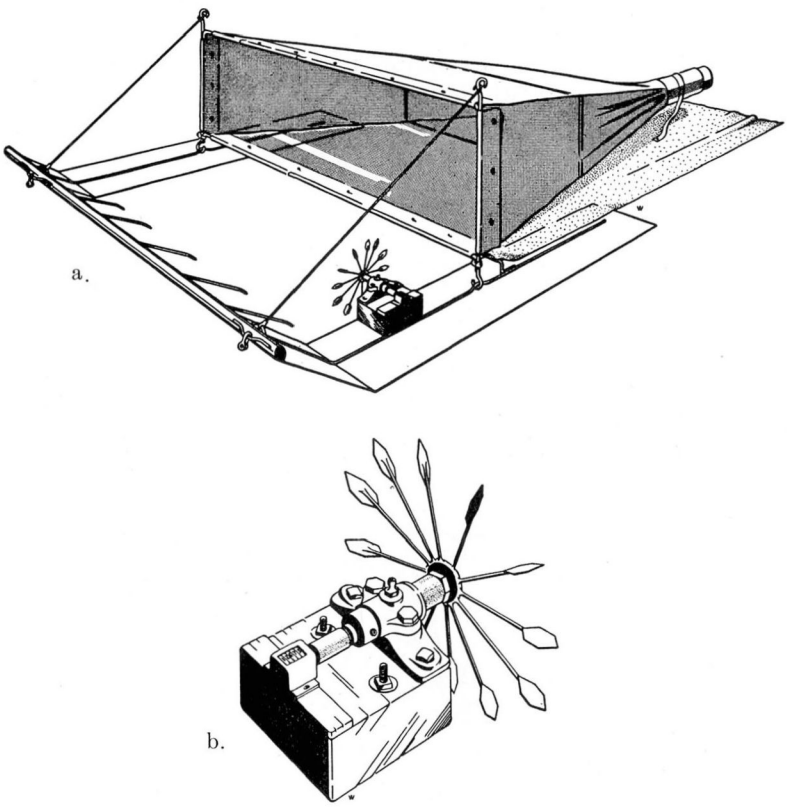

FIGURE 10.—*Epibenthic dredge*
a. view of ensemble; b, detail of the bottom walker.
(Courtesy R. Bieri)

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Alaskan waters in connection with the king-crab fishery (King, 1949; Ellson, Knake, and Dassow, 1949; Ellson, Powell, and Hildebrand, 1950). The potential information to be obtained from study of a trawl fishery has yet to be gained, however. As Merriman and Warfel (1944, p. 230) remarked, the holistic approach has been neglected in the analysis of trawl catches. Most such work is done by fishery biologists, with some special aim in view. In an investigation of the variation in trawl catches made by the same gear under uniform conditions, Barnes and Bagenal (1951) found that the variations in the catches were more indicative of population concentrations than of variations in the operation of the gear. Thus a trawl handled under uniform conditions would appear to have about the same reliability as a plankton net. A mathematical analysis of variability in trawl catches has been made by Taylor (1953).

SAMPLING THE MACROFAUNA OF MID WATERS

An otter trawl, or its variant, the paranzella (which is operated from two vessels in tandem), is, when appropriately rigged, an efficient mid-water fishing device and is now being widely used in the North Atlantic fisheries. A variation designed for use in Pacific waters is essentially a square trawl with four small boards, one at each corner, attached to the usual bridle and otter boards. Another variant of the trawl is the Isaacs-Kidd midwater trawl, designed specifically for collecting bathypelagic organisms (Fig. 11). This net, which functions like a large plankton net, is a cone-shaped net 10–15 feet wide, with a spreader bar or beam at the top and attached to a diving vane at the lower edge. A perforated can or a standard meter net may be attached to the cod end.

In operation the IKMT has proved to be reliable and foolproof. It is very stable and is easily handled from a vessel of moderate size (using a suitable boom) in general sea conditions. It is the only device developed so far which is efficient in collecting specimens at some depth at relatively high speed (4.6 kt) using a reasonable amount of cable. (Isaacs and Kidd, 1953).

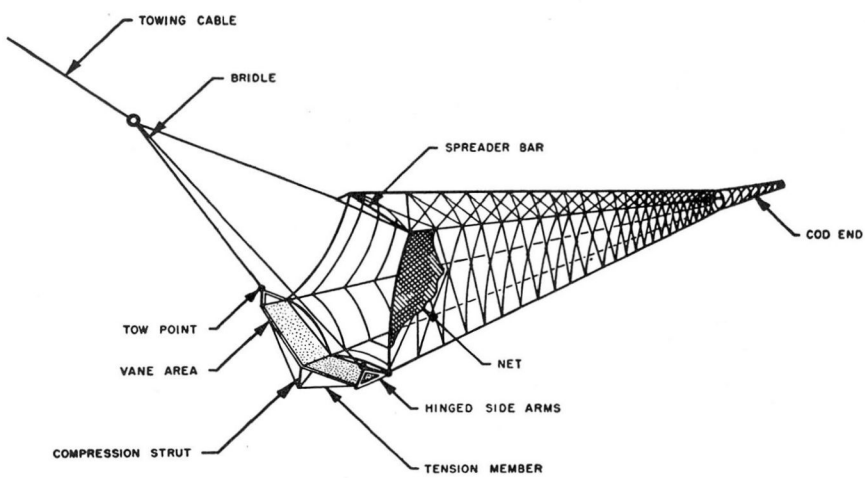

FIGURE 11.—*Isaccs-Kidd midwater trawl*

From Isaacs and Kidd (1953)

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This is not to say that the instrument is perfect; the problem of bringing up delicate fish and invertebrates from great depths at such speed in satisfactory condition is still to be solved, and the actual operating speed is only 1 or 2 knots, but even in its present experimental stage the net has brought up many rarities and shows promise of contributing materially to our knowledge of the life of the bathypelagic regions. Research is now under way with a view to constructing a closing arrangement so that the trawl would not fish while being hauled in; as with all such open nets that fish while being towed, the chief difficulty is in being certain of the actual depth from which the various species were taken.

It was discovered accidentally that the midwater trawl operated successfully as a dredge on soft bottom, and some effort has been made to design a deep-sea dredge on the same general principle. This is still in the experimental stage, and the preliminary model has not behaved according to expectations.

MISCELLANEOUS COLLECTING APPARATUS

Collecting apparatus is limited only by the ingenuity of the collector and the available material, and it is useless to itemize all the diverse contraptions that have been designed and sometimes used.

One of the standard methods hitherto unmentioned is the trap. Essentially an adaptation of one of the most ancient of fishing devices, the lobster pot, it consists simply of a baited cage with a restricted entrance. The most elaborate traps were used by the Prince of Monaco for fishing in deep water, and small traps manufactured of wire netting are the most useful collecting apparatus in Arctic regions where a hole must be bored through the ice. Modifications, consisting of half bottles, have been used successfully for trapping young bottom stages by Thorson (1946); these can be arranged at various levels on a rope.

If fished for certain intervals, traps can supply data for assessing the populations of the organisms, and such data are used in crab and lobster fisheries in particular. (Thomas, 1952; 1954).

Filters have been recently introduced in marine studies to assay the quantities of particulate organic matter suspended in sea water; the Goetz filter extracts particles down to 2 μ on membranes of cellulose acetate and nitrate (Fox, Isaacs and Corcoran, 1952). Results of these investigations are summarized in Chapter 14.

A filtering device of quite another variety is the interstitial fauna pump designed by Delamare Deboutteville (1954); this is essentially a well point constructed to suck the microscopic creatures of sand beaches into a chamber at the base of the apparatus.

MEASUREMENTS OF PHOTOSYNTHESIS

Data on rates of biological processes are not easy to obtain in the sea, primarily because of the difficulty of repeating observations precisely. Such observations also require that an expensive investigation be duplicated, and this may be economically impossible. Some attempts have been made to devise inexpensive methods which would provide data on the rate of biological activity in the sea, of which the best known are the light- and dark-bottle method for measuring photosynthesis by the production of oxygen in the light bottle (Gaarder and Graan, 1927), and the C^{14}

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uptake technique (Steemann Nielsen, 1951; 1952). In both methods the data obtained refer to the activity of phytoplankton in the upper layers of the sea, and the relation of such measurements to the rates of activity of midwater and bottom organisms is yet to be determined.

Both methods have certain defects, and there has been some controversy about the validity of the data as well as the conclusions concerning the amount of organic production in the sea derived from these methods. It is pointed out, for example, that measurement of respiration in a bottle cannot be corrected for the artificial limitation of nutrients in the water sample, while the C^{14} technique requires a number of correction factors for background activity, absorption, etc. (Ryther and Vaccaro, 1954). Nevertheless, these methods are being widely used, especially the C^{14} method, which is easy to use on shipboard. A long-term observation station has been established on a Danish lightship, for example, to provide comparable data on the rate of production throughout the year.

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Chapter 5

General Features of the Oceans*

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INTRODUCTION

Detailed descriptions of specific aspects of the oceans are presented in other contributions to this volume. It is the purpose of this chapter briefly to review some of the major geographic features of the oceans and to outline the principal characteristics that must be included in any description of an open ocean or coastal area. Although the treatment will be largely qualitative, some attention will be devoted to the processes that control the regional characteristics and seasonal variations. It is only through a proper understanding of the influences of these processes that any rational attempts can be made to reconstruct the oceans of the past. In many of the problems our knowledge and understanding are so fragmentary that the answers we desire are still remote, but a better understanding of the basic features may point the way for further study and research on those topics that are particularly critical. The treatment will proceed from a discussion of the ocean features that depend principally upon latitude and atmospheric circulation to the influences that control the conditions in relatively small coastal areas.

FEATURES THAT DEPEND ON LATITUDE

It is an obvious fact that many of the physical, chemical, biological, and geological features of the oceans vary with latitude. In some instances the relationship is a relatively simple one, as in the case of average surface temperatures, while in others, such as the distribution of plankton organisms or the nature of marine sediments, the relationships are obscured by the influences of factors that may not be directly related to latitude.

For certain of the more easily observed surface feature there exist compilations of data that have been issued in atlaslike publications by such agencies as the U. S. Navy Hydrographic Office, the U. S. Weather Bureau, and similar organizations in other countries. Most such compilations show average monthly conditions, and from them it is possible to obtain a nearly complete picture of the annual cycles of surface temperatures, currents, ice distribution, waves, and the principal atmospheric features in different areas. However, even these data are scanty or lacking in many regions, because they are based on observations made from merchant vessels and consequently they are concentrated on the main trade routes. For other features of the sea surface, such as salinities, the amount of data is so scanty that only the gross pattern of distribution is known and the number of observations is generally inadequate to attempt any monthly analysis. For many other characteristics of interest, such as the distribution of plankton, the regional coverage, let alone seasonal details,

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is so fragmentary that it is impossible to show even the major features. In part, this is due to lack of observations, but the situation is further complicated by the variety of methods that have been employed in the collection and examination of the samples, so that it is difficult to convert the results of different investigators to a common standard. (*See* Chapter 4.)

Some of the features of the oceans have been observed for approximately 100 years, but in most instances data before 1900 are sparse. It is only in a relatively few areas, and for a few types of observations, that there are sufficient data to permit any analyses for long-term trends or for quasi-periodic variations.

These comments should emphasize the fact that not only are there vast areas of the oceans that still must be surveyed but also that observations must be repeated at frequent intervals in order to evaluate the nature and amplitude of the annual variations and of year-to-year differences. When it is remembered that the oceans are three-dimensional and that the repeated observations must be extended into the depths, the tremendous magnitude of the task can be recognized.

Beneath the sea surface the available data are even more sparse. Vast regions are virtually unknown and, with the exception of a few areas where periodic systematic surveys have been conducted, we do not have any idea of the nature and magnitude of the seasonal variations and year-to-year differences. It is fortunate, however, that horizontal gradients are small and that below a few hundred meters the seasonal changes are so slight that for many purposes it is satisfactory to combine data taken at different times and to *assume* that steady-state conditions prevail. The validity of such an assumption can be established only when sufficient observations of high accuracy have been made to demonstrate that there are no significant long-term changes. Changes in the atmospheric conditions can also have profound effects on the deep-water conditions.

Only during the past few decades has attention been focused upon both short- and long-period variations in climate and even more recently upon changes in the oceans. The observations of Ahlmann and others on the retreat of the glaciers during the interval 1920–1940 led to the detailed analysis of both meteorological and oceanographic records with the result that greater attention is now being paid to the nature of time variations in addition to the more conventional treatment of average conditions.

Because of their relative abundance, surface-temperature data have been examined with some care, and all such analyses reveal that statistically significant variations have occurred during the period of observation. No attempt has yet been made to bring together these features on an ocean-wide basis. Iselin (1955) has emphasized the possibility that measurable but slow changes in the character of the deep water of the North Atlantic may have occurred during the past 50 years, and he has urged that world-wide surveys be made from time to time to determine the nature and magnitude of these apparent changes.

With the foregoing qualifications and restrictions in mind, it is desirable to examine some of the better-known characteristics of the sea surface as functions of latitude. Wüst *et al.* (1954) have made such an analysis of surface temperatures and salinities.

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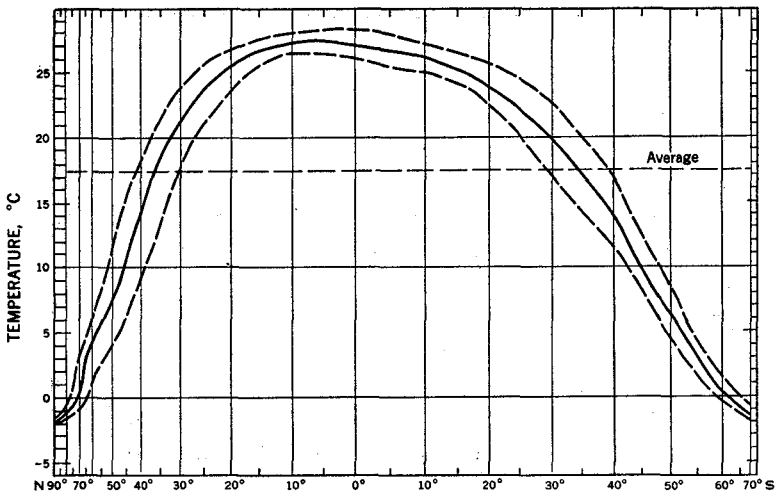

FIGURE 1.—*Mean annual temperatures of the surface ocean waters*

Approximate annual range is represented by the envelope based upon data for February and August. After Wüst *et al.* (1954).

Figure 1, taken from their paper, shows the mean annual surface temperature as a function of latitude. The scale for latitude has been adjusted so that it actually is a measure of the ocean areas as a function of latitude, and the area under the curve permits one to estimate the average surface temperature of the ocean to be 17.54°C. Added to the data from Wüst *et al.* are curves showing the approximate annual range of temperature (from Sverdrup *et al.*, 1954). These are based on the temperatures for February and August. The annual range is relatively small (less than 2°C.) in the tropics and increases in middle latitudes to maxima of 6°C. in the Southern Hemisphere and 9°C. in the Northern Hemisphere and then decreases again in the higher latitudes. Physical or biological phenomena affected by surface temperatures are, therefore, subject to the greatest seasonal variations in middle latitudes, and it is in these regions that we may expect to find the largest differences from year to year and where the effects of climatic changes may be most conspicuous.

The data presented in Figure 1 may be used for a first approximation of the surface-temperature characteristics as functions of latitude. More detailed estimates involve other factors to be described later. Wüst *et al.* (1954) present information for the three major oceans as well as the world averages given in Figure 1.

Average surface salinities as a function of latitude are shown in Figure 2. The latitude scale is the same as in Figure 1 (and also for Figures 4, 5, and 6), and the mean surface salinity is 34.73 ‰. The variation of salinity with latitude is more complicated than that of temperature, showing a minimum in low northern latitudes, maxima in about 20°–30°, and decreasing in higher latitudes but having marked differences between the two hemispheres. Although the average salinities for the three oceans do not differ materially, the maxima are higher in the Atlantic (about 37 ‰) than in the Pacific and Indian oceans, where they do not exceed 36 ‰. Relatively

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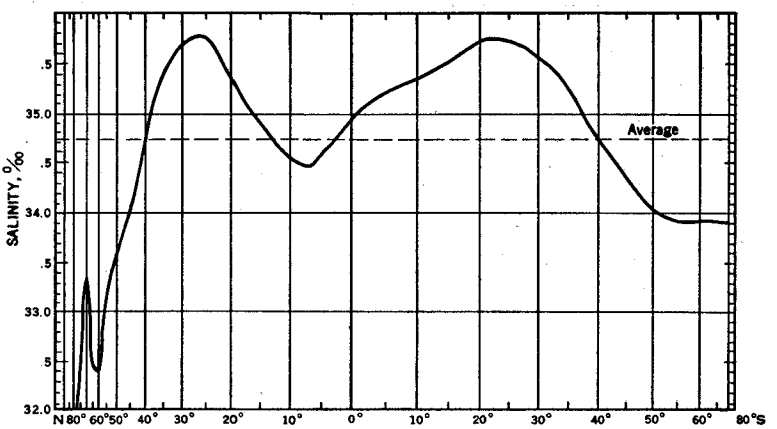

FIGURE 2.—*Mean annual salinities of the surface ocean waters*
After Wüst *et al.* (1954)

few data are available to show the seasonal variations in salinities, but these are believed to be small except in coastal regions in higher latitudes and near the mouths of large rivers (Schott, 1935; Fleming, 1955).

Because of the importance of surface currents to navigators, there exist quite detailed compilations of these movements. Sverdrup (1954), among others, has emphasized the similarity between the patterns of circulation of the surface waters and the climatic winds. Because of the importance of the winds in controlling the surface circulation and because of the relationships between the winds and other characteristics of the oceans, their general features will be briefly reviewed. Figure 3 shows a schematic diagram of the wind systems that would prevail on a water-covered earth. In this hypothetical model both the horizontal flow and the general features of the vertical circulation are shown, the latter in profile. The Northeast Trades and Southeast Trades occupy zones between the equator and approximately 30°N. and 30°S. Between 30° and 60° are the zones of the Westerlies, and poleward from these are the Easterlies. The two Trade-wind systems are separated by a low-pressure belt, the Equatorial Low or Doldrums, a region of light variable winds and calms. The belts of high pressure centered on 30°N. and 30°S. are the Subtropical Highs or Horse Latitudes. These are also characterized by light variable winds and calms. The Subpolar Lows at about 60°N. and 60°S., and the Polar Highs surrounding the poles complete the general features of the pressure distribution. With such a system of winds it may be assumed that the surface-water circulation in each hemisphere would be characterized by two westward-flowing streams in the zones of the Trades and Easterlies separated by an eastward-flowing current in the zone of the Westerlies. Munk (1950) and Hidaka (1955) have shown how the main features of the ocean circulation can be computed if the nature of the winds and the shape of the oceans are known. Such an approach is of obvious value in reconstructing the winds and currents of past ages.

The systems of winds and currents outlined above are not realistic, and other factors must be taken into account to describe even the broad features of the ocean

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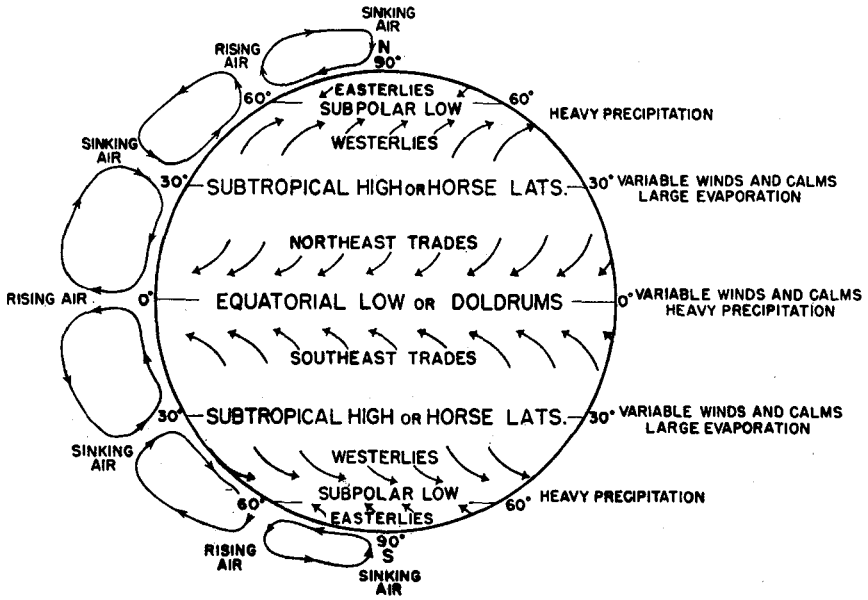

FIGURE 3.—*Schematic wind system for a hypothetical, water-covered earth*

Names are shown for major winds and for zones of rising and sinking air. Vertical air movements are indicated in exaggerated profile on left side of diagram.

circulation. However, the hypothetical systems do provide a first approximation and serve as a framework that can be modified to the extent demanded by the amount of detail required. A closer approximation to actual conditions may be achieved by considering the modifications to both the atmospheric and ocean circulations that arise from the geographic distribution of land and water areas in the earth's surface.

Because of the importance of the water exchange between ocean and atmosphere, it is essential to recognize the main features of the latitudinal variations of evaporation and precipitation that have also been reviewed by Wüst *et al.* (1954). The vertical circulation of the atmosphere indicated in Figure 3 shows that there are three belts of rising air corresponding to the Subpolar Lows and the Doldrums, and heavy precipitation can be expected in these regions. On the other hand, descending dry air in the Subtropical High belts can be expected to induce conditions leading to large evaporation. Figures 4 and 5 based on Wüst *et al.* (1954) show the annual average precipitation and evaporation over the oceans as functions of latitude. The general features just mentioned are shown by these data, although there are some shifts in the latitudes of maxima in rainfall. The rainfall maximum in the Doldrums is at about 7.5°N., and the maxima in the Subpolar Lows are in about 50°N. and 45°S. rather than at 60°. Wüst *et al.* have computed that the average annual evaporation amounts to 97 cm and the precipitation to 90 cm. The volumes of water involved are 351,200 km³/year and 324,000 km³/year respectively. The difference of 27,200 km³ represents the net excess of rainfall on land that is returned to the ocean by rivers and runoff. The data in Figures 4 and 5 show that there are large latitudinal differences in both evaporation and precipitation, and in Figure 6 the difference between these two varia-

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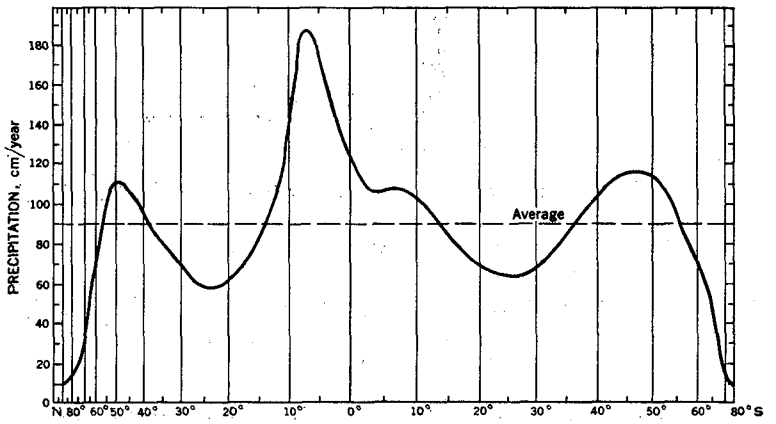

FIGURE 4.—*Average annual precipitation on the oceans as a function of latitude*
After Wüst *et al.* (1954)

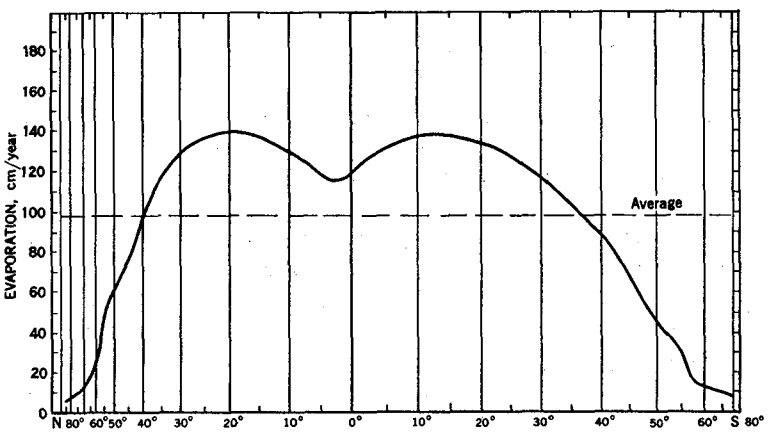

FIGURE 5.—*Average annual evaporation from the oceans as a function of latitude*
After Wüst *et al.* (1954)

bles has been plotted. This shows that there is a net dilution in low northern latitudes (in the Doldrums) and in latitudes above 40°N. and 40°S. with maxima in about 50–60° corresponding to the position of the Subpolar Lows. Evaporation exceeds precipitation in the Trade Wind zones and in the lower-latitude portions of the Westerlies with maxima corresponding in latitude to the Subtropical Highs in about 25°–30°N. and 25°–30°S. Comparison with the salinity data in Figure 2 shows that the salinity has a close relationship to the difference between evaporation and precipitation, and it is possible to derive simple linear relations between these two variables (Sverdrup *et al.*, 1954; Wüst *et al.*, 1954).

In the foregoing discussion the general latitudinal variations of surface temperatures, salinities, winds and surface currents, evaporation, and precipitation have been briefly reviewed. No attempt will be made to describe in any quantitative way the various physical processes in the atmosphere and ocean and the interactions be-

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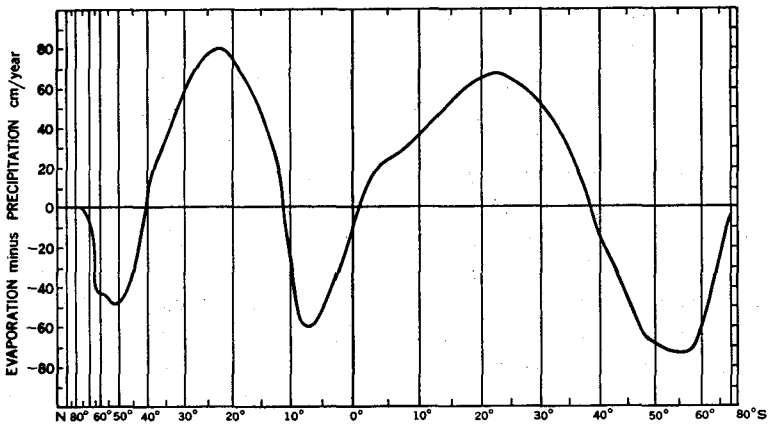

FIGURE 6.—*Excess of evaporation over precipitation as function of latitude*
Based on data in Figures 4 and 5. After Wüst *et al.* (1954)

tween the two systems that control these distributions of properties. The problems of the heat and water-vapor exchange have been reviewed by Sverdrup (1951; 1954) and Jacobs (1951a; 1951b). If it is assumed that there is no progressive change from year to year, there must be a balance between the total amount of heat received by the oceans and the amount lost. However, as Sverdrup has shown, there is an appreciable transport of heat in the oceans with the flux from lower to higher latitudes. Similarly, as can be seen from Figure 6, there must be a net transport of water toward the belts of the Subtropical Highs to compensate for the excess evaporation in these regions.

It is beyond the scope of this discussion to describe the seasonal variations that depend on latitude. Most of these ultimately depend on the annual cycle in the relation of the earth and sun and on the changing intensities of the incoming solar radiation in different latitudes. These are reflected not only in the direct effects on the physical characteristics but also on the seasonal sequence of plant and animal life. The changing atmospheric conditions also induce seasonal changes of smaller amplitude in the oceans.

One of the chief features of the oceans is the sluggish character of the vertical circulation—that is, the convective motion and interchange of water at different depths. In this respect the ocean is very different from the atmosphere that is thermodynamically active and where it is the unstable density distributions that produce large-scale vertical movements of the air and, through the conversion of thermal energy into kinetic energy, provide the driving power for the wind systems. Except in high latitudes where cooling and the formation of sea ice may induce vertical convection during winter months, there is generally an increase of density with depth that results in a stable situation that can be broken down only if energy is provided for mixing.

The heating of the surface layers by the sun or dilution by rainfall or runoff from land tend toward further stabilization and even greater resistance to mixing. The processes of cooling and evaporation (and formation of sea ice) tend to increase the

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density of the surface waters, and where the two processes act together or where water of high salinity is cooled there will be convective overturn. In the lower and middle latitudes these processes do not penetrate to very great depths and are generally referred to as factors that modify the surface layers in ways that are represented by the annual cycle of conditions at the surface. In most open-ocean areas the annual variations are limited to the uppermost layers, and variations in temperature, salinity, and other properties rarely extend to more than a few hundred meters. In the higher latitudes where the cooling in winter will reduce surface temperatures, and particularly if ice is formed, the density will be increased to a point where in certain areas it will sink to depths of several thousand meters and thus form the bottom and deep water of the great ocean basins. Water of intermediate densities formed in similar ways will sink to moderate depths and form the intermediate water strata of the oceans. Descriptions of the properties of these different types of water, their modes of formation, and areal distribution have been described by Sverdrup *et al.* (1954).

Because of the inherent stability of the ocean waters the following generalizations may be made:

(1) The densest water available to any ocean basin will occupy the deep portions of the basin.

(2) Water of different origins will be arranged vertically in strata with decreasing densities toward the surface.

(3) Waters of equal density will tend to spread horizontally so that lateral gradients in properties will be small compared to vertical gradients.

(4) Unless replaced with water of equal or higher density, the subsurface waters will tend to stagnate (that is, to have their dissolved oxygen content depleted or completely utilized by biological processes).

(5) Processes that remove from the lighted surface layers trace materials essential for plant growth will result in depletion of these substances so that plant growth and general biological fertility will be slight except in regions where mixing or vertical movements bring these materials to the surface.

(6) To produce vertical mixing, energy is required. In the open ocean kinetic energy imparted by the winds in creating waves is probably the largest source of such energy. In inshore waters and on the continental and insular shelves the tides and wind-generated waves are the principal sources of energy for vertical mixing.

These generalities have been enumerated because they are essential to an understanding of conditions in the oceans of today and must be invoked in any attempts to reconstruct past conditions, and because they help clarify some of the striking differences that exist between conditions in the open oceans and those in enclosed seas and other coastal regions. (*See*, for example, the descriptions of conditions in the Baltic Sea, Chapter 24, and in the Black Sea, Chapter 25.)

INFLUENCES OF THE LAND MASSES

In the foregoing sections we have reviewed features of the oceans that are primarily functions of latitude, but even these are affected to some extent by the shapes, sizes, and geographic relationships of the oceans and the land masses. For our immediate purposes we must consider the following features:

(1) Most of the land is in the Northern Hemisphere. The principal result is that the atmosphere and oceans of the Southern Hemisphere correspond more closely to the theoretical model of the water-covered earth. A second result is that the meteorological equator is located somewhat to the north of the geographic equator.

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(2) The main ocean areas are represented by a wide continuous belt surrounding Antarctica with three marginal "gulfs" extending northward to form the Atlantic, Pacific, and Indian oceans. The Southern Ocean provides the connections for the exchange of water between the three oceans. The consequence of this division of the earth's water surface into three main areas is that most of the ocean waters circulate in large closed gyrals instead of in continuous latitudinal belts.

(3) The inequalities in the widths and their different latitudinal dimensions have marked effects on the oceanography of the three oceans. For all practical purposes the Pacific Ocean can be considered as isolated from the Atlantic in Lat. 66°N. at the location of Bering Strait. On the other hand, the Atlantic Ocean includes the Polar Basin and extends across the North Pole. The Indian Ocean, however, does not extend northward beyond about 25°N. Thus all three oceans will have essentially similar conditions in the higher southern latitudes, and differences that exist between the Atlantic, Pacific, and Indian oceans must be related to their different northward extents and to their different widths.

(4) The land masses and their size, shape, topography, and geographic relations have their influence on the oceans chiefly through the effects they exert in modifying the atmospheric circulation, in supplying dissolved solids and sediments, and in diluting certain coastal regions by the discharge of large volumes of river water. Probably the most significant effect, and the one that is most noticeable in the Northern Hemisphere, is the monsoon effect that tends to produce onshore movement of air masses in summer and offshore movement of air during the winter. All continental land masses have such an effect.

The climatic zones on land are in general dependent upon latitude, topography and distance from the oceans and, in coastal areas, upon the local ocean conditions. The wind zones shown in Figure 3 can still be recognized over both land and water areas, but they show marked seasonal variations due to monsoon effects. Over the ocean areas they tend to form a series of rotating systems (Figure 7). This more realistic pattern of the winds is reflected in the nature of the principal surface currents.

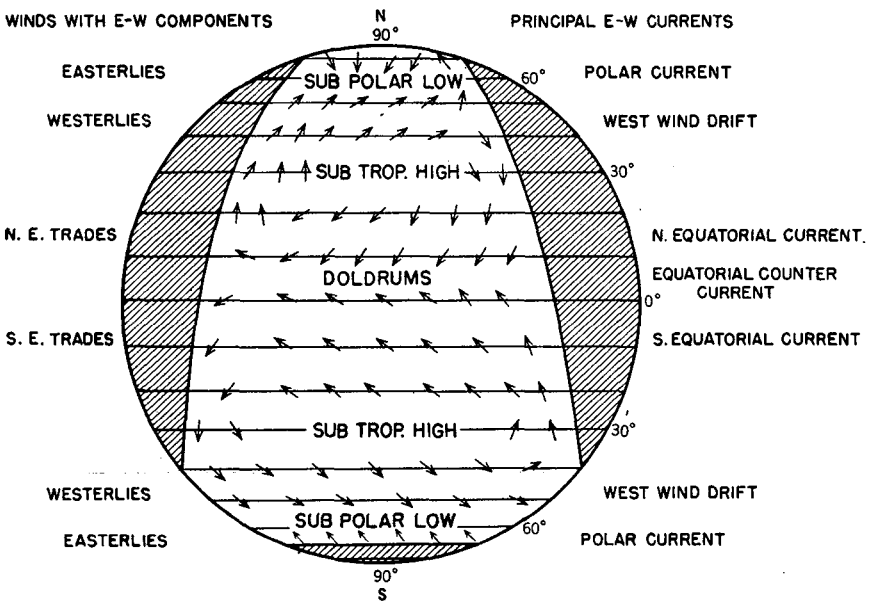

FIGURE 7.—*Schematic average wind circulation over a hypothetical ocean extending from 70°S. to and beyond the North Pole*

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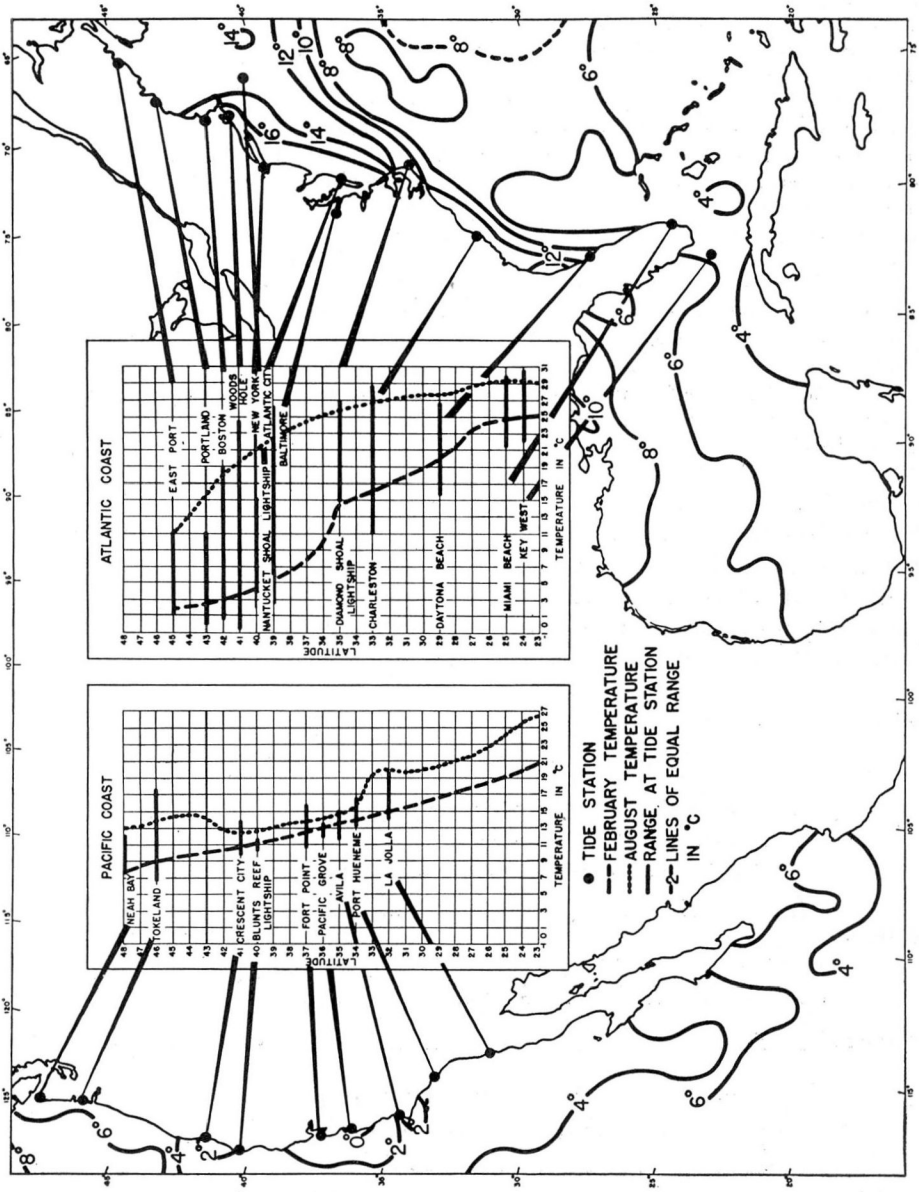

FIGURE 8.—*Annual range of temperature of the surface waters off the west and east coasts of the United States and Mexico*

Inset diagrams show winter and summer temperatures near the coast and at tide stations. Fleming and Elliott (1956)

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Relatively strong flows in north-south directions carry warm water into higher latitudes on the western sides of the oceans and carry cool water toward the equator on the eastern sides of the oceans, completing the current gyrals in both hemispheres. The flow of cold water is reinforced by the upwelling that occurs along certain ocean margins, notably off California and the western coasts of South Africa and South America. The combined effects of the modified circulation and air movements restrict the significance of the generalized latitudinal distributions of temperature and salinity shown in Figures 1 and 2. Although these distributions can be taken as representative of mid-ocean areas, it is necessary to reconsider the conditions in the eastern and western portions of the oceans. Only the northern oceans have been examined in any detail. Schott (1935; 1942) has demonstrated the effects of currents and upwelling, and Jacobs (1951a; 1951b) has shown the greatly modified processes of heat and water exchange. Fleming and Elliott (1956) have compared conditions on the Pacific and Atlantic coasts of the United States and Mexico (Fig. 8). The consequences of the modified atmospheric and oceanic circulation are as follows:

(1) The annual range of temperature in mid-latitudes on the western sides of the oceans is much greater than on the eastern sides. This is largely due to colder temperatures in winter on the western sides of the oceans, when under the influence of the winter monsoon, and to the fact that upwelling in summer on the eastern sides keeps temperatures relatively low (Fig. 8).

(2) Surface salinities in the western parts of the mid-latitudes are generally higher than in the eastern portions. This is in part due to the poleward transport of higher-salinity water but is modified by two additional processes: (1) the higher evaporation in the western portions where dry air from the continents moves over the relatively warm waters, and (2) the higher precipitation that is characteristic of the eastern sides of the oceans. Figure 9 shows the annual excess of evaporation over precipitation for the northern Pacific and Atlantic Oceans.

Examination of the data in Figure 6 shows that there is an excess of precipitation in latitudes above 40°N. and 40°S. Consequently there must be a net transport of water toward the lower latitudes in order to maintain the balance of water. This is maintained by the relatively dilute surface currents that are best demonstrated by the California Current and, in the western North Pacific, by the Oyashio. Some compensation is also effected by the movement of dilute water toward the equator at intermediate depths. Sverdrup (1954) has also stressed the fact that in order to maintain the heat balance there must be a poleward transport of heat in both hemispheres. The warm currents that flow into higher latitudes in the western parts of the oceans are the principal way in which this heat is transferred.

Although the features described above are characteristic of all oceans, there are significant differences among the three oceans that can be related to the following three features:

(1) The differences in air circulation resulting from the great width of the Pacific compared to the Atlantic and Indian oceans.

(2) The differences in the water balance between the North Pacific and the North Atlantic. Examination of Figure 9 shows that the Northern Pacific is an area of net dilution, whereas in the North Atlantic the evaporation exceeds the precipitation. This very important difference is reflected not only in the higher surface salinities in the North Atlantic but also in entirely different types of vertical circulation.

(3) The differences in the northern limits of the three main ocean areas. The northern isolation

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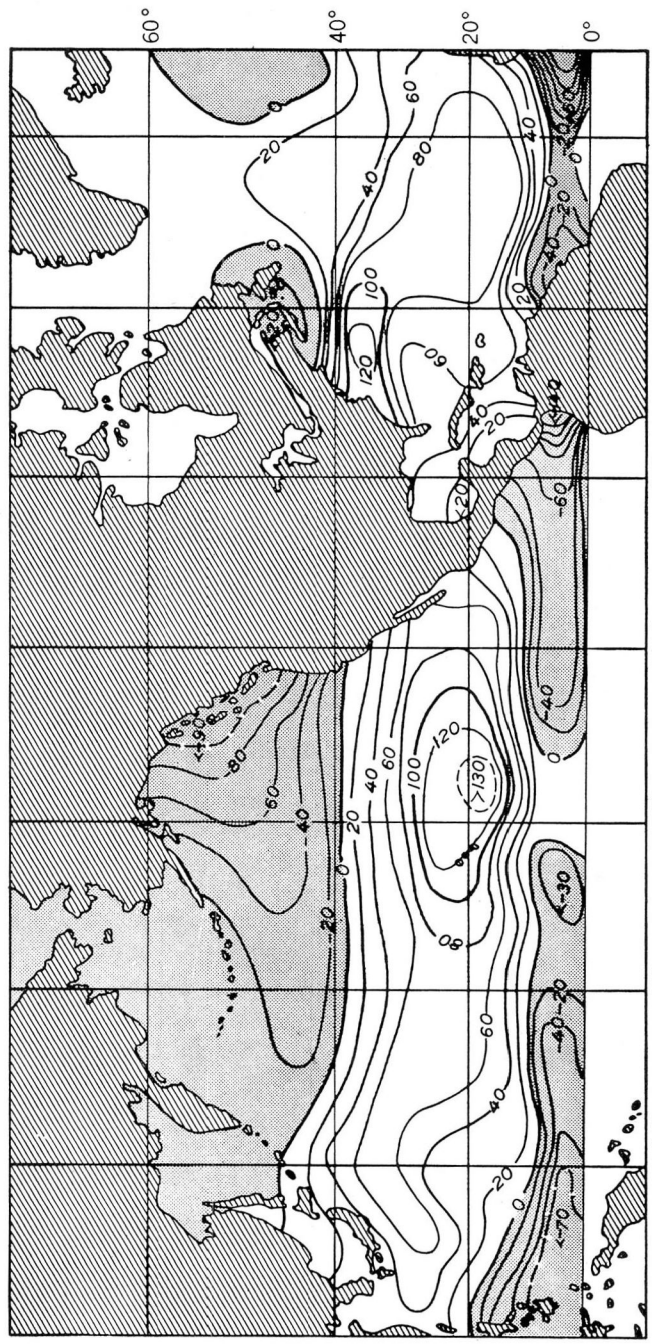

FIGURE 9.—*Annual evaporation minus precipitation over the North Pacific and North Atlantic oceans*
Shaded ocean areas indicate net dilution. Units: centimeters per year. After Jacobs (1951b)

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of the Pacific in about 66°N. and the excess precipitation in the northern portions mean that even though temperatures are reduced to freezing (about −1.8°C.) the water is still of relatively low density and forms an intermediate water at rather shallow depths (Sverdrup *et al.*, 1954). On the other hand, in the Northern Atlantic there is a definite northward transport of high-salinity water that is cooled and in certain areas further concentrated by the formation of sea ice. This leads to the formation of very dense water that sinks and fills much of the deep basin of the North Atlantic.

Emphasis has been placed on the conditions that can be related to latitude and to the eastern and western parts of the oceans, and finally on some of the conditions that differ from ocean to ocean because of differences in size and geographic relations of the three main ocean areas. In addition to the direct effects reflected in the distribution of conditions at the surface, there are also major differences in subsurface conditions and even in the distribution of recent deep-sea sediments that can probably be attributed to the varying processes affecting the sea surface. As stated previously, conditions in the southern portions of the three oceans are, in general, rather similar, and it is in the northern hemisphere that the greatest differences are apparent. In comparison with the other oceans in both hemispheres, the North Atlantic has a vertical circulation closely similar to that of the oceans in the Southern Hemisphere. However, there is apparently a greater transport of surface water poleward, and as this sinks it affects the distribution of dissolved plant nutrients, so that their concentration in the North Atlantic is conspicuously low. The fact that no deep or bottom water is produced in either the North Pacific Ocean or North Indian Ocean has a number of consequences. Because of the more sluggish deep-water circulation the dissolved oxygen content of the deep water is conspicuously lower in the North Pacific, and associated with it are a higher carbon-dioxide content, a lower pH, and higher contents of the plant nutrients.

CHARACTERISTICS OF INSHORE REGIONS

The discussion so far has dealt with the major features of the oceans, and no attention has been devoted to the semi-enclosed seas and coastal features. The relationships described can be used to characterize some of the general features of temperature and salinity, but local topography, seasonal volumes of river discharge, and tides, among other factors, will combine to make any one region unique in some respects.

One of the most significant factors in a coastal region is the balance between evaporation and precipitation and local runoff. Where there is an excess of precipitation and runoff there must be a net outflow of water. This customarily results in a nontidal outflow of diluted surface water and a slow inflow at depth. On the other hand, where there is an excess of evaporation the opposite type of circulation prevails. Examples of areas where there is excess evaporation are the Mediterranean, the Red Sea, and the Persian Gulf. All are characterized by high salinities, but only the last two have high temperatures. Because of the large amount of heat involved in evaporation, these regions all lose sensible heat, and the outflowing water is cooler than the inflowing surface water. On the other hand, regions that are diluted are usually heated, and the outflowing surface water is warmer than the water flowing in at depth. In attempting to describe the characteristics of a coastal area it is therefore of paramount importance to establish the water budget for the water area in

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question. In contrast to the Mediterranean type are regions with net dilution such as the Black and Baltic seas, the fjords, estuaries, etc. (*See* Chapter 23.)

Second among important factors that influence local coastal conditions is the extent of isolation of the region. On an open-ocean coast the oceanographic features will not differ appreciably from those in the adjacent deep ocean, and the same will apply to conditions near oceanic islands. On the other hand, seas, gulfs, and other more or less land-locked regions will differ more as they are more nearly isolated. The same principle applies to the isolation in depth that will result from the presence of sills or shoal obstructions that block the water exchange at depth. The importance of the water budget and sills on the water exchange in basins has been reviewed by Fleming and Revelle (1939) and by Sverdrup *et al.* (1954).

Certain features of a coastal region can be predicted, or at least correlated, if the geological history of the adjacent land is known. This will not only indicate certain aspects of the topography but will give some indication of the types of sediments that will characterize the area.

In coastal areas tides are also important controlling factors. In general, tides are larger and the tidal currents are stronger in coastal areas than in the open ocean. However, this is by no means always true, because there are areas such as the Black, Mediterranean, Japan, and Baltic seas that are almost tideless. At the other extreme is the Bay of Fundy, with tides of 50 feet, and a number of regions where tidal ranges exceed 25 feet. There is no latitudinal pattern in the range of tides and no simple rule for estimating their range. Such features are therefore unpredictable except where near-by observations are available. The effects of isolation can be seen in the "tideless" areas, and the large tides can usually be explained in terms of the topography of the individual areas. *See* Plate 1 of Chapter 18 for a map of tidal characteristics and ranges.

Tidal currents are in part dependent upon the range in tide but must be considered in terms of type of tide and more particularly as they are related to the tidal prism, that is the volume of water that must pass a given cross section in order to add or remove the volume of water entering and leaving the shoreward end of the system. As an example of this, there are strong tidal currents in the Straits of Gibraltar although the range of tide in the Mediterranean is extremely small.

The range of tide is itself an important local feature, as it exposes different levels of the beach to attack by waves and will affect the intertidal organisms. (*See* Chapter 18.) Similarly, tidal currents have direct effects on erosion and deposition affecting the bottom and coast line. However, most important of all is the energy provided by the tidal movements that, where tidal currents are strong and the topography irregular, will produce intensive vertical mixing and break down the vertical stability and thus in turn modify the temperature and salinity distribution and the volumes involved in the nontidal water exchange.

A comparison of temperature and salinity and other conditions in the Norwegian fjords with those in such an area as Puget Sound, Washington, shows that in the fjords where the tides are small the water is highly stratified and there is an outflow of a shallow very dilute layer and a slow inflow of saline water at depth. On the other hand, in Puget Sound where the tidal range is fairly large and the tidal currents

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strong, there is active mixing and consequently a nontidal outflow of a large volume of diluted water and a corresponding large inflow of saline water. The Baltic Sea with its small tides is extremely dilute, but regions with stronger tides but comparable precipitation and runoff are of much higher salinity (Barnes *et al.*, 1954; Waldichuk, 1955).

Three important controlling factors have been mentioned in discussing the characteristics of inshore areas: the local water balance, the isolation of the area, and the tides and tidal currents. A fourth factor is the nature of the adjacent land area and the underlying sea floor. The topography of the land will, in part, affect the local precipitation and runoff and the winds. The nature of the land surface and the amount of vegetation will influence the supply of sedimentary debris. These four factors are paramount in determining the oceanographic features of a coastal or inshore area. Extremes in any one of them may exert an overwhelming influence, but, in general, on the continental margins the coastal and inshore areas will differ from the adjacent open sea in the following respects. In the coastal and inshore areas,

(1) The annual range of temperature is greater, and the inshore waters are warmer in summer and cooler in winter.

(2) Sea ice is more likely to occur in the higher latitudes.

(3) The surface salinities are lower, except in areas of upwelling.

(4) Because of the lower surface salinities the stability of the water column is greater or may develop earlier in the season. The gradients in temperature, salinity, and other properties are steeper and at shallower depths.

(5) Because of the supply of terrigenous materials, and large plankton populations, the transparency of the water is less.

(6) The rates of sedimentation are higher.

(7) The local variability in topography, types of substrate, water balance, tides and tidal currents, etc., results in coastal conditions that are more variable in both space and time.

(8) There is a greater variety in both plants and animals.

(9) There is a higher productivity and greater abundance of both plants and animals.

(10) There is greater likelihood of extreme changes in both physical and biological conditions that can result from changes in sea level, landslides, floods, tsunamis, sea ice, violent storms, etc.

DESCRIPTION OF OCEAN AREAS

In a description of an area on land there are many terms employed that may involve the geology, the topography, the climate, and the vegetation. Such a vocabulary is lacking when we attempt to describe an area of the ocean, whether it be far from land or a coastal region. The general terms like bay, gulf, sea, etc., have little significance. Zoogeographers and ecologists designate certain typical marine environments in terms of characteristic organisms and have related these to such features as the temperature conditions (*e.g.*, Ekman, 1953). Others, such as Schott (1935; 1942), have attempted to combine both physical and biological features to designate certain natural regions. However, these by name alone do not describe the conditions prevailing in these regions. Elliott (1952) has proposed certain ocean regions that can be defined in terms of surface properties and climatic features. Such systems do not reveal the complete picture, and it is therefore essential to use some type of outline when attempting to describe an individual area, to compare two or more regions, or to reconstruct a past environment. The following outline is comprehensive, but the

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major topics should be touched upon whether the description is only a brief paragraph or fills a volume.

DESCRIPTIONS OF MARINE ENVIRONMENTS

The following items must be considered in describing the major features of a marine environment. The order of presentation will depend on the nature of the region and the purposes of the description.

(1) General features
Latitude, longitude, boundaries, relation to land, size, shape, depths, etc. Purpose of description. Sources of information.
(2) Climatic features and hydrology
Winds and weather including cloudiness, precipitation, etc. Rivers and seasonal runoff.
(3) Water circulation
Currents, flushing, upwelling, etc.
(4) Tides and tidal currents
Type and range of tide. Features of tidal currents, mixing and scouring. Relations to topography.
(5) Physical and chemical properties
General distribution and variability of temperature and salinity. Properties depending on temperature and salinity. Properties that vary independently such as transparency, plant fertilizers, and dissolved gases.
(6) Geological features
Shape, topography, and geological history. Nature of sediments and their sources.
(7) Surface features
Waves, surf, ice, icebergs.
(8) Biological features
Plants and animals; types and abundance. Intertidal forms. Plankton. Bottom life. Fisheries. Migratory populations.
(9) Special features
Seismic and volcanic activity. Tsunamis and storm surges. Red tides. Effects of human activity.

There is no significance to the order in which the items are arranged, and the emphasis on the various topics varies depending upon the purpose of the description. The outline has been planned with coastal areas in mind, and for a region in mid-ocean many of the topics can be omitted because they are irrelevant.

The outline for the description of ocean areas is an ideal rather than a reality. Schott (1935; 1942) has given the only comprehensive descriptions of the oceans from a geographical point of view. The basic information often exists in the voluminous reports of large-scale expeditions or systematic regional surveys and in the data reports and atlases published by various national organizations. The value of such descriptions has been stressed by the author (1948). Regional studies that review the state of existing knowledge have recently been compiled by Barnes *et al.* (1954) and Galtsoff *et. al* (1954). A brief analysis of conditions in the Northern Pacific has been prepared by Fleming (1955).

PRODUCTIVITY OF THE OCEANS

Detailed features of the distribution of properties affecting the types and abundance of life are presented elsewhere in this volume. However, it is desirable to mention some of the features that may control the total plant productivity of the oceans and

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certain of the major features of the regional fertility. The problem has been under investigation for a number of years, but our knowledge is still fragmentary both in regard to the factors affecting productivity and to the regional differences. For most ocean areas depletion of plant nutrients in the surface layers is believed to be the chief factor limiting plant productivity, and consequently the processes that will return these essential substances to the sea surface control the total productivity. These processes are chiefly winter mixing, upwelling at coastal boundaries and at current divergences, and the general upward displacement that must result from the formation of deep and intermediate water, and, in coastal water, tidal mixing. Some estimates of production have been made, most recently by Steemann-Nielsen (1954). These have been used to construct Figure 10, which shows in a semiquantitative way the major features of the regional productivity (Fleming and Laevastu, 1955). The values are given in units of grams of carbon/m^2/year. Although these values are estimates of the total plant production—that is, the gross amount of photosynthesis—they do not give any measure of the standing crops of either plants or animals, although it can be assumed that there will be a qualitative regional agreement. Furthermore, the values represent annual totals and do not indicate the large seasonal variations that are the conspicuous feature of life in the middle and higher latitudes where available light, temperature, and the self-shadowing that occurs with dense phytoplankton populations will greatly limit the rates of photosynthesis at various times of the year. In the Antarctic and Northern Pacific waters depletion of plant nutrients is not the factor that limits the amount of plant growth.

In Figure 10 data for plant productivity are based on conditions in deep water and do not necessarily reflect the higher productivity that can occur in coastal waters and over shoals and around oceanic islands. In all such regions an increased supply of nutrients to the surface waters can result from mixing associated with the currents and particularly with the tidal currents. Furthermore, the abundance of life on the shallow bottoms represents a reservoir of the essential plant nutrients that are made available as a result of metabolic activities.

RECONSTRUCTION OF PAST ENVIRONMENTS

The writer has indicated some of the principal features of the oceans and of the processes that control them. Some attention has been devoted to the factors that are significant in coastal regions. Any attempts to reconstruct the patterns of conditions in the seas of the past must follow similar lines of treatment. Because of the paramount importance of climatic conditions as they affect the interchange of heat, water, and momentum between the atmosphere and the oceans, it is essential that these conditions be established before any reconstruction of past oceans is possible. Paleoclimatologists have so far devoted their attention to situations existing over the land, and more comprehensive studies are now needed.

Iselin (1955) has shown the possible significance of relatively minor climatic fluctuations that may influence the formation of deep and bottom water and has suggested that such waters are formed only during periods with extremely cold winters. However, it is felt that the water budgets rather than temperatures are the most important factor, because freezing temperatures will always be achieved in high

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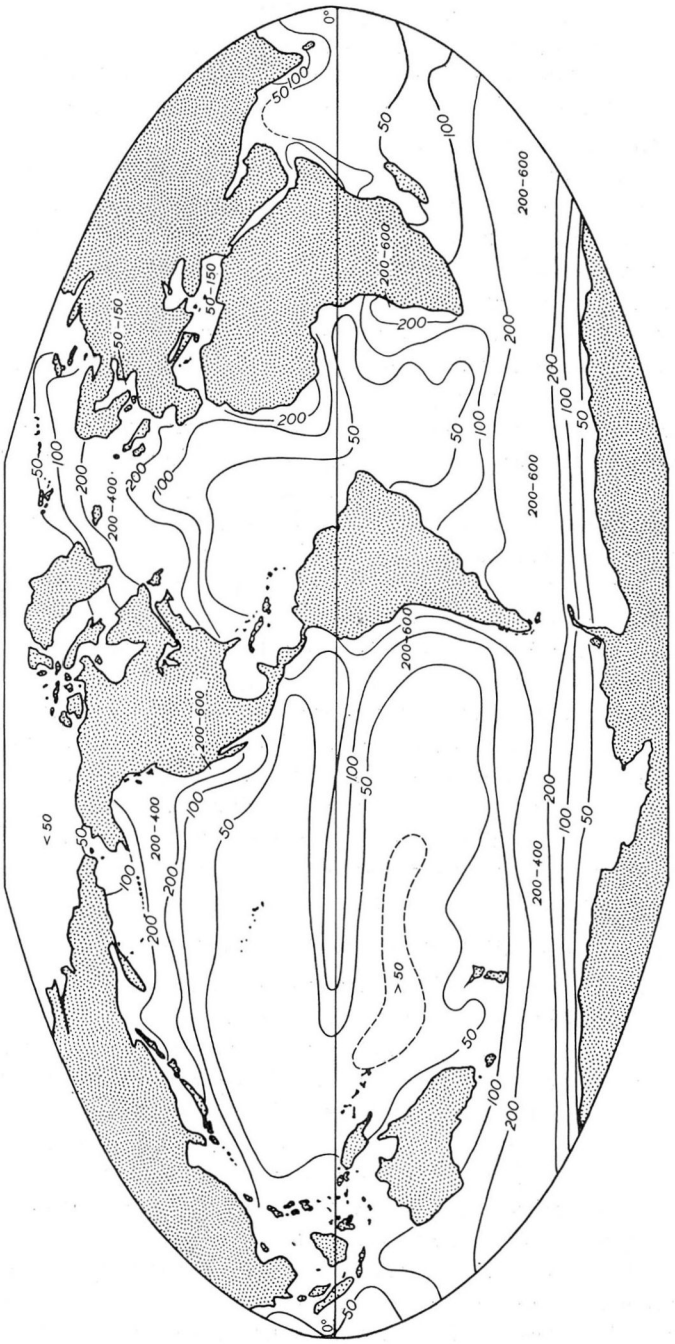

FIGURE 10.—*Estimated annual photosynthetic productivity of the oceans*
Units: grams of carbon/meter²/year

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latitudes, and the density of the surface water in winter will be determined by its salinity. Conditions under which there is an accumulation of continental ice will thus favor the formation of deep water, whereas when the glacial ice is retreating, as it has in recent decades, these conditions may be less favorable for the formation of very dense water.

Perhaps this particular problem can be emphasized by using the estimated lowering of sea level that accompanied the greatest advance of the ice during the Pleistocene. Let it be assumed that there was a lowering of the sea level of 100 m. This is approximately 3 per cent of the mean depth of the oceans (3800 m), so it can be estimated that the mean salinity of the oceans would have been increased by about 1 ‰. The present deep waters of the oceans have salinities slightly less than 35.0 ‰. If the more saline water (about 36 ‰) were chilled to the freezing point, an extremely dense water would have accumulated in the ocean basins. It is then interesting to consider why traces of this water are no longer present. One possible explanation is that this water was gradually warmed by the flow of heat from the earth's core and possibly by biological respiration until it became sufficiently light to mix with the overlying waters or to be displaced by newly formed bottom water. Under such conditions a temperature inversion of between 5° and 10°C. might have developed. Such a mass of stable deep water could, therefore, have had temperatures of 5° to 10°C. and would probably have been stagnant. If only the flow of heat from the earth is considered, it would require an interval of the order of 10,000 years to break down the stable stratification.

It is further of interest to note some of the other general features that may have accompanied the accumulation and melting of the continental ice during the Pleistocene. Estimates indicate that the alternate accumulation and melting of land ice probably occurred at rates that would correspond to the removal from and addition of water to the oceans of the order of 1mm/year. This is approximately 1/1000 of the total precipitation or evaporation as described earlier and indicates that no large-scale changes need have occurred in the rates of evaporation or precipitation. The records of the climatic changes are undoubtedly written in the accumulations of sediments in middle and higher latitudes. Kullenberg (1952) has been utilizing the salinities of the interstitial waters to attempt to reconstruct past salinity conditions in the Mediterranean and Baltic seas. Studies of this type will undoubtedly do much to help reconstruct the climates and oceanography of the past.

CONCLUSIONS

One tenet of geology is that "the present is the key to the past." This is equally true in oceanography, because only in the present-day ocean can we establish the patterns of conditions and quantitatively evaluate the effects of the controlling factors. With such an understanding it will be possible to take the information of the geologist, the paleontologist, the glaciologist, and the paleoclimatologist and reconstruct the oceans of the past. All such data will be fragmentary, and it is the task of the oceanographer, or of the paleo-oceanographer of the future, to weld them into an integrated and dynamic whole. The unity of the seas in space is well recognized. There

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is a similar unity in time, because the history of the ocean is continuous, not interrupted as is the history of the lands that have been alternately submerged and elevated. Furthermore, there is a unity of subject matter and an intimate interdependence of all aspects of the oceans, whether they be physical, chemical, biological, meteorological, or geological. Emphasis in this chapter has been placed upon some of the major geographic features of the oceans. Only from an integrated picture of the present oceans, and an understanding of the controlling processes, can we proceed to rational reconstructions of the oceans of the past.

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Chapter 6

Solar Radiation, Submarine Daylight, and Photosynthesis

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INTRODUCTION

Solar radiation is probably the most fundamental ecological factor in the marine environment: it is the source of energy utilized by plants in the manufacture of the complex organic substances upon which the metabolism of the sea depends. The degree of availability of this energy directly controls the amount of organic matter synthesized, for, no matter how favorable other factors may be, this amount will be limited by the relatively low efficiency of the photosynthetic process. An important "by-product" of photosynthesis is the production of oxygen. This contributes appreciably to the amount of dissolved oxygen in sea water and plays an important role in plant and animal metabolism and in the oxidation of inorganic and organic substances. The diurnal light cycle in the photic zone of the sea is, in some organisms, a tropistic stimulus and is the cause of the well-known vertical migrations of certain plants and animals. In addition to these roles, light is also necessary for the formation of certain plant and animal pigments. Solar radiation is likewise responsible for the heating of the oceans, and temperature profoundly affects all metabolic processes in animals and plants.

The various wave lengths (different colors) of sunlight range from the infra-red (24,000–760 mμ), through the red (760–650 mμ), orange (650–600 mμ), yellow (600–550 mμ), green (550–500 mμ), blue (500–450 mμ), violet (450–400 mμ), to the ultraviolet (400–280 mμ). In sea water light of different wave lengths is absorbed at different rates, and various plant groups manifest different abilities to utilize light of different qualities.

INSTRUMENTATION AND HISTORICAL SURVEY

One of the earliest methods used to estimate water transparency was to lower a white or light-colored disk into the sea, noting the depth at which the disk disappeared (Ciladi and Secchi, 1865). The Secchi disk, as it is now called, is still employed by investigators who desire a simple but rough estimate of transparency. Atkins and Poole (1930) found that the extinction coefficient for visible light ($k_{vis.}$) could be approximated from Secchi disk measurements; $k_{vis.} = 1.7/D$, where D is the maximum depth of Secchi disk visibility. Investigations carried out by Le Grand (1939), Clarke (1941), and Gall (1949) have further demonstrated the appreciable deviations from this formula.

Submarine daylight was first measured photographically in the late nineteenth century by Fol and Sarasin (1884; 1885; 1886) and by Forel (1887). The greatest depth in the Mediterranean at which these investigators recorded faint residual

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daylight was about 400 m, and they also noted a decrease in this depth with decreasing solar altitude. Helland-Hansen (Murray and Hjort, 1912) was able to record residual daylight down to a depth of 1000 m in the north Atlantic by employing more sensitive emulsions than were available to his predecessors. In 1911 Bertel successfully adapted a spectrophotometer to underwater use and made qualitative studies of chromatic extinction. Knudsen (1922) refined Bertel's technique, making possible quantitative measurements under conditions of relatively high light intensity. Recently Jerlov and Koczy (1951) employed a simple quantitative photographic technique for measuring submarine daylight at moderate depths (*ca.* 200–500 m).

The light-sensitive property of selenium was probably first used to measure submarine daylight by Regnard (1891) although his measurements are of historical interest only. Shelford and Gail (1922), Shelford and Kuntz (1926), Poole (1928), and Atkins and Poole (1930; 1931) have successfully adapted selenium tubes (both vacuum and gas-filled) for quantitative use. The light-sensitive cells employed by these and other early investigators required an external power source for their operation, a feature that made the construction of photometers and their operation somewhat difficult and troublesome. The use of self-generating selenium barrier-layer photocells in submarine photometers was apparently first investigated in 1933 (Atkins and Poole, 1933); this and subsequent trials proved so successful that by 1938 their use was recommended by a special committee appointed by the International Council for the Exploration of the Sea (Atkins *et al.*, 1938). Since then virtually all submarine photometers have employed this type of cell.

The modern submarine photometer (Fig. 1A) consists essentially of a water-tight enclosure containing a photocell mounted behind a clear glass window. Provision above the window on the outside of the housing is made to accommodate various color filters, reducing screens, and a diffusing disk. This underwater unit is usually suspended by an electrical cable which also connects the photocell with a deck galvanometer. A similar photocell is usually mounted on the deck of the vessel so that incident solar radiation can be measured simultaneously with subsurface illumination. Instruments of this type, along with filter recommendations, and standardization techniques, have been described by Atkins *et al.* (1938) and Jerlov (1951). An excellent though slightly more elaborate instrument has been used by Steeman Nielsen (1951) with considerable success in ecological studies.

This type of instrument, when used with various color filters, enables one to measure light intensities in different spectral regions and calculate vertical extinction coefficients (k). The photometer may be used without color filters and vertical-extinction coefficients for total energy calculated (Johnson and Kullenberg, 1946). Instruments of this type give a measure of the sum of the absorption and a fraction of the scattering of the downward-travelling light. If a measurement of beam extinction (c) is desired, an instrument called a transparency meter (Fig. 1B) must be employed (Pettersson, 1934; 1936; Jerlov, 1951). This instrument contains its own carefully regulated light source, the beam from which is reflected by a mirror back to a photocell and measures total scattering (except that in a forward direction) and total absorption. Such an instrument has been frequently employed in coastal waters and is particularly useful to the biologist as it gives a measure of the organism content

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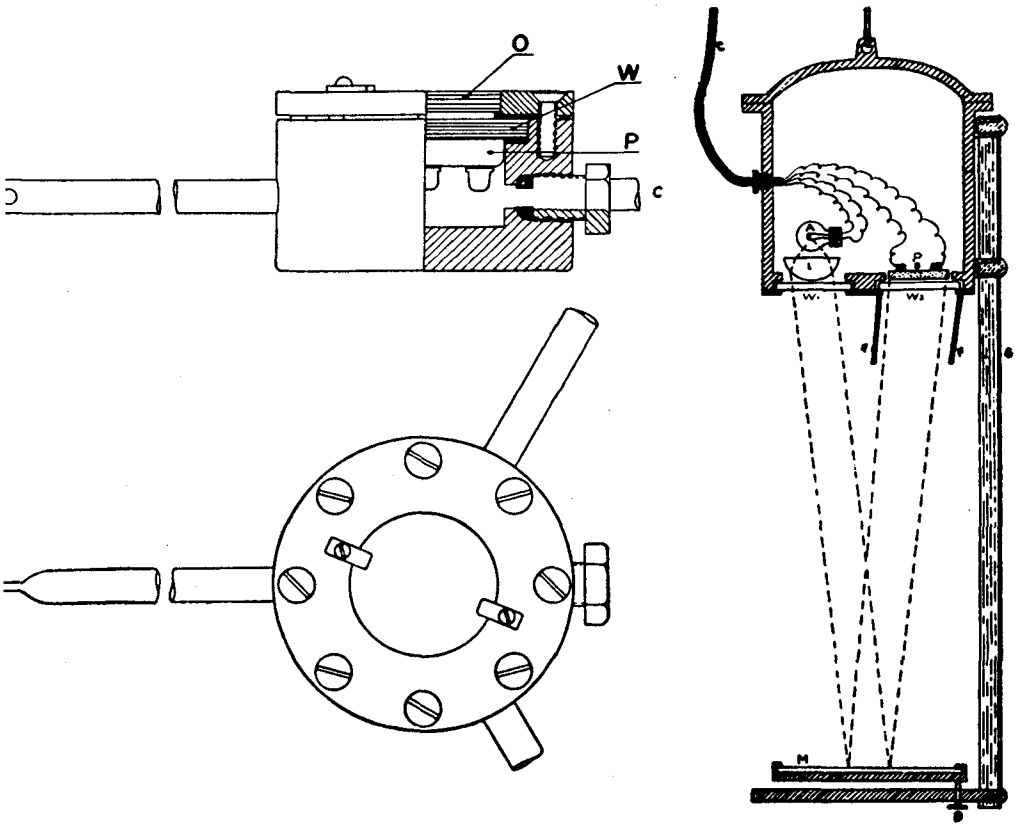

FIGURE 1.—*Instruments*

(A) Plan of a small submarine photometer. From Jerlov (1951)
(B) Plan of a transparency meter. From Pettersson (1936)
A, lamp; C, electrical cable; L, lens; M, mirror; O, filters, etc.; P, photocell; W, window.

of the water, something the Secchi disk and the submarine photometer will not consistently do. Other submarine photometers with certain modifications are employed if the angular distribution of submarine daylight is to be measured (Atkins and Poole, 1940; Poole, 1945; Johnson and Liljequist, 1938), or if the penetration of ultraviolet light is to be studied (Jerlov, 1951).

None of the above-mentioned instruments will discriminate between absorption by particles and absorption by dissolved substances. While such measurements are of interest to the biologist, they are not normally obtained in routine ecological investigations. An excellent account of the methods employed for separate measurements and a summary of the existing data are given by Jerlov (1951; 1953a; 1953b).

In the following two sections an attempt has been made to summarize our knowledge of the optical properties of sea water and those facets of the solar-radiation problem that seem pertinent as background material. References have been kept to a

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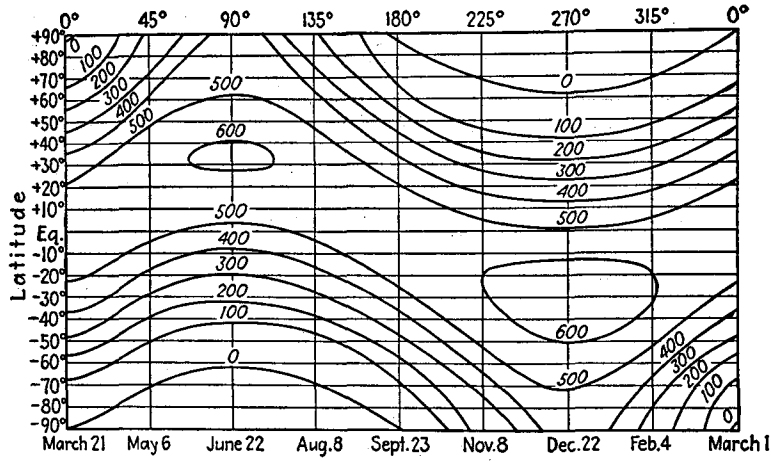

FIGURE 2.—*Daily insolation in calories per square centimeter at the earth's surface when the atmospheric transmission coefficient is 0.7*

From Haurwitz (1941)

minimum. In the discussion of optical properties the author has liberally used data and information presented in Jerlov's recent papers (1951; 1953a; 1953b) which summarize and evaluate the results of previous investigations in addition to presenting the complete set of observations he obtained on the recent Swedish ALBATROSS expedition.

SOLAR RADIATION

The spectral-energy distribution of solar radiation received at the outer limits of the earth's atmosphere is presented in Figure 2. Radiation with wave lengths both exceeding and falling below the limits depicted in this figure does occur; in fact the range of the optically measured spectrum extends from 0.22 to 24 mμ, but the very long and very short wave lengths are relatively unimportant (they constitute only roughly 5 per cent of the energy of the incident radiation). The total amount of energy that reaches the outer limit of the earth's atmosphere (the solar constant) probably does not exceed 2.0 gram calories/cm^2/min: the new Smithsonian value for the average solar constant is 1.90 which is 0.04 gm cal/cm^2/min less than their previous value. Variations from this average figure do, of course, occur, but these variations are very small ($\pm$1.0 per cent) and are usually ignored.

Both the quantity and quality (color temperature) of solar radiation reaching the earth's surface vary with time and place (Figs. 2, 3). These changes in quality and quantity are induced by a number of factors: the angle of the sun, absorption and reflection (by gasses, water vapor, dust, and clouds), scattering, and multiple scattering. Of these, the most important is reflection from and absorption by clouds. Estimates of the amount of solar energy reaching the earth's surface vary considerably depending upon how and under what conditions the measurements were taken, but on the average 65 per cent of the incident radiation reaches the earth's surface. This value may rise to 80 per cent on cloudless days or even higher when the sun shines

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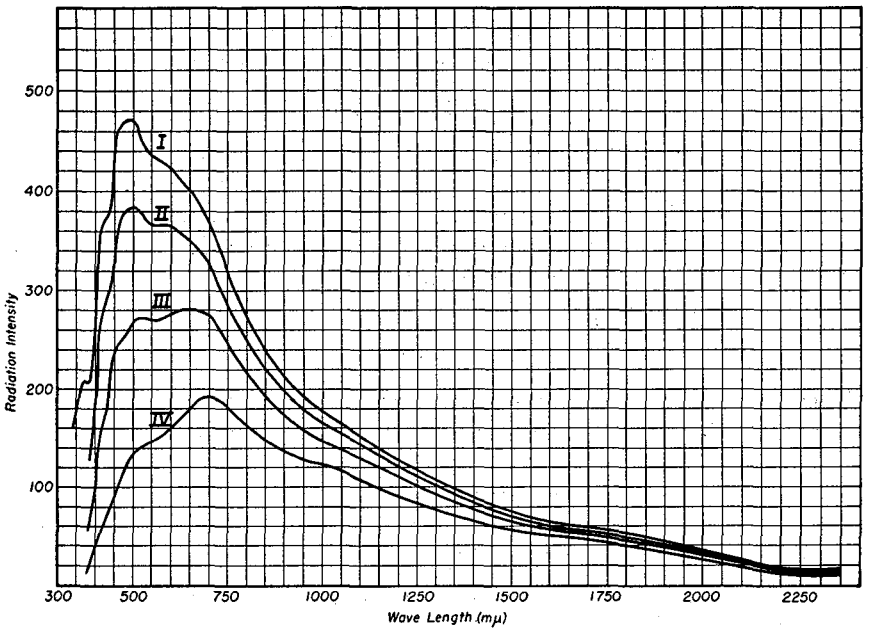

FIGURE 3.—*Normal spectral curves of solar radiation*

I, air mass 1.1 (Zenith distance, Z = 25°); II, air mass 2.0 (Z = 60°); III, air mass 3.0 (Z = 70.7°); IV, air mass 5.0 (Z = 78.7°). After Kimball (1924).

through scattered clouds, or be cut down to 20 per cent or less on dark overcast or rainy days. Sverdrup *et al.* (1942) have published a table based on Kimball's computations which gives the best available estimates of the average amount of energy incident upon the sea surface in different localities during various months of the year (Table 1).

PENETRATION OF WATER BY LIGHT

The amount of incident radiation that enters the sea is dependent upon the amount of radiation immediately above the surface and the reflectivity of the surface. The angle of incidence of the radiation largely determines the amount of radiation reflected. For high solar altitudes reflectivity is quite low and continues to remain relatively low until the sun comes to within 10°–20° of the horizon (Table 2). When the sky is overcast the reflectivity averages about 10 per cent regardless of solar altitude (Nieburger, 1948; Burt, 1953). When the sea is rough enough to produce white caps the albedo of the water surface increases to about 31 per cent (Fritz, *in* Malone, 1951).

As a beam of light passes through a medium, in this case sea water, the intensity of the beam decreases in the direction of the beam as the light is both scattered and absorbed. In pure water, scattering would be caused by the water molecules only. The effect of temperature on the absorption of light is small, except in the infra-red region, and can be ignored. Likewise, the dissolved salts occurring in sea water can be ignored as they cause only slight variation from absorption coefficients in pure water (Sverdrup *et al.*, 1942).

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In oceanography the rate at which downward radiation decreases with depth (per meter) is called the extinction coefficient and is defined as follows:

$$k \text{ or } c = 2.30 (\log I_{\lambda,z} - \log I_{\lambda,(z+1)})$$

where k or c is the extinction coefficient as measured by the submarine photometer and transparency meter, respectively, and $I_{\lambda,z}$ and $I_{\lambda,(z+1)}$ represent intensities at a specified wave length (λ) on horizontal surfaces at depths z and $(z + 1)$ meters (Sverdrup *et al.*, 1942). To give a more concrete idea of the reduction of light with depth, it is convenient to use transmission per meter (T) instead of extinction. The term T is defined as follows:

$$T = e^{-k}$$

The extinction of daylight in the sea is caused by absorption (by the water itself, by particles, and by dissolved substances) and by scattering (by the water and by

TABLE 1.—*Average amounts of radiation from sun and sky*

Expressed in gram calories per square centimeter per minute, which reaches the sea surface during various months. From Sverdrup *et al.* (1942)

Latitude	Longitude	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
60°N	7°E–56°W	.002	.053	.125	.207	.272	.292	.267	.212	.147	.074	.006	.0
60 N	135–170 W	.005	.078	.155	.208	.269	.260	.242	.185	.127	.077	.015	.0
52 N	10 W	.048	.089	.148	.219	.258	.267	.251	.211	.160	.104	.062	.041
52 N	129 W	.053	.091	.135	.185	.246	.250	.230	.214	.158	.097	.058	.039
42 N	66–70 W	.094	.138	.212	.272	.306	.329	.302	.267	.230	.174	.115	.086
42 N	124 W	.100	.151	.210	.286	.331	.360	.320	.274	.231	.174	.113	.092
30 N	65–77 W	.146	.165	.238	.285	.317	.310	.301	.282	.239	.188	.169	.142
30 N	128–130 E	.141	.153	.199	.241	.258	.238	.256	.260	.219	.178	.153	.135
10 N	61–69 W	.254	.276	.299	.305	.272	.276	.285	.292	.287	.269	.248	.239
10 N	116 E–80 W	.226	.257	.292	.278	.255	.239	.240	.242	.247	.237	.224	.219
0	7–12 E	.239	.248	.244	.230	.210	.196	.188	.194	.220	.240	.239	.235
0	48 W; 170 E	.261	.265	.282	.297	.309	.300	.300	.340	.366	.362	.339	.278
10 S	14 E; 36–38 W	.329	.328	.301	.254	.219	.206	.232	.278	.312	.324	.317	.320
10 S	72–171 E	.290	.308	.315	.289	.266	.253	.269	.306	.332	.313	.301	.303
30 S	17 and 116 E	.452	.406	.340	.254	.186	.148	.166	.214	.274	.362	.401	.430
30 S	110 W	.380	.330	.260	.209	.162	.130	.145	.176	.237	.321	.340	.390
42 S	73 W; 147 E	.343	.297	.223	.154	.104	.085	.092	.135	.186	.264	.310	.348
52 S	58 W	.289	.237	.167	.112	.062	.039	.049	.097	.150	.222	.273	.302
60 S	45 W	.213	.171	.105	.056	.011	.0	.003	.054	.111	.156	.204	.221

TABLE 2.—*Percentage of total incoming radiation from the sun and sky which on a clear day is reflected from a horizontal water surface at different solar altitudes*

From Schmidt (1915)

Altitude of the sun (°)	10	20	30	40	50	60–90
Percentage reflected	28	14	8	6	5	4

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TABLE 3.—*Comparison between transmission (per cent) per meter for double-distilled water and mean transmission per meter for clearest ocean water and for the depth ranges indicated*

The depths Z_{10} and Z_1 are those at which the percentage of light is 10% and 1% of the surface value, respectively. From Jerlov (1951)

Wave length mμ	Double-distilled water (Clark and James, 1939)	Clearest ocean water			
		0–10 m.	0–Z_{10} m.	0–Z_1 m.	Z_{10}–Z_1 m.
310		86	86	86	86
375	95.6	96.3	95.7	95.0	94.0
400	95.8	97.2	96.4	95.8	94.7
425	96.8	97.8	96.9	96.3	95.3
450	98.1	98.1	97.2	96.7	95.8
475	98.2	98.2	97.3	96.8	95.9
500	96.5	97.2	96.4	95.9	95.2
525	96.0	96.1	95.1	94.7	94.2
550	93.3	94.2	93.4	93.4	93.4
575	91.3	92	92	92	92
600	83.3	85	85	85	85
625	79.6	74	74	74	74
650	75.0	70	70	70	70
675	69.3	65—	65	65	65
700	60.7	58	58	58	58

particles). In other words

$$c = a_w + a_p + a_y + s_w + s_p$$

where c is the total extinction coefficient (as measured with the transparency meter), a is the absorption coefficient for water (w), particles (p), and dissolved substances (y), and s the scattering coefficient for water itself (w) and particles (p). If the part of the total extinction due to the water itself (c_w) is subtracted we obtain

$$c - c_w = a_p + a_y + s_p.$$

As mentioned previously the submarine photometer measures total absorption (A) but only a fraction (y gamma) of the scattering (S).[1]

$$K = A + yS$$

Jerlov's data (1951) indicate that in clear, oceanic water y equals about ½ and scattering is produced by relatively large particles.

Actual measurements of a_p and s_p at various wave lengths in the clearest oceanic water reveal that scattering by particles (s_p) is relatively high whereas absorption by a_p particles is very low. As scattering does not greatly affect vertical extinction (as measured with the submarine photometer) and as absorption by particles and dissolved substance is low, extinction in water of this type will be caused largely by absorption of the water itself; in other words $c_w \doteq k$. In Table 3 the

[1] Since light is scattered in all directions a certain amount impinges upon the photocell of this instrument whereas in the transparency meter the photocell records only that light which has travelled in a direct path from its self-contained light source.

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transmission values for double distilled water and the clearest oceanic water are presented as a function of wave length and in the latter case, also, of depth. From a comparison of these values it can readily be seen that the clearest oceanic water is nearly as transparent as double-distilled water; in fact, in the blue-violet end of the spectrum, oceanic water appears to be more transparent than double-distilled water. According to Jerlov (1951) this is because the transmission values for distilled water include the effect of molecular scattering (which is most pronounced in the short wave lengths) which tends to reduce transmission somewhat. In the clearest oceanic water the amount of scattering is relatively high but does not appreciably affect transmission values. The data in Table 3 also reveal that transmission first decreases with depth and then becomes nearly constant. The decrease in trans-

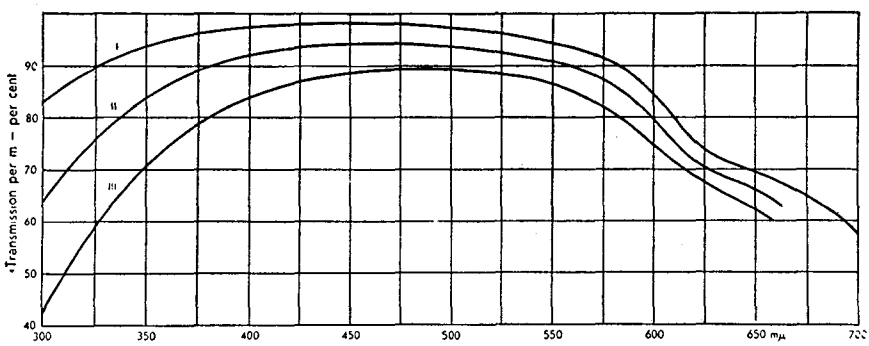

FIGURE 4.—*Normal transmission curves for different types of oceanic water*
Zenith sun. From Jerlov (1951)

mission observed in turbid oceanic water (Fig. 6) is due to absorption by yellow substance and also to a_p. In turbid oceanic water particles are more abundant and larger than in clear oceanic water; while both $a_p + s_p$ increase in such circumstances only the increase in a_p affects transparency.

A still greater decrease in transmission occurs in coastal water (Figs. 4, 5). Clarke and James (1939) concluded that the suspensoids and filterable materials contained in coastal water were responsible for the difference, as these materials exerted a selective action which is most pronounced in the shorter wave lengths. Utterback (1936) likewise observed greater absorption in the shorter wave lengths in coastal water. Kalle (1937) showed the presence in sea water of a water-soluble yellow pigment ("yellow substance"), whose absorption curve would account for the observed increase in extinction in the blue end of the spectrum and also demonstrated this substance to be most abundant in coastal waters. The most recent investigations support Kalle's observations, and it is now fairly certain that this substance is probably chiefly responsible for the high extinction in the shorter wave lengths encountered in turbid oceanic water and coastal waters.

The most recent transmission values (for the upper 10 m) for different types of ocean and coastal water have been obtained by Jerlov (1951) and are presented in Tables 4 and 5 and in Figures 4 and 5. While variations among the various types are considerable, certain generalizations can be made. Sea water is fairly opaque to red light (*see also* Sverdrup *et al.*, 1942) and quite transparent to blue and green. Further-

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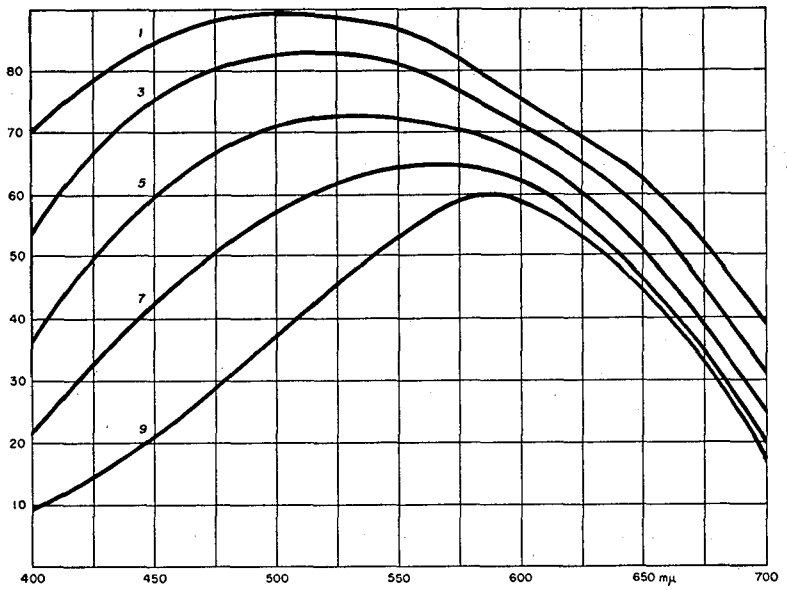

FIGURE 5.—*Normal transmission curves for various types of coastal water*
Solar altitude 45°. From Jerlov (1951)

more, oceanic water is relatively more transparent to blue than green light, whereas the converse is true in coastal water.

Curve I in Figure 4 (also Table 4) represents the clearest oceanic water, while curve II is characteristic of tropical and subtropical oceanic water of relatively high turbidity. Curve III applies to temperate oceanic water. Still greater opacity might be expected in arctic waters (Jerlov, 1951). An examination of these three curves shows absorption to be a selective process, with the short-wave portion of the spectrum relatively more reduced than the long-wave portion. This selectivity, owing chiefly to the presence of the aforementioned yellow substance (which is presumably a stable plant-degradation product), is not so pronounced in oceanic water as it is in coastal water. The source of this yellow substance in oceanic water is difficult to trace. Turbid oceanic water is usually associated with upwelling areas. These areas are also very productive. The yellow substance may be produced *in situ*, or it may be carried

TABLE 4.—*Normal transmission values (per cent) per meter for ocean waters and with the sun at the zenith*
From Jerlov (1951)

Type of ocean water	Wave length mμ														
	310	375	400	425	450	475	500	525	550	575	600	625	650	675	700
I	86	96.3	97.2	97.8	98.1	98.2	97.2	96.1	94.2	92	85	74	70	65	58
II	69	89	92	93.5	94	94	93.5	92.5	90.5	87.5	80	71	67		
III	50	79	84	87	88.5	89	89	88.5	86.5	82.5	75	68	63		

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TABLE 5.—*Normal transmission values (per cent) per meter for coastal waters, with a solar altitude of 45°*

From Jerlov (1951)

Type of coastal water	Wave length mμ						
	400	450	500	550	600	650	700
1	70.0	84.6	88.6	86.9	75.4	62.8	38.8
2	64.5	81.8	86.5	85.0	74.1	61.1	36.9
3	54.1	75.5	82.1	81.1	71.6	57.7	32.7
4	45.0	68.4	76.9	76.8	69.4	54.6	28.9
5	36.6	60.5	71.1	72.4	67.1	51.9	25.7
6	29.0	51.7	64.1	68.1	64.8	49.4	23.0
7	21.8	42.3	56.5	63.6	62.6	47.4	20.9
8	15.2	32.3	47.6	58.3	60.8	46.0	19.6
9	9.7	21.7	37.5	53.5	59.0	45.2	19.1

to the surface from mid-depths by the upwelling process or transported from place to place by currents (Jerlov, 1951).

The differences between oceanic and coastal water and among coastal-water types are due very largely to this yellow substance. A large amount of yellow substance finds its way into the coastal water via rivers, although not all rivers carry large amounts of it. Tropical rivers carry less yellow substance than do the Scandinavian rivers. The Nile, for instance, contains relatively small amounts. The Amazon, however, is an exception and is quite rich in this substance as are the Scandinavian rivers (Jerlov, 1951).

The extinction and transmission values we have been discussing give information only about the vertical component. An organism suspended in sea water in the photic zone receives light from all directions. Scattering in oceanic water is nearly restricted to the ultraviolet, blue, green and yellow-green portion of the spectrum. Practically no orange or red light is scattered. Poole (1945) and Johnson and Liljequist (1938) have studied the amount and quality of light scattered both horizontally and vertically. Their results show that in oceanic water, when the sun is at the zenith, 5–7 per cent of the blue and violet light (465 and 375 mμ) is scattered upward. The total amount of upward scattering increases with decreasing solar altitude. In coastal water the scattered light has a somewhat different spectral composition and contains more red and orange. These differences may be attributed to the differences in abundance of particles. In oceanic water most of the scattering is caused by water molecules, and only very small amounts of orange and red light are scattered. In coastal water, however, particles are much more numerous, and they effect relatively more scattering in the orange and red than do water molecules.

Considerably more light is scattered horizontally than vertically. In the waters off Plymouth, Atkins and Poole (1940) found the ratio of the total horizontal to downward illumination to be between 73 and 84 per cent. In two sets of observations in the Sargasso Sea, Jerlov (1951) found that H/V for blue light ranges only between 56 and 77 per cent; at different depths in the Baltic and Skagerrak to average 73 per

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cent; in the Mediterranean, 63 per cent. These workers found that the H/V ratio remains approximately constant with depth, and according to Atkins and Poole (1940) it is independent of solar altitude. These observations indicate that the directional character of subsurface radiation is lost very slowly with increasing depth. Even at a depth of 500 m, Helland-Hansen (Murray and Hjort, 1912) found that the vertical radiation is considerably more intense than the horizontal.

So far the discussion has been limited to the way in which sea water absorbs and scatters light of different colors; in addition to the changes in quality with depth, the biologist is interested in the penetration of energy. Extinction and transmission of energy can be expressed in the same manner as are extinction and transmission of radiation intensity.

According to Sverdrup *et al.* (1942), 100 gm. cal./cm.^{2}/hr. of incident radiation penetrates the sea surface on a clear day with the sun at the zenith; the value for energy entering the sea with a solar altitude of 45° is approximately 70 gm. cal./cm.^{2}/hr. (Jerlov, 1951). Jerlov has calculated and plotted the transmission of energy in the various types of sea water mentioned above (Figs. 6, 7). These values apply to

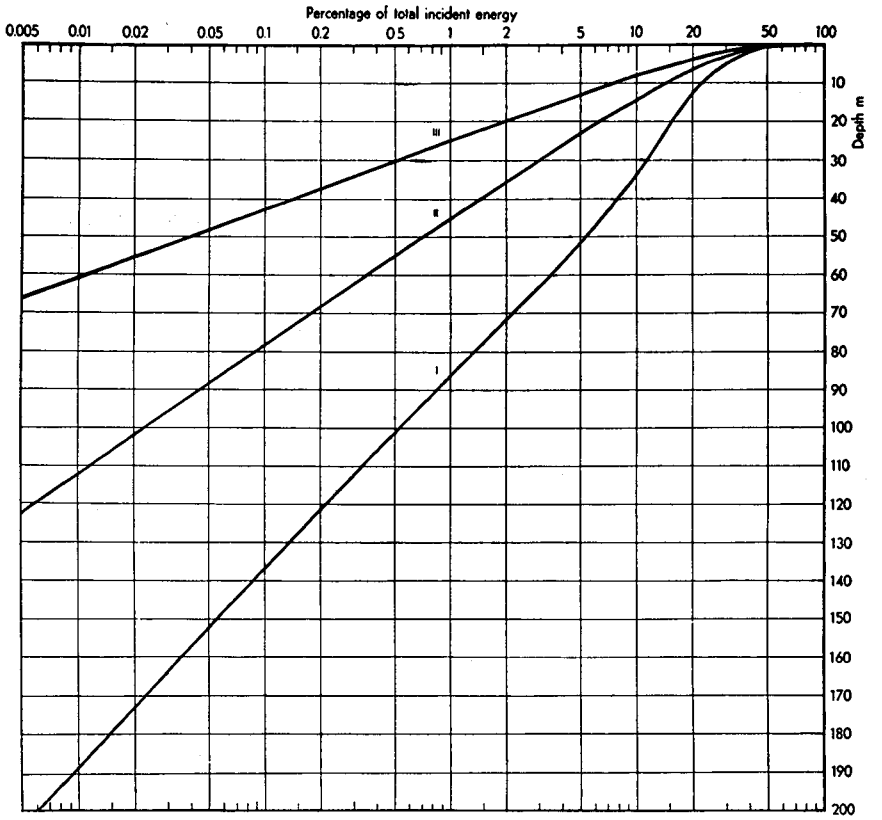

FIGURE 6.—*Percentage of total incident energy at different depths in different types of ocean water*
Zenith sun. From Jerlov (1951)

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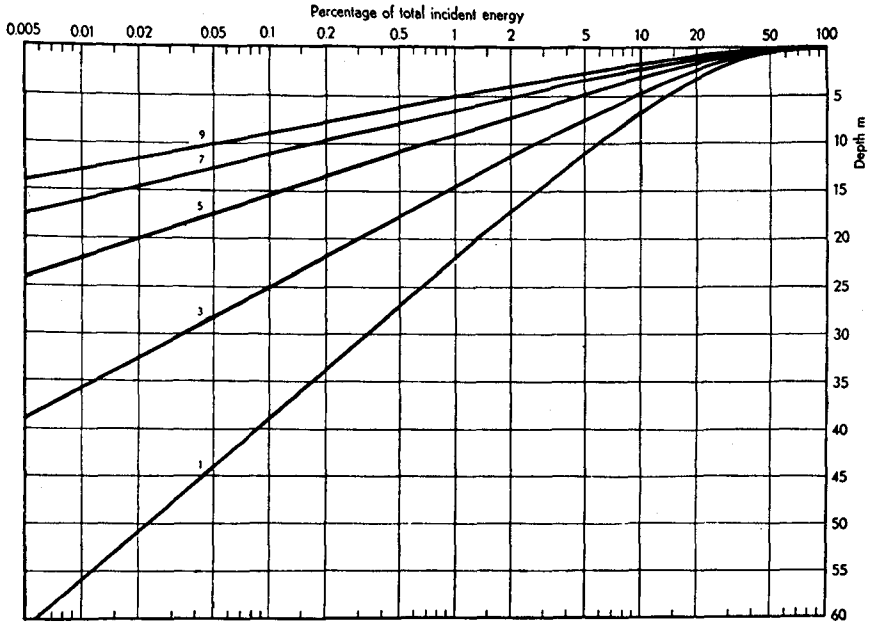

FIGURE 7.—*Percentage of total incident daylight energy in different types of coastal water* Solar altitude 45°. From Jerlov (1951)

the vertical component only. Jerlov estimates that these values should be increased by 20 per cent for oceanic water and by 30 per cent for coastal water to obtain the total energy that would be received by an organism in the photic zone.

SUBMARINE DAYLIGHT AND PHOTOSYNTHESIS

The intensity of submarine daylight decreases slowly with depth; yet it is convenient for the biologist to regard the ocean as being divided horizontally into "lighted" and "unlighted" zones—the photic and aphotic zones. Within the photic zone, there is enough light to permit algae to carry on photosynthesis, whereas in the aphotic zone there is not. It is impossible to set an intensity or depth limit that separates these zones. The light requirements for photosynthesis vary with the quality of the light and the plant species and their physiological condition. Similarly, a depth limit cannot be set because the intensity of sunlight at any depth will vary widely with solar altitude, turbidity, time, geographic position, and season.

In the sea one encounters two distinctly different types of plants: the microscopic free-floating or weakly motile pelagic organisms called the phytoplankton, and the attached algae and their epiphytes which inhabit the inner sublittoral and supralittoral zones. The phytoplankton consist almost exclusively of acellular algae: the diatoms, dinoflagellates, minute naked flagellates (the "mu" flagellates), coccolithophorids, and a few green and blue-green algae. The importance and distribution of the photosynthetic bacteria are not sufficiently understood to warrant discussion here.

Photosynthesis, as is well known, is an endothermic photochemical process in which

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solar radiation serves as the energy source. Solar energy absorbed by the plant pigments passes through the pigment complex providing the energy necessary for the reduction of carbon dioxide into organic matter. The role of carbon dioxide and the path of carbon-dioxide reduction is far more complex and need not concern us here (*see* Smith, 1949) as CO_2 probably never becomes a limiting factor in plant production in the sea. The quantity and quality of light absorbed by the plant is dependent upon the types of pigments present, their concentration, and the quantity and quality of the incident radiation. Pigments must be present if photosynthesis is to take place, but this alone is not a sufficient condition; other systems within the cell must also be active.

All of the photosynthetic phytoplanktonic organisms contain in their plastids one or more chlorophylls accompanied by varying kinds and amounts of carotenoid pigments. Detailed studies of pigment composition and the physiological activity of plastid pigments are available for only a few species of phytoplankton. The relevant data concern diatom pigments and their photosynthetic role and an incomplete analysis of two dinoflagellates, *Peridinium* and *Prorocentrum micans*. In diatoms and *Peridinium* chlorophylls *a* and *c* are present (Strain, Manning, and Hardin, 1943); chlorophyll *b* is apparently missing or present only in very minute quantities. The principal diatom carotenoid is the xanthophyll fucoxanthin. In *Peridinium* and *Prorocentrum micans* the principal xanthophylls appear to be diadinoxanthin and peridinin or sulcatoxanthin (H. H. Strain, *cf.* Franck and Loomis, 1949; Pinckard *et al.*, 1953). Many investigators have found evidence that in addition to chlorophyll fucoxanthin participates in the photosynthetic reaction (Dutton and Manning, 1941; Dutton and Duggar, 1943; Jenkin, 1937; Montfort, 1940; Stanbury, 1931; Tanada, 1951; Wassink and Kersten, 1946) although it is only in the past few years that this can be said to have been definitely proven. Quantum-yield studies (*see especially* Tanada, 1951) reveal that light ranging from 400 to 700 mμ can be utilized in the photosynthetic process by the diatoms with nearly equal quantum efficiency. In terms of energy this process will always seem more inefficient in the blue end of the spectrum as the energy per quantum varies inversely with wave length (Rabinowitch, 1951).

In addition to light quality, the intensity of the light must be considered. Once again the data are scanty and are further complicated by the fact that some investigators have determined the effect of various intensities of white light upon division rate, while other investigators have determined the intensity effects of white and monochromatic light upon oxygen production as measured by either the Winkler method or by Warburg's manometric technique. It is impossible to compare these results. Available evidence indicates that division rate reaches a maximum at lower light intensities than photosynthesis. Division-rate studies indicate that different species have different optimal intensities: *Peridinium triquetrum*, *ca.* 107 f.c. (Braarud and Pappas, 1951); *Biddulphia mobilensis*, *ca.* 172 f.c.; *Carteria* sp., *ca.* 344 f.c. (Schreiber, 1927); *Cryptomonas* sp., *ca.* 450 f.c.; *Peridinium* sp., *Prorocentrum micans*, and *Prorocentrum gracile* all about 180 f.c. (Barker, 1935).[2]

Braarud (1937) cultured a number of diatoms at 86 and 161 f.c. and found no

[2] As indicated, these last four organisms were investigated by Barker, and the light values given were obtained by taking foot-candle measurements directly from an illumination set-up equivalent to that employed by Barker.

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evidence of inhibition at the 161 f.c. level. Jenkin (1937) found that photosynthesis as determined by the Winkler method was inhibited in *Coscinodiscus excentricus* at 10 gm. cal./cm.^{2}/hr. (approximately 7700 f.c.) and was optimal at 1.8 gm. cal./cm.^{2}/hr. (approximately 1200 f.c.). *Biddulphia regia* showed similar responses (Jenkin, 1937). Preliminary studies at Scripps Institution of Oceanography have shown photosynthesis, as measured by the manometric method, to be saturated in the dinoflagellate *Gonyaulax polyedra* at about 800 f.c. (Haxo and Sweeney, 1955). Wassink and Kersten (1946) found photosynthesis in *Nitzschia* sp. to be saturated at *ca.* 6000 f.c. In experiments carried out by Steeman Nielsen (1937) the photosynthesis of natural populations was measured at various light intensities. Photosynthesis in temperate and boreal plankton was saturated at about 750 f.c. and remained constant up to about 2150 f.c., but at high levels there was a noticeable decline in carbon-dioxide consumption.

These data on photosynthesis and growth reveal that at low and intermediate intensities photosynthesis and growth are proportional to the light intensity; as the intensity is increased, saturation is reached asymptotically. Additional increases in the intensity do not increase photosynthesis, and a point is eventually reached when the rate decreases markedly with increasing illumination.

Illumination in turbid and average coastal water at a depth of 5–10 m reaches an intensity of about 700 f.c. at noon (Sverdrup *et al.* Table 92, p. 776, 1942)—the average intensity is presumably less, and it is approximately at this depth that productivity is highest. In very turbid water photosynthesis will be maximal much nearer the surface where the illumination will approximate 700 f.c. As we have seen, at light intensities above 2150 f.c., photosynthesis is inhibited. Illumination values exceeding 2150 f.c. are common in the immediate vicinity of the surface, and then production is less here than at some intermediate level.

The results discussed thus far pertain to neritic, temperate to boreal species or populations. In oceanic water the situation is somewhat different. E. Steeman Nielsen (1952) found maximum production in oceanic tropical waters at about 10 m, and in controlled experiments with natural populations saturation occurred at about 3200 f.c. Riley (1939) found maximum production in the clear water of the Tortugas region between 10 and 15 m. These data certainly indicate that oceanic populations, at least in tropical areas, have considerably higher saturation intensity values than do neritic populations.

Biological oceanographers and plant physiologists are also interested in the intensity or depth at which oxygen production and consumption (respiration) at a given moment balance one another. These are called the compensation intensity and compensation depth. Another term frequently encountered in the literature is the compensation point which is defined by Jenkin (1937) as the depth at which oxygen production is sufficient to meet respiration requirements for 1 day (24 hours). In actual practice these definitions are not followed closely, and the compensation point is frequently considered to be equivalent to the compensation depth (Clarke, 1936; Clarke and Ostler, 1934).

In a natural population the compensation depth is affected by the physiological characteristics of the autotrophic plants making up the population and varies with the

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species composition of the population and the relative abundance of autotrophs and heterotrophs. Respiration and photosynthesis decrease with temperature, but, as a downward change in temperature depresses respiration more than photosynthesis, there is a slight lowering of the compensation depth with decreasing temperature (Sverdrup *et al.*, 1942). The increase of photosynthetic rate with temperature is more pronounced at high light intensities. Riley (1949) discusses the importance of light and temperature in some detail and believes that these factors affect nutrient requirements.

The compensation intensities for a few phytoplankton are known: for *Biddulphia mobilensis* (Schreiber, 1927) *ca.* 10 f.c., for *Coscinodiscus excentricus* (and presumably *Biddulphia regia*) about 36. f.c. (Jenkin, 1937), and for *Gonyaulax polyedra* 200 f.c. (Haxo and Sweeney, personal communication). Measurements made by lowering cultures into the sea give the following compensation depths: *Skeletonema costatum* 2.5–12 m in the turbid inner Oslo Fjord (Rustad, 1946), *Coscinodiscus excentricus* 45 m in the English Channel (Jenkin, 1937). Typical of measurements with natural populations are the following values: in turbid coastal water 1–12 m (Clarke, 1936; Steeman Nielsen, 1937; 1951), in clear coastal and turbid oceanic water 25–45 m (Clarke, 1936; Clarke and Ostler, 1934; Jenkin, 1937; Riley, 1947) although this depth may be reduced during a bloom. Not many observations have been made in clear oceanic water, but Riley (1939), taking into consideration all the data available, believes that the compensation depth in the Sargasso Sea lies at about 150 m and in more northern oceanic waters at a depth of about 50 m. Riley further states that the light intensity at this depth is about 0.5–1 per cent of the incident radiation.

The quantum yield of photosynthesis in green plants has been reported to drop off sharply above 700 mμ although there is some evidence that wave lengths up to 832.5 mμ may be effective in *Chlorella* phtosynthesis (Rabinowitch, 1951, p. 1153–1158). It is doubtful that radiation above 700 mμ is of great importance in the sea as this long-wave radiation is very rapidly filtered out in even the clearest oceanic water. Quantum yields also fall off beyond the violet end of the spectrum (365–400 mμ). The transparency of clear oceanic water to radiation falling below 315 mμ may be important in vitamin D production in certain animals and plants although very little is known about this subject (Johnson and Levring, 1947; Jerlov, 1951).

Certain dinoflagellates are phototactic, and their vertical distribution may be partially explained as a result of phototactic movement. Hasle (1950) has shown that vertical migrations of certain dinoflagellates occur in nature and that diurnal migrations of as great as 5–10 m are possible. Of the four organisms investigated by Hasle, two (*Ceratium tripos* and *C. fusus*) left the surface during the day and returned at night, while the other two (*Gonyaulax polyedra* and *Prorocentrum micans*) rose to the surface during the day and returned to deeper water at night. The peculiar hydrographic and light conditions in inner Oslofjord may have tended to exaggerate these migrations, but Hasle believes migrations of this sort occur generally although it is not yet possible to say how many dinoflagellate species participate in such migrations nor how great the vertical distance traversed may be. Unfortunately no information concerning the wave-length specificities of phototaxis is available for these organisms.

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PIGMENTS, PHOTOSYNTHESIS, AND CHROMATIC ADAPTATION IN LITTORAL ALGAE

The principal pigments found in the littoral algae are summarized by groups in Table 6. The role of some of these is not known, but certain generalizations can be made concerning the photosynthetic activity of some of them. In the green marine algae, Haxo and Blinks (1950) found evidence of photosynthetic sensitization not only in the region of chlorophyll absorption but also in the region where carotenoid absorption predominated, although the carotenoids are not so active as the chlorophylls. These authors do not attempt to determine which were the active carotenoids.

Quantum studies by Emerson and Lewis (1943) with *Chlorella* revealed that oxygen production remains essentially constant throughout the visible spectrum except in the region of dominant carotenoid absorption (*i.e.*, 480–520 mμ). Investigations by Moore and Duggar (Franck and Loomis, 1949) again with *Chlorella* revealed essentially the same situation. These data indicate the active participation of pigments other than chlorophyll in photosynthetic sensitization. Essentially the same situation, though even more pronounced in the region of fucoxanthin absorption, was revealed by Haxo and Blinks (1950) when brown algae were used as test material. Light absorbed by the xanthophyll fucoxanthin led to oxygen production, as apparently did, to a lesser extent, light absorbed by other carotenoids in the 420–500 mμ region. In 1883 Engelmann provided evidence to show that light absorbed by the phycobilins (the red and blue-green pigments in the red and blue-green algae) was utilized in photosynthesis. Observations by Emerson and Lewis (1943) and Haxo and Blinks (1950) and others have shown that Engelmann was indeed correct. More interesting, however, is the observation of Haxo and Blinks (1950) that the direct sensitization of chlorophyll and carotenoids plays only a subordinate role in oxygen production in the red algae and that photosynthesis is most effectively sensitized by the phycobilins whose maximum absorption occurs in the 495–630 mμ region. The available evidence indicates that the phycobilins are not direct sensitizers but that the energy absorbed by the phycobilins is transferred to chlorophyll (Duysens, 1952).

The photosynthetic responses of the littoral algae to variations in light intensity are naturally very similar to those of the phytoplankton, but, although the light curves are of the same type, the intensity which produces saturation is generally higher in the former. In the brown alga *Fucus serratus* saturation of photosynthesis

TABLE 6.—*Principal pigments of the littoral algae*
From Franck and Loomis (1949)

Plants	Chlorophylls	Carotenes	Principal Xanthophylls	Phycobilins
Blue-green algae	a	$\beta \pm \alpha$	Myxoxanthin, myxoxanthophyll, Lutein, Zeaxanthin	present
Green algae (except *Siphonales*)	a + b	$\beta \pm \alpha$	Lutein, Neoxanthin, Violaxanthin	absent
Green algae (*Siphonales*)	a + b	$\alpha \pm \beta$	Siphonein, Siphona xanthin, Lutein, Neoxanthin, Violaxanthin	absent
Brown algae	a + c	$\beta \pm \alpha$	Fucoxanthin, Violaxanthin	absent
Red algae	a + d	$\beta \pm \alpha$	Lutein, Zeaxanthin	present

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occurs at about 2500 f.c.; among the green algae, in *Rhizoclonium* somewhat above 1500 f.c., in *Hormidium flaccidum* at about 600 and 240 f.c. for light and shade-adapted cells, and in *Chlorella* between 1500 and 2000 f.c. (these values are taken from Rabinowitch (1951) but are the results of various investigations). In the green alga *Ulva lactuca* saturation occurs at about 1500 f.c. (F. T. Haxo, personal communication) and in the deep-growing red alga *Delesseria* at about 100 f.c. The compensation intensities for a number of marine algae are also quoted by Rabinowitch (1951): in green algae the values ranged between 17 and 45 f.c.; in two brown algae, between 34 and 40 f.c.; and in three red algae, from 27 to 30 f.c.

The most important factor determining the saturation intensity is the adaptation of the plant to strong or weak light (Rabinowitch, 1951) which may be determined genetically but is subject to modification in at least some cases. Photosynthesis is saturated in shade-adapted plants (umbrophiles) at lower intensities than in heliophiles, and likewise compensation intensities are usually lower for umbrophiles than heliophiles. Littoral algae living at great depths in the sea, particularly the red algae behave as umbrophiles and may even be injured by exposure to high light intensities (Rabinowitch, 1951; *see also* Haxo and Blinks, 1950).

Speculations as to the reasons for the common occurrence of red algae in deep water, brown algae at mid-depths, and green algae near the surface have been in the literature for many years. (*See* Rabinowitch, 1945; 1951 for references.) Originally, two alternative explanations were offered: (1) that this vertical distribution has been determined by an adjustment by the plant to the intensity of the prevailing light—Oltmann's theory—; and (2) that this vertical zonation is due to the adaptation of the algae to the predominant quality of the prevailing light—Engelmann's theory. Currently the importance of both types of adaptations is recognized.

Adaptations permitting algae to survive well below the sea surface have apparently been achieved in two ways—by the development of photosynthetically active accessory pigments which are complementary in color to the prevailing light (such adaptations are exemplified by deep-growing red algae) or by an increase in the chlorophyll concentration which enhances absorption in the middle of the spectrum (such adaptations have been made by deep-growing green algae—*see* Strain *in* Franck and Loomis, (1949) and Strain (1950). Presumably adaptation to weak light could also take place by a significant decrease in respiratory rates, but not enough data are available to evaluate the importance of such an adaptation.

These adaptations are genetically determined, but within the genetic framework is a capacity for individual variation which tends to adjust the pigment complex of an individual to existing conditions. The concentrations of pigments of the same species vary in individuals growing at different depths (Rabinowitch, 1945) presumably in response to variations in the intensity as well as in the quality of the prevailing light. Thus, red and brown algae found growing near the surface may be almost green. In other algae adaptations may occur by an increase in the total concentration of pigments rather than by changes in the relative amounts of the individual pigments or by an increase in thallus thickness (Fogg, 1953). Factors such as the ability to withstand surf action, desiccation, etc., may also be decisive in determining the vertical distribution of the littoral algae.

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Chapter 7
Salinity

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COMPOSITION OF SEA WATER

The oceans are primarily solutions of metallic salts. Organic materials are present in minute amounts, and atmospheric gases are in solution in varying amounts. The concentrations of dissolved nitrates, phosphates, and silicates are relatively minute and variable and are therefore excluded from ordinary salinity determinations. The chief metallic salts (those of Na, Mg, Ca, K, Sr) are present in such constant proportions that for most purposes a simple analysis of one component, the chloride, is sufficient in any ocean for determination of the total salinity, the specific gravity, and the proportions of various salts. Salinity is defined as "the total amount of solid material in grams contained in one kilogram of sea water when all the carbonate has been converted to oxide, the bromine and iodine replaced by chlorine, and all the organic matter completely oxidized" (Sverdrup, Johnson, and Fleming, 1942, p. 50). It is expressed by the symbol ‰ (parts per thousand). Sets of tables for these determinations, based on the formula, salinity $= 0.03 + 1.805 \times$ chlorinity, have been prepared and constitute one of the standard tools of the oceanographer (Knudsen, 1901).

The average total salinity of ocean water is about 35 ‰, but it is slightly different in the various oceans. In the mid-Pacific, for example, the surface salinity is 35.5 ‰; in mid-Atlantic, 37.0 ‰, and in the Red Sea it is about 40 ‰. The Laguna Madre of Texas and the Crimean Sivash are among the saltiest marine lagoons of appreciable size on earth. Readings of 50–80 ‰ are common, and in places salinity is 104 ‰. In various tropical regions, such as the Bahamas and West Indies, certain shore ponds only intermittently connected with the sea have salinities up to 155 ‰.

Near the mouths of great rivers and in bays the proportions of salts in solution are slightly different. Nevertheless, the composition of oceanic and coastal waters is very similar and is markedly different from that of lakes and rivers and such inland salt waters as the Dead Sea (Tables 1, 2). The salts draining into the sea are not in the same proportion as those already present; the most pronounced difference is that the most abundant salt in the ocean is sodium chloride, whereas in rivers and typical inland waters it is calcium carbonate. Semi-enclosed seas, such as the Baltic and Black seas, have proportions similar to oceanic water, but their total concentration is less, whereas the isolated Caspian Sea is markedly different, especially in sulfate content (Table 3). Excess salinities are uncommon in the oceans. Low salinity occurs in polar seas and next to land, usually in bays, sounds, and estuaries, where fresh

† Deceased, December 11, 1956.

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TABLE 1.—*Common constituents of sea water and typical freshwaters, %*

	Normal sea water		Hard fresh water (3)	Soft fresh water (3)
	(1) (pH 8.17)	(2)		
Cl^-	19.630	18.9799	0.041	0.019
$SO_4^=$	2.701	2.6486	0.025	0.007
Br^-	0.066	0.0646		
F^-	0.001	0.0013		
CO_2, H_2CO_3	0.001			
HCO_3^-	0.116	0.1397		
$CO_3^=$	0.012		0.119	0.012
H_3BO_3	0.022	0.0260		
$H_2BO_3^-$	0.005			
Na^+	10.770	10.5561	0.021	0.016
Mg^{++}	1.298	1.2720	0.014	0.00053
Ca^{++}	0.408	0.4001	0.065	0.010
K^+	0.387	0.3800	0.016	—
Sr^{++}	0.014	0.0133		
Salinity	35.161	34.3159	0.301	0.065

(1) From Rubey (1951); (2) From Sverdrup *et al.* (1942); (3) From Baldwin (1937).

TABLE 2.—*Percentage of dissolved salts in various waters*

After Rankama and Sahama (1950) and Clarke (1924)

Constituent	Sea water	Lake and river water (average)	Jordan River near Jericho	Dead Sea north end	Bear River near mouth	Great Salt Lake
CO_3	0.41*	35.15	13.11	Trace	21.53	0.09
SO_4	7.68	12.14	7.22	0.31	8.16	6.68
Cl	55.04	5.68	41.47	65.81	32.36	55.48
NO_3	—	0.90	Trace	—	—	—
Ca	1.15	20.39	10.67	4.73	10.12	0.16
Mg	3.69	3.41	4.88	13.28	4.76	2.76
Na	30.62	5.79	18.11	11.65	20.54	33.17
K	1.10	2.12	1.14	1.85		1.66
Fe_2O_3, Al_2O_3		2.75	1.45	—	2.53	—
SiO_2		11.67	1.95	Trace	—	—
Sr, Br, H_3BO_3	0.31					
Br				2.37		
	100	100	100	100	100	100
Salinity, ‰	35.0	.146	.770	192.15	.637	203.49

* As HCO_3^-

water drains into the sea. Except along the arid coasts of the earth, a margin of water of lowered salinity borders all continents.

Inland salt lakes and mineral springs vary so much in salt composition and proportions that we cannot generalize about them, and a lake may also differ from its

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TABLE 3.—*Percentage of dissolved salts in various semi-enclosed and inland seas*

Data from Clarke (1924); for the sea water, from Rankama and Sahama (1950)

Constituent	Sea Water	Baltic Sea	Eastern Mediterranean	Black Sea	Caspian Sea	Aral Sea
Cl	55.04	55.01	55.30	55.12	42.04	35.40
Br		0.13	.16	.18	.05	.03
SO_4	7.68	8.00	7.72	7.47	23.99	30.98
CO_3	0.41*	0.14	0.19	0.46	0.37	0.85
Na	30.62	30.47	30.51	30.46	24.70	22.62
K	1.10	0.96	1.12	1.16	0.54	0.54
Rb		0.04			0.02	0.02
Ca	1.15	1.67	1.19	1.41	2.29	4.02
Mg	3.69	3.53	3.81	3.74	5.97	5.50
Fe, SiO_2, PO_4		0.05		0.03		0.04
Sr, Br, H_3BO_3	0.31					
	100	100	100	100	100	100
Salinity, ‰	35	7.21	38.36/41.15	18.2/22.2	12.94	10.84

* As HCO_3^-

principal tributary in salt content (Table 2). The data presented in Tables 1, 2, and 3 are at best close approximations. Further information on the salt content of various seas and inland waters may be obtained from Clarke (1924) and from treatises on geochemistry (*e.g.*, Rankama and Sahama, 1950).

The salt content of sea water modifies its physical properties, some of which are of considerable ecological significance, comparable to the well-known effect of the temperature of maximum density on the character of fresh-water lakes. The temperature of maximum density of water of 0 salinity is 4°C, while at 35.5 ‰ it is lowered to −3.8°C. The freezing temperature of water declines less rapidly with increased salinity, and at 35.5 ‰ this value is about −1.96°C (Fig. 1). This is the initial freezing point at which a few ice crystals appear. The intersection of these curves at 24.695 ‰ and −1.332°C is considered an important characteristic of natural waters by Knipovich (1938), who sets the demarkation between brackish water and ocean water at this point. However, the lower values of these curves are not encountered in nature, and any attempt to set an arbitrary limit to the third decimal is less satisfactory than one based on the biota or other field correlates.

COMPOSITION OF SEA WATER IN THE PAST

The salts in the sea are the result of leaching and land drainage and addition from the magma throughout the ages plus original salt in the primeval oceans. Until recently the oceans were generally considered to have been quite dilute in early stages, becoming progressively more saline with passage of time, with temporary reversal between glacial epochs when the ice-caps melted. Murray (1895) notes that, according to evidence of Precambrian rocks, radiolarians were more abundant then than now. This suggests that early seas were more acid and less saline than today. Schuchert and Dunbar (1937) say ocean salinity must have increased gradually

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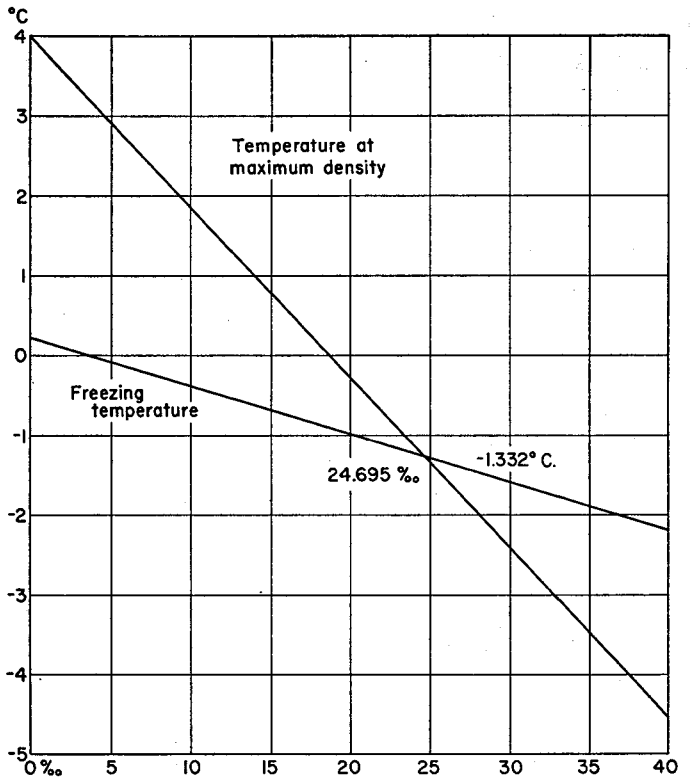

FIGURE 1.—*Physical properties of water at various salt concentrations*
After Knipovich (1938)

throughout geologic time. They emphasize that the older estimates of the rate of erosion and increase of salinity were too high.

Raymond (1939) says

> Various lines of evidence indicate that when the oceans were first fit for organic occupancy they were somewhat acid, and that the first plant and animal skeletons were siliceous or chitinous. Somewhat later, when animals had progressed as far as the stage of the primitive brachiopod and trilobite, the waters had become neutral or slightly alkaline but were still 'fresh'; that is, salts were present in parts per million rather than in parts per thousand. In the course of time calcium bicarbonate has become more abundant in marine waters, and animals have been confronted by an increasingly difficult physiological situation. . . . The Ordovician was the time of the first abundant secretion of carbonate of lime by animals.

In the deeper oceans this may not have happened until the Cretaceous, coincident with a possible increase in the total volume of the ocean in Mesozoic times (Walther, 1911). In any case, more limestone was deposited after Ordovician times, and this can be explained by the supposition that the seas had formerly been comparatively fresh or that the temperatures were lower. Probably the salinity of the oceans, at least during the early stages of life, was somewhat lower, and perhaps more variable near shore.

Conway (1943; 1945) has offered a hypothesis that explains the increased deposi-

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tion of limestone after the Ordovician as a result of the removal of potassium by organic activity. Two main hypotheses based on the assumption of an ocean of constant volume are examined in some detail by Conway (1943). According to one, the initial salinity was zero, and the other assumes a constant salinity but changing inorganic patterns. Because of the great length of time involved and the nature of the reactions, the composition of the ocean at the dawn of the Cambrian is approximately the same according to both hypotheses.

On the other hand the available evidence as to ion tolerances and other requirements suggests that life in the sea, except possibly in the earliest stages, could not exist in a medium much different in its ionic proportions from modern sea water. This implies that the composition of the ocean throughout the fossil record has been fairly stable, and recent work of geochemists and geologists supports this implication. In a recent summary of the problem of the history of sea water, Rubey (1951) concludes that, while there is evidence of some change in the composition of sea water, these changes appear to be of secondary importance.

Rubey's (1951) summary of the available geochemical evidence indicates that the amount of CO_2 in the atmosphere and oceans has remained relatively constant throughout much of geologic time and that there has been an increase in volume of the oceans; it is suggested that the water, CO_2, and most of the anions of marine waters have been derived from the volatile constituents of cooling magmas, accompanied by subtraction of carbonate by sedimentation at about the same rate. A variation in the salinity of the oceans in the magnitude of 20 per cent ± (*i.e.*, 27–42 ‰) would have little effect on the CO_2 balance between the ocean and atmosphere, but, if the CO_2 entering the ocean were to increase suddenly, so as to release for example only one one-hundredth of the CO_2 locked in sedimentary rocks, many marine species would probably be exterminated as a result of the increased acidity. As Rubey points out, relatively minor changes in the concentrations of some of the common ions of high buffer capacity of sea water would be followed by large changes in the pH. While there may have been times in the past when the CO_2 equilibrium has been upset, Rubey's presentation of the data does not suggest salinities much lower than 27 ‰ or a pH less than 7.0 for ancient marine environments.

OSMOSIS

The most significant property of sea water in relation to the ecology and physiology of orgnisms depends on the fact that it is a complex solution of salts. With increase in salinity there is a decrease in the vapor pressure of the solution. The corresponding increase in the differential between the vapor pressure of less saline water and that of more saline water results in a diffusion gradient, if the two solutions are in a closed container. The resulting phenomenon, in which equilibrium between the two solutions is theoretically attained by migration of water molecules from the dilute to the concentrated solution, is known as osmosis. Usually this is explained as the process of diffusion of molecules through a membrane which permits molecules of the solvent but not of the solute to pass, a condition known as perfect semipermeability. This is a special case of osmosis. If the solute is an electrolyte, such as sodium chloride, the differential will be greater than for a solution containing a nonelectrolyte such as sucrose, when molecular densities are equal.

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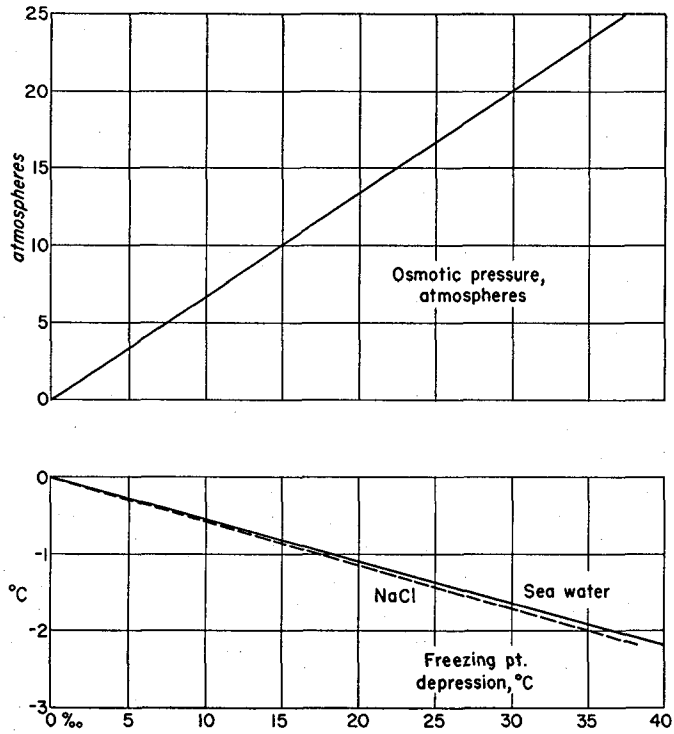

FIGURE 2.—*Osmotic pressure and freezing depression of sea water and NaCl solutions*

The essential action in osmosis is expressed by Fick's law of diffusion—*i.e.*, the rate of diffusion of a substance across a given cross section of a system is proportional to the gradient at that section. Osmosis is usually thought of in terms applying to the more concentrated solution, although the active agent is the water diffusing into a region of *lower concentration of water* in a closed system or through a semipermeable membrane. While osmotic pressure is theoretically expressed in terms of atmospheres of the solution being acted upon, the related colligative property of freezing point lowering (Δf) is more easily determined and is widely used in physiological work (Fig. 2).

Diffusion coefficient is inversely related to molecular size. In general the permeability of external membranes, especially of animals, to nonelectrolytes is so small compared to water and inorganic ions that it can be ignored. Osmotic pressure of blood plasma of vertebrates is approximately 7.6 atmospheres. Such pressure could develop only if the plasma were separated from the pure solvent by a perfectly rigid and semipermeable membrane. These conditions are never fulfilled in the living organism, and the theoretically possible osmotic pressures of internal solutions in organisms do not develop.

In living systems the semipermeable membrane of the theoretical case of osmosis is approximated by the cell or tissue membranes, and the primary problem of life in aquatic media is the maintenance of the optimum concentration of water and

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salts in the internal body fluids through osmoregulation. Some areas of natural membranes may be osmotically inactive, reducing the total cross section available to osmosis, or the membrane may be capable of selecting certain electrolytes and holding back others, and may in some cases be capable of operating against the diffusion gradient. In addition the membranes are not rigid. Furthermore, permeability may vary from time to time in living membranes. Water generally passes through them much more rapidly than do the common salts, and when osmotic control or balance is lost certain organisms and eggs may swell to the point of fatality or bursting in a hypotonic solution. Since the problem of osmoregulation is discussed in detail by Bayliss (1927), Krogh (1939), Höber *et al.* (1945), Prosser *et al.* (1950), Heilbrunn (1952), and others, only some of the more essential aspects, with reference to marine and estuarine problems, are reviewed here.

OSMOREGULATION IN INVERTEBRATES

Aquatic organisms may be roughly classified according to their ability to tolerate salinity changes, or by their ability to maintain their internal fluids at a certain concentration. Such salinity tolerances are not necessarily related to osmoregulatory ability. Many euryhaline organisms have no capacity for maintaining their internal concentrations against external changes, and others may simply be impermeable. Those that do not maintain a given internal concentration are classed as poikilosmotic, and organisms that actively maintain an internal concentration distinct from that of the external medium are homoiosmotic.

Most marine invertebrates have fluids isotonic with the surrounding water and have no osmotic problems as long as they remain in sea water. Such animals, however, are limited to the relatively narrow ranges of oceanic salinities and cannot survive prolonged periods of decreased salinity. Some marine invertebrates function like natural osmometers and absorb water from dilute salinities with a resulting increase of their total volume. They may do so under experimental conditions for several hours before being killed. In this category are found many marine protozoans, invertebrate eggs, and some sipunculids.

When transferred to waters of different salinity the American oyster, *Crassostrea virginica*, adjusts fairly well over a range from 3 to 35 ‰ (the new salinity) in a few hours. In such cases adjustment must be on a cellular level. Similar organisms, osmotically labile insofar as slight environmental changes are concerned, perform little actual work in adjusting themselves to the external environment, and the body fluids passively change with the salinity of the environment.

In some animals, including certain echinoderms and mollusks, the increase in volume is limited by loss of salts through the membranes, thus demonstrating a limited ability to adjust to changes in osmotic pressure. Similar osmotic regulation, of sufficient degree to permit life in a changing environment such as an estuary, but of basically simple character, is also found in such animals as the polychaetes *Nereis diversicolor* and *Neanthes virens* (Beadle, 1931; Ellis, 1937; 1939). Under such conditions there is a steady decline in salt content, which must be harmful if too long maintained, and the control of the internal concentration is only partly effective.

Increased oxygen consumption normally occurs when organisms are subjected to lower salinities, and it is usually stated that osmotic work can be recognized or meas-

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ured by the increase in O_2 consumption (*cf.* Beadle, 1931; Scheer, 1948; Schlieper, 1929). Beadle (1931) attributed the initial increase in respiration to muscular activity in resistance to swelling, and Pieh (1936) believes that increased O_2 consumption in a hypotonic environment may be a result of hydration of body tissues. However, these factors can hardly account for all the increased O_2 consumption in lower salinities for osmoregulation breaks down under anaerobic conditions or upon the addition of 0.001 M cyanide (*cf.* Prosser *et al.*, 1950, p. 15). Both anaesthetized and unanaesthetized *Gammarus* utilize more O_2 in dilute salinities, and crawfish use 30–40 per cent more O_2 in fresh water than in isotonic sea water (Prosser *et al.*, 1950, p. 32); these authors suggest that part of the extra energy may be used for salt and water movements against the gradient and part for maintenance of low permeability in membranes.

There also seems to be some ionic selection in organisms which otherwise show little regulatory ability. Oysters will maintain in their blood a different and inverted ratio of Mg to Ca from that of water of lowered salinity, while nevertheless being isotonic with it (E. J. Lund, personal communication). Similarly certain Crustacea will maintain a higher percentage of K and much lower percentage of Mg than the sea water (Macallum, 1903; 1910; 1926). Bethe (1934) has shown that a crab, *Carcinides maenas*, had a Ca/Mg ratio of 0.94 in artificial sea water after 139 hours. When transferred to artificial sea water lacking calcium the ratio dropped to 0.51 in the same time. The animal lost calcium, but not completely, and evidently the system tried to conserve it. The animal was returned to the first solution, and after 10 days the ratio was 1.4. Several other examples of ionic regulation are listed by Scheer (1948).

One well-studied example of osmoregulation is that of the triclad worm, *Procerodes* (formerly *Gunda*) *ulvae*. This flatworm is found in Devonshire estuaries where there

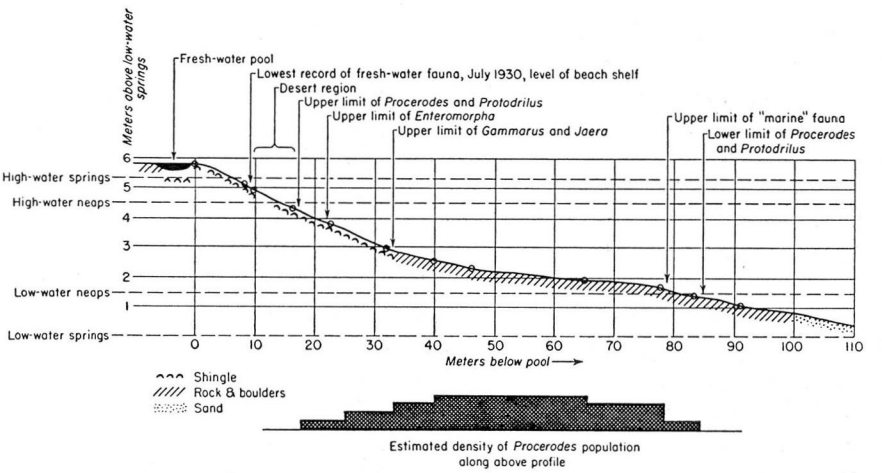

FIGURE 3.—*Distribution of* Procerodes ulvae *along the salinity gradient*
After Pantin (1931a)

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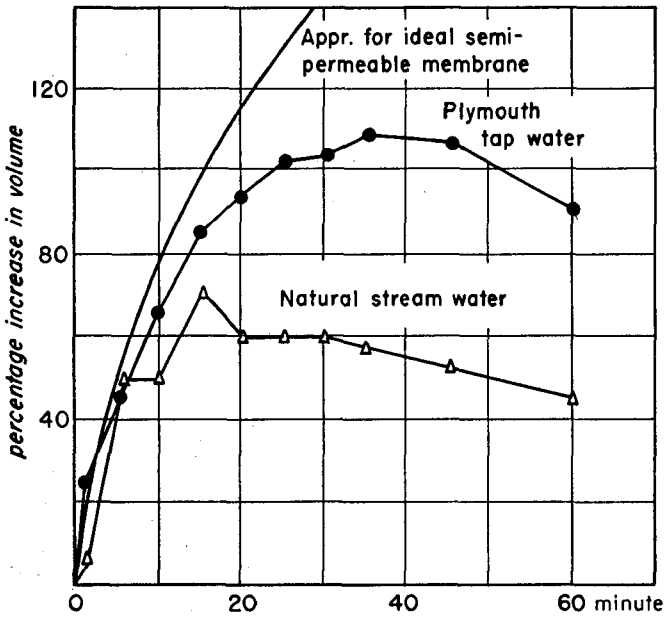

FIGURE 4.—*Comparative volume increase of* Procerodes *in tap and natural stream water*
After Pantin (1931b)

is a daily fluctuation between marine and fresh-water conditions. It occurs most abundantly about half way betweeen high- and low-tide levels (Fig. 3). Experiments demonstrated that, when placed in distilled water or very soft tap water, the worm increased in volume until it burst. In natural stream water, or water to which $CaCl_2$ has been added, the worms increased about 75 per cent in volume and then decreased slightly, and survived for several days (Weil and Pantin, 1931). The data indicated that the membranes of *Procerodes* are only partly permeable, and that calcium inhibits permeability of the membranes (Fig. 4). This is only part of the mechanism; the effective control over volume increase is the storage of excess water in vacuoles in the cells lining the gut (Beadle, 1934).

Some marine invertebrates exhibit evidences of considerable control over the total salt content of their fluids. The shore crab, *Carcinides maenas*, varies its respiration rate with the salinity of the surrounding medium, and it can endure considerable dilution. The shore mussel, *Mytilus edulis*, on the contrary, cannot keep up the molecular concentration and dies probably from the effects of asphyxiation. Duval (1925) found that, when *Carcinides maenas* was transferred from dilute sea water (Δf 1.4°) to a still more dilute solution (Δf 0.63°), the Δf of the blood fell from 1.75° to 1.3° in 26 hours and then remained constant for 15 days. Schlieper (1929; 1930) has shown that the same situation holds for the worm, *Nereis diversicolor*, and that certain marine animals are actively homiosmotic in dilute sea water—*i.e.*, they do work to maintain their body fluids at certain densities by excreting water. Certain of the more specialized Crustacea seem to have quite effective osmoregulation. Panik-

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kar and Viswanathan (1948) have shown that *Metapenaeus monoceros* maintained the NaCl of the blood very close to the same value, while the salinity fluctuated from 6‰ to 30‰.

Marine invertebrates can be divided into four classes on the basis of osmoregulation. The first group is not tolerant of salinity variation. A second group makes little effort to maintain internal salinities at initial levels but can undergo wide changes. Adjustment is apparently at the cellular level. A third group exerts relatively feeble osmotic control and can withstand only moderate salinity variation. A fourth has rather efficient osmotic control and can maintain internal salts, and thus can undergo wide salinity variation. There is, of course, considerable intergradation among the groups.

In many animals adapted to life in estuaries and brackish water, osmoregulation is localized in certain organs or accomplished by specialized development of the excretory or respiratory systems. The flatworm *Gyratrix* has a relatively complex flame-cell excretory apparatus in fresh water. In brackish water it is reduced, and the bladder and ampullae are lacking, while in sea water the nephridial system is lacking (Kromhout, 1943). In *Nereis diversicolor*, for example, it is supposed that the nephridia, which are larger than in related species restricted to oceanic salinities, prevent salt loss by excreting hypotonic urine and thus assist in osmoregulation (Schlieper, 1930). In various Crustacea the size of the antennal or "green glands" is related to the concentration of the external medium. In fresh-water crayfish, which must maintain an internal concentration hypertonic to the environment, the green glands are large, with long nephridial canals providing a comparatively large surface for salt resorption from the urine. In the closely related lobster (*Homarus*) which is restricted to the sea or only slightly diluted salinities, the nephridial canal is short and unspecialized. This is even more strikingly shown by the antennal glands of *Gammarus pulex*, a fresh-water amphipod, and *G. locusta*, an estuarine and marine species (Fig. 5). Marshall and Smith (1930) state that the young of some marine teleosts in brackish water gradually lose the glomerulus of the kidney as they grow older and move out to deeper, saltier water.

The gills of estuarine and fresh-water crabs are reduced in number or size, thus

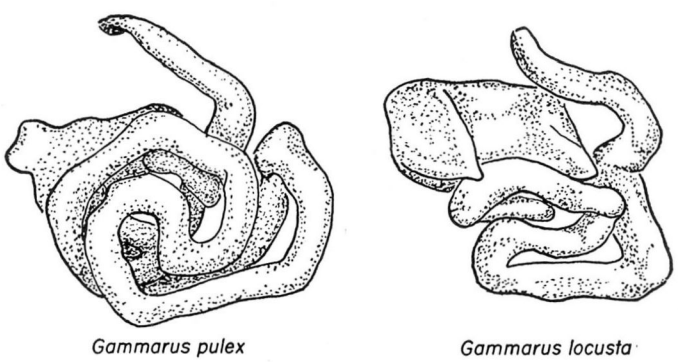

FIGURE 5.—*Comparative sizes of antennal glands of two species of* Gammarus
After Schlieper (1933). Left, *G. pulex* from fresh water; right, *G. locusta*, an estuarine species.

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limiting the total area of membranes through which diffusion of body fluids or external salts may occur (Pearse, 1929a; 1929b).

There are indications that osmoregulatory ability may be influenced by temperature; Broekhuysen (1936) found an inverse correlation between temprature and salinity tolerance in *Carcinides maenas*, and Ehrenbaum (1890) found that *Crangon vulgaris* migrates into brackish waters in spring and returns to oceanic salinities in winter. (*See also* Havinga, 1930; Broekema, 1942.) These are young animals, and essentially the same movement of young takes place in the blue crab (Churchill, 1919), the white shrimp, *Penaeus setiferus* (Viosca, 1920), and the brown shrimp, *P. aztecus* (Burkenroad, 1939). A general migration of fishes and invertebrates on the Texas coast into lower salinities in the spring and their retreat from these waters as the temperature drops in fall and winter, leaving the young of a few species in the bays, has been described in detail by Gunter (1945; 1950). A seasonal variation in the internal salt concentration of certain Crustacea, with the higher values in winter, has been demonstrated by Panikkar (1940). Laboratory experiments show that, when animals are transferred to lower salinities, survival is better when temperatures are higher (Panikkar, 1951). These various observations, when considered in connection with the well-known richness of tropical and subtropical estuaries as compared with cold-temperate estuaries, suggest that facilitation of osmoregulation by higher temperatures may be one reason for the rich estuarine faunas of the tropics.

The differences in the concentration of internal fluids in relation to the external medium, as indicated by the freezing-point depression, have been determined for many animals and may be summarized as follows: In addition to the marine invertebrates, marine elasmobranchs and hagfishes are isotonic, while the bony fishes as a group are hypotonic to sea water. Fresh-water invertebrates, fishes, and amphibians are hypertonic (Table 4). If the data for various freezing-point depressions are plotted, it is observed that a Δf of 0.6°C, roughly the mean of that found in terrestrial mammals and birds, separates most fresh-water and marine organisms (Fig. 6).

Not all adjustments to salinity changes are osmotic. When the salinity drops too low, mollusks close their shells and await a more favorable period. Oysters very often taste salty, while the surrounding water may be practically fresh. Other animals

TABLE 4.—*General relationships between the internal body fluids and the external medium in various groups of aquatic organisms*

Data from Höber (1945)

	Medium		Internal fluid		Pressure gradient compared to medium
	Δf°	Pressure atmospheres	Δf°	Pressure atmospheres	
Certain marine invertebrates	1.9–2.0	19.4–24.0	1.8–2.1	22–24—isotonic	little or none
Marine elasmobranchs	1.9–2.0	19.4–24.0	2.0	22–24—isotonic	little or none
Marine teleosts	1.9–2.0	19.4–24.0	0.8–1.0	9–12—hypotonic	8–12
Fresh-water invertebrates	0.02	1–2	0.1–0.8	1–9—hypertonic	1–8
Fresh-water teleosts	0.02	1–2	0.55	6—hypertonic	ca 5
Fresh-water amphibians	0.02	1–2	0.4	5—hypertonic	ca 4

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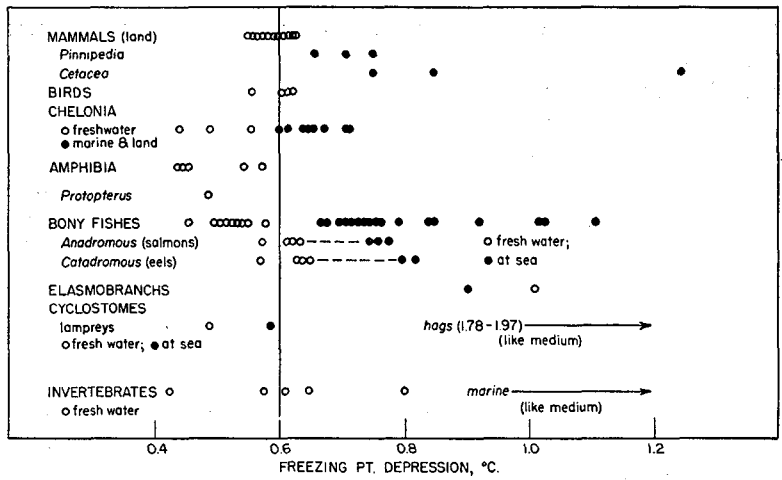

FIGURE 6.—*Freezing-point depression of internal fluids of various organisms*
After Wald (1952)

retreat to the bottom of burrows, and some plug their holes. Existence in a low-salinity environment can continue indefinitely only when short-term or daily changes take place, as with the tide. Thus the animals may feed or become active only at certain times, much as the barnacles between tide marks can become active only when flooded.

Continued low salinities will produce death, although certain organisms such as the oyster can survive fresh water up to 2 weeks, apparently by keeping tightly closed. Nevertheless, extended floods cause mass mortalities in estuarine areas as illustrated by the repeated total destruction of oyster reefs near the lower Mississippi River (*cf.* Gunter, 1949; 1952).

MARINE ALGAE

The problems of osmotic pressures and resistance to osmotic changes in algae have been summarized by Blinks (1951), substantially as follows:

> Some marine algae, *e.g. Valonia* and *Halicystis*, are almost isotonic with sea water. In general osmotic pressure is lower in red algae than in the greens and browns. Some greens may have internal concentrations twice as great as sea water. Such high concentrations would be of advantage in enabling the plant to maintain cell turgor in a hypertonic medium, but would be disadvantageous to a plant in a dilute environment. Some plants are remarkably tolerant of salinity variations, and most algae can stand a range from 0.5 to 1.5 sea water for a matter of hours or even days. Some of the algae living high in the intertidal zone show even greater tolerance for extremes, up to three times sea water for 24 hours, but those lower down, near mean tide level, only withstand up to 2 times sea water. Deeper water algae are even less tolerant. Algae tolerate slow changes more readily than rapid changes, but some estuarine species withstand rapid changes without plasmolytic response. This is also the case for algae living in high salinities—*e.g., Dunaliella* in brine ponds.

IONIC BALANCES

Each of the component ions in the complex mixture called sea water has specific properties. Although the total concentration of salts in an organism may be isotonic

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with the external medium, as in the marine invertebrates generally, the actual proportions of ions may be different, particularly in the tissues. According to Cole (1940), the pH of fluids of worms, clams, and echinoderms which are isotonic with sea water is more or less lower than that of sea water. Prosser *et al.* (1950) present data on the concentrations of the most common ions in the body fluids, in reference to that of the external medium, for a number of marine and fresh-water animals. Such concentrations may vary seasonally, or with sex or age, in a given animal, and ratios may change under experimental conditions. As is to be expected, concentrations in such marine invertebrates as ascidians and echinoderms may vary with the time of collection and the state of the tide (Valente and Bruno, 1951).

As pointed out in the case of *Procerodes*, calcium is important to aquatic organisms in inhibiting the permeability of membranes. In fresh waters deficient in calcium, trout eggs are very sensitive to handling and easily lose their impermeability to water, which causes them to swell and burst. In all animals loss of blood calcium is followed by loss of tonus and reflex activity. There is some indication that marine fishes which invade fresh water do so much more often where the waters are high in calcium (Breder, 1933; 1934); many marine fishes are found in Florida streams, which are rich in calcium, and one species of marine pipefish is distributed over most of the peninsula (Gunter, 1942). It has been suggested that culture of *Chanos chanos*, a euryhaline fish widely used in fish ponds in southeast Asia, may be enhanced by adding calcium to the ponds to increase tolerance of the fish to low salinities (Panikkar, 1951). On the other hand, Odum (1953) has presented evidence that the distribution of marine fishes on the Florida peninsula is related to the concentration of chloride in the water rather than of calcium.

In general, ions cross natural membranes in a series which corresponds to their mobilities: $K^+ > Na^+ > Ca^{++} > Mg^{++} >$; $Cl^- > SO_4^=$, but diffusion rates alone do not account for the differences found within the fluids of organisms (Prosser *et al.*, 1950, p. 91). By varying the proportion of salts in sea water in an experiment with a shark, *Squalus suckleyi*, Quigley (1928) found that the relative increase of NaCl, KCl, or CaCl was not very toxic, but that "the most toxic solution was sea water with added salts."

Young (1938) found better survival in solutions of mixed salts than in those containing only one salt. There are many other examples in physiological literature. In general, NaCl or KCl acting alone are somewhat poisonous, and these effects are neutralized by calcium, thus giving rise to the terms ionic antagonism and ionic balance. Similar salt antagonism is observed in marine plants; *Laminaria* tissue may be killed in pure NaCl or $CaCl_2$ solutions although it can be maintained in a mixture of 97.5 NaCl and 2.5 $CaCl_2$ (Blinks, 1951). The initial work on ionic balance and antagonism was done by Sidney Ringer 72 years ago and led to discovery of the now famous Ringer's solution. Electrolytic dissociation was unknown then, but "it was clearly recognized by Ringer that the effects of calcium and potassium salts were due to the calcium and potassium components of the salts added" (Bayliss, 1927, p. 208).

The active secretion or retention of ions against gradients has been demonstrated for many marine animals, although some may finally prove to be examples of complex

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equilibrium phenomena which are essentially mechanical in nature. (*See* Prosser *et al.*, 1950, Chapter 3, for a summary.) In general, in passing from simple to more complex animals, the greater becomes the relative excess of potassium and the relative deficiency of magnesium.

Bunge (1902, p. 102) made the suggestion that the high NaCl content of blood of land vertebrates is an inheritance from marine ancestors. The similarity in ionic ratios between body fluids of animals and of sea water independently inspired Macallum's (1903; 1904; 1910; 1926) famous theory that the present composition of the blood or internal fluid in a given animal is related to the concentration in the sea at the time the circulatory system of its ancestral type was closed off from direct communication with the external medium. He based his theory on determination of ionic ratios for three marine invertebrates—*Aurellia*, *Limulus* and *Homarus*—and several vertebrates—four fishes, an amphibian, and two mammals. Rogers (1927) has succintly presented the general theory as follows:

> The first living organisms had the sea for their environment. Every cell doubtless came into contact with this fluid which was at the same time the source of its food and oxygen supply. As cells began to be associated in smaller or larger masses, channels were left between them through which the water of the sea might find passage. Animals a little further along the scale of development shut off their body cavities, vascular and otherwise, from direct communication with the sea, but did not succeed in freeing the cells from the necessity of getting their food and oxygen supplies from a solution. The fluid shut within the animal body furnished the immediate environment of the cells; it took the place of the sea in the environment of the organism. It has been seen that the fluid becomes more and more complex as one passes in review from lower to higher forms. And while the internal fluid sea, bathing the individual cells, has become more complex and able to play a greater variety of functions in the life of organisms, there are certain features in which it harks back to the primitive conditions which must have existed millions of years ago.

On the other hand, the idea that blood represents a form of ancient sea water, implying that its ionic proportions are fixed in genetic combinations inherited for millions of years, is not received enthusiastically by some physiologists. Baldwin (1937) points out that Macallum failed to consider the maintenance of ionic balance as a dynamic process, and the fact that the blood concentrations of various animals is so similar indicates that the environment itself has not greatly changed. Wald (1952) observes that Macallum did not have any data for fresh-water invertebrates. The internal concentrations and ionic proportions of body fluids of fresh-water invertebrates are nearer to those of mammals than to marine invertebrates; the Mg/Ca ratio in particular is about the same as that found in vertebrates. On the basis of Macallum's theory, if it can be carried that far, this would mean that fresh-water invertebrates and ancestral mammals left the sea about the same time; Wald prefers to consider this an example of "convergent evolution on a molecular level."

On systematic grounds alone, it is obvious that various groups of fresh-water invertebrates have migrated from the sea at different times. For example, decapod shrimp of the family Atyidae appear to have left the sea in Jurassic times, whereas the superficially similar Palaemonidae are in the process of active emigration (Ortmann, 1902). Experiments by Edmonson (1929) on atyids and by Panikkar (1941) on palaemonids, indicating that the atyids have very slight capacity for resisting salinity increases as compared with the palaemonids, provide corroborative physiological information for Ortmann's contention, which was based principally upon morphology and geographical distribution. Since low osmotic pressure is an advantage in fresh water, Wald's (1952) suggestion that fresh-water invertebrates "have adopted repeatedly as low a fluid osmotic pressure as is compatible with the intrinsic needs of animal tissues" is reasonable.

Macallum's hypothesis, especially as related to the origin of mammalian blood plasma, has also been roughly handled by some geochemists. Such "superficial evolutionism", as Conway (1943) calls it, can be supported only by the most unlikely hypothesis of the ocean's history, and, by whatever reasonable hypothesis chosen, the sodium content of the Cambrian-Ordovician seas must have been three times that of mammalian plasma. "In what manner then could a proposed value corresponding to mammalian plasma then be still defended? With such a view it will be necessary to reject completely the origin of the oceanic halogen from the original atmosphere, since the figure to be accounted

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for is already so low that any appreciable fraction deriving from an acid neutralization would be untenable at the outset. It will be necessary then to find some explanation as to why the ocean contained only 280 Mg/litre salinity up to four-fifths of its age and received the remaining 854 in the last fifth. . . . What evidence is there then for believing that the mean weathering over four-fifths of the oceanic age was only 6 per cent of that in the last fifth of this age? This is a problem that may be left to those holding like Macallum that the inorganic content of vertebrate or mammalian plasma repeats that of the early Palaeozoic seas, but it may be said here that the evidence from the sedimentary strata would appear to be decisively against such a view" (Conway, 1943, p. 207). According to Hutchinson (1944), Conway has disposed "once and for all of the hypothesis that the body fluids of homoiosmotic animals represent samples of sea water collected at the time when their body walls became impermeable to electrolytes." However, these criticisms were unintentionally answered by Rubey's (1951, p. 1114) conclusion "that several lines of evidence seem to indicate some actual changes in the composition of sea water and atmosphere with time. Yet the more closely one examines the evidence, the more these changes appear to be merely second-order differences"; and the theory of the derivation of oceanic halogens from the primitive atmosphere seems to be pretty well rejected.

Furthermore, land animals possess blood salts quite different from their environment and maintain them under difficulty, while any great variation of the salt components leads to death. Thus the composition of the internal fluids seem to be rather rigidly fixed, whether by genes or not, and it is doubtful if the fundamentals of vertebrate physiology have changed throughout the ages. And, "whatever may be the final decision on the question, the fact remains that sea water, diluted to the same osmotic pressure as the blood, is a very effective physiological solution, although the amount of magnesium is unnecessarily great" (Bayliss, 1927, p. 210). Furthermore, Macallum's theory fits into the general course of organic evolution, as any theory of the origin of the blood must. The ancestors of land vertebrates left the seas, possibly as far back as the Cambrian, and there has been no lack of time for changes to develop both in the blood and the sea. Taking these matters into consideration, the present authors are considerably more impressed (*cf.* Pearse, 1950) with the similarity between vertebrate blood and sea water, than with the differences pointed out and the criticisms of Macallum's theory noted above.

OSMOREGULATION IN VERTEBRATES

The marine elasmobranchs are the only fishes and indeed the only vertebrates, except the osmotically labile hagfishes, having blood relatively isotonic with sea water. It may in fact be hypertonic to sea water. The actual salt content of their blood is not greatly different from that of the bony fishes. They make up the difference by maintaining a high content of urea in the blood, which raises the osmotic pressure to approximately that of sea water. When entering fresh water the euryhaline elasmobranchs lower urea content of the blood and thus drop the internal osmotic pressure rather quickly. The marine teleosts are the only fishes with blood hypotonic to the medium.

In general, most fishes are stenohaline, and the fresh water and marine teleosts die very quickly when transferred to the other medium, but many of them can acclimatize to slow changes. Herre (1929) has cited the instance of an American cyprinodontid fish introduced into the Philippines, which became accustomed to living in salt ponds in which the salinity rose to 87 ‰. On the Texas coast another cyprinodontid, *Cyprinodon variegatus*, has been found active and alive in shore ponds at specific gravities equivalent to sea water of 144 ‰ (Simpson, unpublished data). Many experiments that demonstrate the phenomenon of acclimatization to slow increases of salinity have been performed under laboratory conditions. Some fresh-water fishes, which do not naturally enter salt water, can become accustomed to concentrations of full sea water (Myers, 1949). Rawson (1946) introduced whitefish and pickerel into a lake

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that had a salinity nearly half that of the ocean, and both species thrived. Similarly, stenohaline marine fishes can be slowly introduced to considerable dilutions of sea water, but they will not become accustomed to fresh water. Most observers are agreed that death of marine organisms subjected to low salinities seems to result from inability to take up sufficient oxygen.

Black (1951) has given an excellent summary of the chief features of osmoregulation in fishes. Certain teleost fishes may undergo wide variations of salinity in nature. Loeb and Wasteneys (1915) showed that over wide changes of salinity the blood of *Fundulus* remained relatively constant. The milk fish, *Chanos chanos*, carries on active chloride regulation and maintains an internal concentration of chloride within range of 0.5 per cent although the external medium ranges from nearly fresh water to about 50‰ (Panikkar, 1951). The catadromous eel, *Anguilla*, has a Δf of the blood of 0.56 to 0.63 in fresh water and 0.64 to 0.74 in sea water. The marine teleosts cannot absorb external water against a concentration gradient, and they must perforce drink sea water for their bodily needs, chiefly the kidney function. The excess salt is then excreted through the gills, against a concentration gradient (Keys, 1931). Smith (1929) has shown that urea and various nitrogenous wastes also pass through the gills in fresh-water fishes.

Fresh-water fishes have a different problem of osmoregulation. Since they are hypertonic to the medium they absorb water, and the kidney flow is very copious. They must excrete water continuously. The same holds for marine animals in estuarine areas. In this connection we should again mention the observation of Marshall and Smith (1930) that the young of some marine teleosts in brackish water gradually lose the glomerulus of the kidney as they grow older and move out to deeper saltier water. The adults may be aglomerular. Conversely, the pipefishes (Syngnathidae) have aglomerular kidneys, but several species invade fresh water. At this point it should be noted that young marine fishes have a greater predilection for entering fresh water than the adults (Gunter, 1947b); possibly the young are physiologically better capable of coping with the more dilute medium.

The skin and even the mucus surrounding a fish are relatively impervious to the inflow of water and salts. Injury to the skin of marine fishes is often followed by rapid intake of water or salts and osmoregulatory difficulties (Grafflin, 1931). The fresh-water fish becomes waterlogged, while the salt-water fish loses water and in effect dries up. To some extent the fresh-water fish must work physiologically so as not to get an oversupply of water, while the marine fish must struggle to maintain its water. The transition from one physiological state to the other takes place at the salinity osmotically equal to that of fish blood, which is approximately 14–15‰. Salt-water fish subjected to fresh water lose salts, take up water, and decrease oxygen intake initially, and those which die seem to do so through anoxemia (Keys, 1931b). Those that survive finally cease losing salts and re-establish the former respiratory rate. Keys gave evidence that killifish with larger gill surface tended to survive and that this ability also coincided somewhat with higher metabolic rate, which apparently allows for rapid adjustment.

According to Keys (1933) euryhaline fishes, such as the eel, *Anguilla*, act like marine teleosts when in sea water—that is, they drink sea water and excrete salt

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through the gills—and act like fresh-water fishes when in fresh water by absorbing water and excreting it through the kidneys. Stenohaline fishes probably lack the salt-excreting cells or the necessary functional ability of the kidney.

Koch and Heuts (1943) found that two subspecies of the European stickleback, *Gasterosteus aculeatus gymnurus* and *G. a. trachurus*, were normally quite euryhaline and could maintain blood Cl at a constant level in water ranging from 0 to 3.7 per cent NaCl, and even higher (4.6%) in *trachurus*. However, during sexual development the osmoregulatory power was greatly diminished, and the fishes would not survive in 2.6 per cent NaCl. Such osmoregulatory breakdowns may be related to the migrations of fishes and other animals, during the breeding season, into restricted salinity ranges. Possibly, the wide-ranging adults become restricted during the breeding season to the narrower environmental limits suitable to eggs and larvae, as a prelude to spawning.

THE ORIGIN OF VERTEBRATES

Vertebrate remains are apparently absent from Cambrian rocks, and those vertebratelike remains (*i.e.*, the ostracoderms) found in Ordovician strata are said to occur in fresh-water deposits. Based on a detailed analysis of the character of the fossil record in North America, Romer and Grove (1935) concluded that the earliest vertebrates were inhabitants of fresh waters, that the placoderms originated in fresh water, although the arthrodires moved into the sea in the lower Devonian, and that the sharks invaded the sea in early Devonian times. According to this study the more specialized fishes also originated in fresh water, and most of them remained in that medium throughout Devonian times. This theory of vertebrate origin was previously advanced by Chamberlin, Barrell, and other geologists. The literature is reviewed by Romer and Grove. Physiological evidence for the fresh-water origin of vertebrates has been adduced by Smith (1932) from his studies of water balance and kidney function of fishes. Since no fishes and indeed no vertebrates except mammals can secrete urine more concentrated than blood, he has constructed a syllogism as follows: the vertebrate kidney from the elasmobranchs up is functionally sufficient to maintain water equilibrium in fresh water, but deficient because of the absence of hypertonic excretion to maintain this equilibrium in salt water; therefore the kidney must have acquired its functional nature in a medium more dilute than the blood. The elasmobranchs are similar to the bony fishes in composition of the blood and mode of osmotic regulation when both are in fresh water. Therefore, they must have had a common phyletic history in a relatively dilute medium at some remote period.

The theory of the fresh water origin of fishes is accepted by a number of biologists.

> Summing up the case for fishes it seems that we can say that they all originated in fresh water. The presence of a water excreting device in the form of a glomerulus is evidence of fresh water ancestry. The glomerulus degenerated in those teleosts which went to sea, in response to the necessity for conserving water as much as possible, but it persisted in the elasmobranchs, for these forms found in physiological uremia an alternative method of protecting themselves against the loss of water (Baldwin, 1937).

The senior author accepted the theory in all of his writings (*cf.* Pearse, 1950), while the junior author has indicated certain reservations. He pointed out (Gunter, 1938; 1942) that many marine fishes are euryhaline and a fossil in fresh-water deposits is not complete proof of fresh-water origin, and additionally that a greater proportion of euryhaline fishes of today are of more primitive types suggesting that possibly euryhalinity was more prevalent among ancient fishes than it is today. Certain points may be added here.

As Smith recognizes, little is definitely known of the salinity of the early seas, and, regardless of what the general salinity may have been, the vertebrates may have originated in shallow seas at lower salinities near shore. The shallow seas seem to be optimal for marine life today, and most marine animals, both past and present, are adapted to this environment. Osmoregulatory and re-

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spiratory problems are at a minimum for fishes at isotonic salinities, and it appears most likely that the protovertebrate developed in a dilute sea. It is possible that the primitive fishes may have been similar to the modern hagfishes in having blood isotonic with the medium and varying with it. In that case, the typical fish kidney developed later when the blood system "closed" and dilute sea water or fresh water was invaded. Sea water of about 14‰ is isotonic with fresh-water fish blood, and any lower salinity would have been hypotonic, thus satisfying conditions for origin of the kidney. Smith's work gives strong indications that present-day fishes, including the elasmobranchs, had a long phylogenetic history in waters of low salinity, but not necessarily fresh water, and that seems to be as far as the idea can be safely carried. Allee *et al.* (1949), p. 171) also view the fresh-water origin theory with some reservation and maintain that "evidence from optimum salinity. . . points to the sea as the ancestral home of fishes."

SALINITY, DISTRIBUTION, AND EMIGRATION FROM THE SEA

Some organisms near shore in areas of varying salinity are distributed in rather definite zones or communities according to isohaline lines (Yamamoto, 1951; Ladd, 1951). In general the relations between salinity and organisms are evidenced by patterns of distribution, and probably the most important relation of organisms to salinity, so far as the marine ecologist and paleontologist are concerned, is their ability to exist in various salinities. This applied to species, families, and other groups. It is impossible to list them all here, and precise information will have to be derived from Ekman (1935) and works of specialists in the various fields. Pearse (1950) summarized the literature on salinity tolerance of many species, including field studies by Annandale (1922), Percival (1929), Redeke (1922), and Schlienz (1923).

Completely euryhaline organisms, those which can move from fresh water to full sea water or the reverse, are relatively uncommon. Most of them are animals, although some neritic diatoms and estuarine algae can undergo considerable salinity change. Most aquatic species are stenohaline, and only a minority can tolerate a wide salinity range. There is no sharp distinction between the two groups, and any definition is arbitrary because organisms exhibit gradual transitions from one type to the other. The most numerous euryhaline organisms are fishes. Gunter (1942) compiled a list of 143 species including elasmobranchs and cyclostomes from continental North America. A higher percentage of more primitive fishes were euryhaline, but this appears not to hold in the tropics, and marine species were predominant in the ratio of about 9 to 1. Completely euryhaline invertebrates are rare. A few marine Crustacea, including the American blue crab, *Callinectes sapidus*, invade fresh water. It is stated that *Artemia*, the brine shrimp, is an extreme example of euryhalinity, since it can live in fresh water and in salinities of over 200‰ (Allee *et al.*, 1949, p. 171), but this may be a conclusion based on faulty systematics, since there is evidence of at least two, perhaps three, species or physiological races of brine shrimp (Kuenen, 1939), and the form found in fresh water may be genetically separate from the saliniphilous forms.

A better example of euryhalinity may be found in the calanoid copepod *Pseudodiaptomus euryhalinus*, which not only tolerates a salinity range from 1.8 to 68.4‰, without noticeable structural variations, but reproduces successfully at these extremes (Johnson, 1939).

Of more general significance than extreme examples of salinity tolerance is the indication that the populations of lagoons of metahaline salinity are recruited from

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those of meso- or polyhaline bays rather than directly from the ocean itself. This suggests that, once an organism is capable of adjusting itself to salinity changes, its range of tolerance may exceed the usual changes in the immediate environment so that salinity is not the governing factor, and the organism is able to meet unusual conditions and colonize extreme environments.

Salinity limitations on distribution may be exercised on early stages of life histories in accordance with the general law, emphasized by Shelford (1915), that limiting effects of physical factors are often exerted on the reproductive stages or the young. Some estuarine animals, such as the blue crab, *Callinectes sapidus*, and fiddler crabs (*e. g., Uca minax*) can live in or near water that is essentially fresh, but must return to the ocean to spawn, since their eggs cannot develop in fresh water. Sandoz and Rogers (1944) have shown that the eggs of the blue crab, *Callinectes sapidus*, will hatch only at a restricted, relatively high salinity range. The annual migrations of the tropical land crabs (*Coenobita clypeatus*) to spawn in the sea are well known. The adults may live even in deserts (Pearse, 1932). The eggs of the large burrowing land crab, *Cardisoma armatum*, die in fresh water although a few develop as far as hatching, but some will hatch into apparently normal larvae in a mixture of half fresh and half sea water (Cannon, 1923).

The most essential requirement for permanent establishment in fresh or slightly saline waters is the accumulation of food and salts in the egg so that the animal in its most critical stage is relatively independent of the medium; as long as the egg is small and dependent upon the external medium for the salts necessary for development, the adult must return to the sea to deposit it. Thus we find that the eggs of most fresh-water invertebrates are comparatively large, with relatively impermeable shells, or that development is direct (as in many fresh-water decapods), or reproduction is achieved in somewhat specialized ways which are not characteristic of the marine representatives of the group, such as the gemmules of fresh-water sponges, or the statoblasts of fresh-water Bryozoa. There are, however, exceptions. Fresh-water copepods, cladocerans and phyllopods, have small eggs and go through a series of larval stages like those of marine Crustacea.

The young of many animals, usually thought of as marine, require areas of low salinity for nursery grounds. The distribution and abundance of the blue crab and of the commercial shrimp (*Penaeus setiferus*) on the South Atlantic and Gulf coasts are dependent on the presence of estuarine areas. The shrimp spawn in oceanic salinities; the early stages apparently require oceanic water, but the older larvae must reach bay waters or perish. The young shrimp grow up in the low-salinity bays and return to the sea. Pearson (1929) and Gunter (1945, 1950) have shown that roughly this cycle of spawning, growth, and movement in relation to salinity holds true for many important fishes and invertebrates on the Gulf Coast. In general marine animals on such estuarine coasts move offshore as they grow older.

The problem of evolutionary emigration of organisms from the sea into estuaries and fresh water has been reviewed by Pearse (1950), who brought together many details from a large literature. Among the invertebrate groups restricted to the sea are the echinoderms, brachiopods, siphonophores, radiolarians, and corals. The sponges are represented in fresh water by a single family, the coelenterates are repre-

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sented by a few hydroids and anemones in brackish water and two hydroid medusa (*Craspedacusta* and *Limnocnida*) in fresh water, and the free-living Turbellaria are far less numerous in fresh water than in the sea. Among the most characteristic of estuarine and fresh-water invertebrates, at least in warmer latitudes, are the decapod Crustacea. Some crabs are terrestrial as adults. Various mollusks are also common in estuaries, and there are many fresh-water species.

Once the transition from the sea to fresh water has been achieved, it is seldom reversed. Fresh-water invertebrates in particular are stenohaline and do not survive exposure to sea water, and a few euryhaline fresh-water invertebrates are known. In gaining ability to retain salts in hypotonic media they have apparently lost ability to adjust to changes (Adolph, 1925). Myers (1949) has pointed out that fresh-water fishes are very useful in studies of zoogeography because they can be divided into six groups on the basis of salt tolerance. In brief they are called Primary (strictly intolerant), secondary (confined to fresh water, but more salt tolerant—*e.g.*, Lepisosteidae), Vicarious (fresh-water representatives of primarily marine groups), Complementary (fresh-water forms belonging to marine groups, which become dominant only in the absence of the first three, as in some islands), Diadromous (those which enter or leave at a definite state of the life cycle), and Sporadic (those which enter or leave sporadically "and not as a part of a true migration").

Among the few fresh-water invertebrates known to invade salt waters may be mentioned the river shrimps (*Macrobrachium*), which may be found carrying eggs in salinities up to 12‰ (Gunter, 1937) but these, it should be mentioned, are members of the Palaemonidae, and most of the larval stages are suppressed in the egg so that the young are protected from severe osmotic changes. A few insects have managed to colonize the sea, the best known of which are the marine water striders of the genus *Halobates*, related to the familiar water striders of ponds and streams. Most of these are air breathers and as such are not subjected to the full effect of salt water. A few midges and small beetles have colonized the intertidal, but the most conspicuous insect invasion has been of brackish waters. Various Diptera, especially, mosquitoes, are common inhabitants of brackish waters. Some mosquito larvae can tolerate very high salinities, up to 88‰ (King and del Rosario, 1935), and one species, *Aedes mariae*, can live in a range from nearly fresh water to a concentration four times that of sea water; salinity in this case is apparently not the limiting factor, but turbulence, preventing the deposition of eggs and the breathing of the larvae, may be (Margalef, 1949). Many dragon-fly nymphs are found in brackish waters; of 33 species of nymphs studied in the Mississippi Delta and adjacent marshes, 19 were restricted to fresh water, 18 were found in brackish water (0.5 to 20‰), and 1 (*Erythrodiplax berenice*) occurred in salinities from 20 to 50‰ (Wright, 1943). In general, more-specialized insects appear to endure high salinities more readily than primitive types (Buxton, 1926).

The pattern of distribution of species indicates that the comparatively highly saline waters of the sea, or at least of the shallow sea, are optimum. There is a progressive weeding out of stenohaline marine organisms as the sea water declines in salinity (Hesse *et al.*, 1951), and there is little replacement by species from fresh water (Brandt, 1897; Percival, 1929; Pearse, 1936; Gunter, 1945; 1950), and the life

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of estuaries, even at very low salinities, is predominantly marine. While the inhabitants of bay waters can withstand salinity increases, many of them cannot withstand decreases below a certain concentration, and as the salinity decreases the number of species declines. For instance, out of 112 fishes commonly caught on the Texas Coast, Gunter (1945) took 109 species at salinities above 30 ‰, 73 at salinities of 20 ‰ and less, and 39 at salinities below 5 ‰. Ekman (1953, p. 119), has recorded similar decreases in numbers of species for several groups of invertebrates along the falling salinity gradient in the Baltic Sea, and Segerstråle (Chapter 24) has given an even more extensive list. This decline also occurs in salinities in excess of sea water, as in the coastal lagoons of southern Texas and northern Mexico. In short, the number of species falls as the salinity varies from the optimum, which is full sea water. The decrease of species along a falling salinity gradient can be used by paleontologists to determine the direction of ancient salinity gradients (Gunter, 1947a). By utilizing knowledge of the salinity limits of various invertebrates Ekman (1935) has shown that salinity of the Baltic Sea was formerly about 5 ‰ higher than it is today (Chapter 24).

In more stable brackish waters, such as the inner Baltic, there is a stronger element of the fauna derived from fresh waters than is encountered in the fluctuating environment of estuaries as indicated by Remane's (1950) examination of the limnic element of the Baltic. At the other end of the Baltic, Pettersson (1912) has shown that fluctuations of the herring fisheries probably depend on the fact that the fish enter the area only when the salinity is above 32 ‰.

> It seems reasonable to conclude that salinity does not ordinarily function as a limiting factor for animal populations. . . . It can be argued that there is a greater abundance of species and individuals of marine organisms in coastal regions because of the lower salinity existing there. There is a dangerous, and possibly specious, argument *a priori*, however, since the coastal waters may be more favorable in other ways also: e.g., greater food supply. As seems true for pH, it is easy to reach the *ad hoc* conclusion that salinity is an effective factor, but such a conclusion is hard to prove without recourse to experimentation. (Allee *et al.*, 1949, p. 341).

The basis for this statement is not clear. In the first place marine species are not most abundant in coastal waters at low salinities. They are most abundant in coastal waters in full sea water (Gunter 1945; 1950; Yonge, 1949), and in all coastal areas of lower salinity the numbers of species are correspondingly reduced. It is admittedly difficult to differentiate all the factors that determine the presence of organisms within a salinity range. Food or other ecological factors, such as the overpowering effect of temperature, may prevent full extension of organisms into salinity ranges they can tolerate. Elton (1935) has given examples of apparent limitation of *Eurytemora lacinulata* by low salinity which turned out to be really species competition. Gunter (1945) commented on the cyprinodontid fishes which are absent from the Gulf apparently because of lack of cover, but are found in the Laguna Madre at 84 ‰. In the normal bay and sea, with no near-by hypersaline areas, such a distribution would appear to be caused by salinity. Such observations emphasize the complexity and the difficulty of ecology, however, rather than disproving effectiveness of salinity as a limiting factor. Marine ecologists who traverse salinity gradients and note the changes in the flora and fauna are impressed by the correspondence between species distribution and salinity. Field studies of distribution show that the number of species decline as salinity falls, and the weight of physiological evidence strongly indicates

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that salinity is definitely a limiting factor for marine organisms, especially when it varies downward.

In this connection the views expressed by Mars (1950) deserve notice. He pointed out that experiments on salinity tolerance are difficult to carry out properly (and we might add also difficult to interpret) and that field observations yield dependable results, if certain pitfalls are avoided. He added that experimental studies are complementary. Certain difficulties in the application of experimental results to the environmental situation are mentioned by Wells and Ledingham (1940) and Bassindale (1943). In brief, laboratory studies on salinity tolerance do not give complete answers when the results are applied to environmental situations and field observations and experimentation are complementary.

SALINITY AS RELATED TO STRUCTURE AND SIZE

There are various ways in which the excretory and respiratory systems can be modified in relation to the salinity of the environment, such as the enlarged excretory glands of fresh-water Crustacea mentioned above, and the reduced number of gills in crabs in brackish water (Pearse, 1929a; 1929b). One of the most famous cases of structural modification in relation to salinity is that of the brine shrimp, *Artemia* (Kuenen, 1939, and earlier literature), which has recognizable forms, once classified as widely apart as different genera, according to the concentration of the brine. Another case is found in mosquito larvae, in which the anal papillae, which apparently function in ion exchange, are reduced in size as the concentration of the environment increases (Wigglesworth, 1938).

An interesting structural variation was observed by Andrews (1940) in the snail, *Neritina virginea*, involving the brilliance of the shells. In higher salinities he found that the pigment deposition in the shell was less, so that reflection, or brilliance, is greater. The possibility that this may be related to insolation cannot be ruled out, although a relationship between shell pigment and salinity has been reported for *Littorina* with brighter colors in the lower salinities (Andrews, 1940), whereas in *Cardium* the coloration is increased with salinity (Bateson, 1889). Fishes from the hypersaline Laguna Madre of Texas and northern Mexico are notably paler than their congeners from the less salty waters of the bays and the Gulf of Mexico.

Dwarfs of *Neritina* have been found at the lowest and highest salinities of the animal's range (Metcalf, 1930; Andrews, 1940). Ladd (1951) found the largest individuals of the clam, *Rangia cuneata*, in low salinities, which appear to be the optimum for this species, as individuals taken in saltier parts of the bay were smaller. Milne (1940) said the sessile organisms on buoys become less numerous and smaller toward the lower end of their salinity range. He mentioned *Laminaria* and *Mytilus* particularly. Boettger (1950) found smaller mollusks at lower salinities.

According to Newcombe and Kessler (1936) the shell growth of *Mya* is heavier in higher salinities. The reverse is true, however, of the oyster on the Gulf Coast. In the bays oyster shells are thick and often riddled with various shell-boring associates—the clam, *Martesia*, the sponge, *Clione*, the polychaete worm, *Polydora websteri*; in the Gulf, on artificial structures 5 miles offshore, oyster shells are thin and unperforated. On the other hand the oysters in lower salinities, where shell borers

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TABLE 5.—*Maximum sizes of certain mollusks in various parts of the Baltic Sea*
After Brandt (1897)

Species	Bay of Kiel S15 ‰	Finnish Gulf S 5-2‰	Gulf of Bothnia 5-2 S‰
Mytilus edulis	110 mm	27 mm	21 mm
Mya arenaria	100	55–70	36.5
Cardium edule	44	22	18
Tellina baltica	23	17	15

are also absent, are thin-shelled. In this case variation in shell thickness seems not to be necessarily related to salinity. Heavier shell may be a natural concomitant of increased size, and the relationship noted in *Mya* may be another aspect of larger size in optimum salinities rather than a relation *per se* of heavier shell to higher salinity.

General relationships between lowered salinity conditions and reduction of size have been observed by various authors (Boettger, 1950; Picard and Le Roche, 1949; *see also* Segestråle, Chapter 24). The relationship is not necessarily precise, however, for salinities themselves are variable, and other factors obviously complicate the matter. (*See* Table 5, from Brandt, 1897.) For instance, rate of growth and size are related to the length of the growing season, temperature of the water, and the abundance of nutrient salts—all factors that vary locally in an area as large as the Baltic (see Segerstråle) and that are not necessarily correlated with salinity.

There is a clear relationship between salinity and size which holds for the motile organisms of estuaries and the shallow sea. This comes about because of the life cycle and is somewhat different from the relation between salinity and size of mollusks and other relatively nonmotile animals. In general the young animals move into less saline water as soon as they are spawned, and some species must reach the estuarine raising grounds or perish, as in the case of the shrimp, *Penaeus setiferus*. In the low-salinity waters the myriads of young grow and return seaward or to the sea annually when the temperatures drop in the fall. The next year some may re-enter the lower bays, but their numbers are decimated, and they are outnumbered by young. Thus any series of measurements, above the larval and egg stages, which are usually found in high salinities, will show a direct correspondence between salinity and size. This is essentially the relation noted by Ehrenbaum, Havinga, and Viosca, as noted above, but it was first stated by Weymouth, Lindner, and Anderson (1933, p. 17) who said the shrimp, *Penaeus setiferus*, "move, in general, seaward through the summer and fall, so that there is always a gradient of decreasing size from the waters of greater salinity toward fresh water." Gunter (1945; 1950) presented tables or graphs demonstrating the phenomenon in many Gulf Coast fishes and invertebrates. Figure 7 gives some examples.

The question arises whether the relationship is one to salinity *per se* or is merely a fortuitous correlation based on the life cycle. In the first place many aquatic animals move into deeper waters as they grow older. Fresh-water shrimp in the Mississippi River make such a move (Gunter, 1937), and various marine fishes are found in deeper water at larger sizes, although the salinity changes undergone are negligible (Russell, 1942; Matsui and Takai, 1951; Yokota, 1951).

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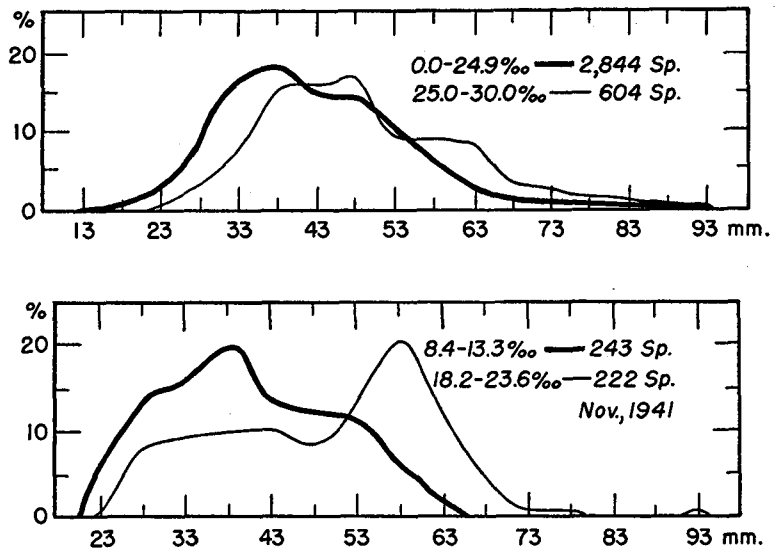

FIGURE 7.—*Size of fishes as related to salinity*

Above, the bumper, *Chloroscombrus chrysurus*; below, the silverside, *Menidia beryllina peninsulae* (from Gunter, 1945).

On the other hand it is the young of the euryhaline fishes that have a predilection for entering fresh water, as has already been mentioned. Similarly, among such salinophilous forms as the Spanish mackerel, the ling (*Rachycentron*), and squid, *Lolliguncula brevis*, and the marine crab, *Callinectes danae*, along the Texas coast the young venture at times into the lower bays. These species have no necessity for entering waters of lower salinity during part of the life cycle. Nevertheless, their wanderings into low-salinity waters conform to the pattern of species which do come into estuarine waters apparently of necessity, in that the young are found at the lowest salinities. Similarly, the fresh-water gizzard-shad, *Dorosoma cepedianum*, goes into salt water, and the larger specimens go into the saltiest water. Certain Gulf fishes and one shrimp come into the bays only in the cooler part of the year, when the salinities are lower than in summer. These are the smaller sizes. In winter when many marine animals have moved into the Gulf, only the smaller sizes of many species remain in the lower salinities and cooler waters. This distribution of different sizes in relation to salinity holds in midsummer as well as in midwinter. Thus the differential size distribution and the slow movement seaward with increasing size is not necessarily caused by the temperature cycle, although it is in the same direction and is probably related to it, for adjustment to low salinities seems to be particularly difficult at low temperatures (Gunter, 1945; 1950).

In brief there seems to be some peculiar predilection of young marine animals for low salinities, which is gradually lost as they become larger, and thus the relationship of salinity and size of motile organisms is probably a real relationship to salinity and not a fortuitous or false correlation. Physiological differences between old and young in the matter of osmoregulation should be detectable, as a final check on the matter. No work has been done on animals which move over the estuarine gradient as part

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of the life cycle. However, Keys (1931b, p. 471) found in work with the Pacific killifish, *Fundulus parvipinnis*, that "Smaller fishes are normally more resistant to abrupt decrease in salinity of the water, and this ability of the smaller fishes is correlated with a high rate of metabolism." The point seems to be significant.

Regardless of the fundamental or physiological causes, this gradient of size and salinity is real and extensive in coastal waters where salinities of waters marginal to land are lower than the sea, and it should be detectable in fossil populations.

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Chapter 8

Temperature

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Temperature is the most important single factor governing the occurrence and behavior of life. Temperature changes affect protoplasm directly and change the physical and biological environment as well. Protoplasm is destroyed at 100°C. and when ice crystals form within it. Some plants live in hot springs where the temperature is at least 85°C, and some deep-sea animals live at perpetual subzero temperatures, but these extremes encompass a relatively narrow range (Fig. 1).

There is a great mass of information available concerning temperature as an ecological factor, but its actual operation is sometimes difficult to evaluate. This is because many of the "temperature" data are simply positions on a column of mercury, without consideration of gradients or duration. The rate of change, or temperature gradient, may be as important to the ecology of an organism as its total summation, its average, or its actual range within a given environment during a period of time.

TEMPERATURE AND THE PHYSIOLOGY OF ORGANISMS

Resistance to chemical reactions is lowered by increase in temperature, hence a rise in temperature speeds up reactions. Biological systems are heterogeneous and involve physical as well as chemical processes. The velocity of reactions in protoplasm is determined by the factor having the slowest rate, which may often be diffusion. For this reason many life processes are not accelerated by a temperature rise as much as chemical reactions are, but the correspondence between temperature coefficients of chemical and biological reactions is often close. At the temperature range at which life processes will go on, which for the majority of marine organisms lies between about 0° and 35°C, the rate is approximately doubled by a 10-degree rise in temperature. However, this is only a rough average, and certain processes may be accelerated anywhere from 1 to 6 times by a 10-degree rise in temperature.

Various attempts have been made to express the rate of biological activity in relation to temperature and to find some handy expression of the temperature relationship in terms of a coefficient or characteristic, and to ascertain the key, or specific, master reactions in the life process by the characteristics of the coefficients. There is an extensive literature of physiological investigation in this field, but it cannot be said that a philosopher's stone has been found. This is doubtless due to the intrinsic complexity of the processes involved.

Three formulae for the interpretation of effects of temperature on physiological processes have been widely used, those of van't Hoff, Arrhenius, and Krogh. The observation that, within favorable limits, physiological processes are accelerated at a constant rate of about two to three times for every 10°C rise in temperature has been called van't Hoff's rule. This figure became the famous Q_{10} of general physiology, but, as Chapman (1931, p. 44) has pointed out, van't Hoff probably never in-

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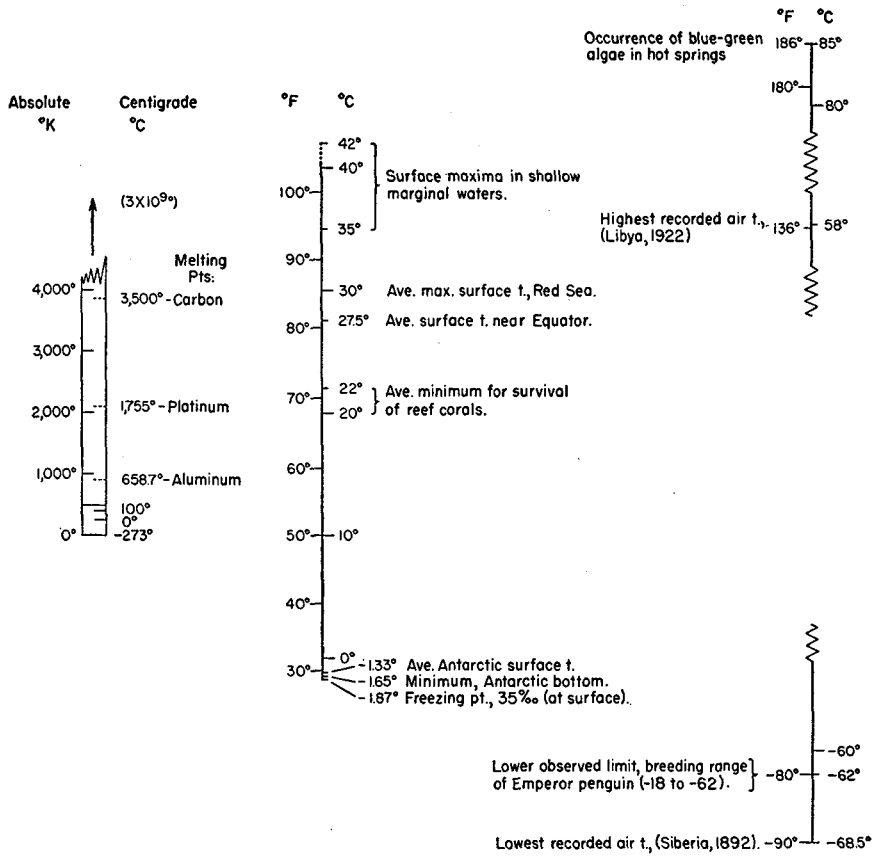

FIGURE 1.—*Temperature ranges in nature*

Left, absolute scale; center, in the sea; right, in air and hot springs, compiled from various sources.

tended his formula to be anything more than a general principle with wide limits of variation. Arrhenius (1915), another physical chemist, changed van't Hoff's formula by basing it on the absolute temperature and introducing a constant to bring Q_{10} closer to 2. Another type of generalization is that based upon the observation that the reciprocal of a time-and-temperature curve is a straight line, and, above the threshold of development, time multiplied by time-temperature is a constant (Sanderson and Peairs, 1914). This has been modified by Krogh (1914), who proposed the formula $V_t + 10 = V_t + K_{10}$. This is now expressed as $V = tK + c$, in which c is the intercept of the reciprocal and the temperature curve. In essence, this means that the speed of the process is a linear function of the temperature. This seems to be the best generalization yet proposed, at least for application in ecology, but like the others it holds only within medial temperatures. Fuller discussions of the measurement of temperature action on physiological processes will be found in Peairs (1927), Jacobs (1928), and Ludwig (1928) or the various texts on general physiology, especially Barnes (1937) and Heilbrunn (1952), and the ecological treatise of Allee *et al.* (1949).

In spite of the difficulty of expressing the effect of temperature in physiology, the fact that Q_{10} lies mostly around 2 indicates that life processes are dominated by chemical rather than physical reactions. The rate of nerve conduction, heart beat, CO_2 production, oxygen consumption, rate of breathing, CO_2 assimilation by plants, rate of egg cleavage, general activity, and other physiological processes have all been shown to be accelerated by temperature.

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Some examples of the effect of temperature on eggs of marine animals are of interest in this connection. Reibisch (1902) gave the following information on the development of cod's eggs (*Gadus morrhua*):

T°C	−1°	+3°	4°	5°	6°	8°	10°	12°	14°
Times in days	42	23	20.5	17.5	15.5	12.8	10.5	9.7	8.5

Hesse *et al.* (1937) say herring eggs develop in 40 to 50 days at 0.5°C and in 6 to 8 days at 16°C. According to Peter (1906), the rate of development of sea-urchin eggs is increased 2.5 times for every 10-degree rise in temperature between 2.5° and 25°C.

Shelford (1929), Chapman (1931), and Allee *et al.* (1949) have discussed the difficulty of assaying the effect of temperature on physiological processes and the difficulty of relating experimental results to ecological conditions. Physiologists must, for the purpose of interpreting results, work with constant conditions while assessing the influence of one variable or rarely two. Further, the one variable is compared from one constant state to another, and fluctuating factors are not used. In nature few factors are constant, and this is particularly true of temperature. It fluctuates during the day, from day to day, and from season to season. These fluctuations are slower and of smaller order in the sea than on the land. There is some reason to believe that organisms do not react to varying temperatures in the same way their actions at constant temperatures would indicate. The "norm" for most organisms is varying conditions. The same set of conditions may also be the "optimum". The hatching of certain insect eggs is accelerated more by a varying temperature than by any constant temperature to which they can be exposed (Ludwig, 1928; Parker, 1930). In addition the history of conditions to which an organism has just been subjected has some effect on how it reacts to the present conditions, as shown by the phenomenon of acclimation. These facts all contribute to the difficulty of using the data of physiology in the interpretation of ecological data, but they are nevertheless the best we have.

TEMPERATURE OPTIMA AND EXTREMES

Plants have, essentially, no temperature-regulating mechanisms. Animals are divided into two groups, the homoiotherms and the poikilotherms—*i.e.*, warm-blooded and cold-blooded; The cold-blooded group is really temperature variable and may be quite warm at times. Mammals and birds have well-developed temperature-regulating mechanisms which keep the body at a very precise temperature. These organisms are at the same time somewhat the victims of their specialization and usually die if the body temperature is much changed for any length of time. All lower vertebrates and the invertebrates are poikilothermic; their body temperature changes with that of the environment. This holds true for all except certain parasites which cannot exist at temperatures different from those of their warm-blooded hosts. Certain poikilotherms, such as some of the higher fishes, have crude temperature-regulating mechanisms that change body temperatures slightly from that of the environment.

In a physical or chemical system the temperature at which the maximum rate of reaction takes place is the optimum temperature. For a living system, however, the optimum temperature might be termed the one at which metabolic processes function at a maximum rate consonant with the maintenance of the system. These vital

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TABLE 1.—*Temperatures lethal to various marine mollusks when submerged*
Compiled from Broekhuysen (1940) and Evans (1948)

Species	Lethal temperature	Locality	Author
		Sublittoral	
Venus mercenaria	45.2	St. Andrews, N.B.	Henderson (1929)
Yoldia sapotilla	34.8		
Musculus niger	34.5		
Pandora trilineata	33.5		
Astarte undata	33.5		
Cardium pinnulatum	33.2		
Crenella glandula	32.8		
Saxicava rugosa	32.8		
Leda tenuisulcata	32–31		
Musculus discors	31.9		
Cardita borealis	31.6		
		Sublittoral to Lower Intertidal Zone	
Patella athletica	41.7	Aberystwyth, Wales	Evans (1948)
Gibbula cineraria	36.2		
		Lower Intertidal Zone	
Littorina littoralis	44.3	Aberystwyth, Wales	Evans (1948)
Littorina littorea	44–41	St. Andrews, N.B.	Gowanloch and
Littorina littorea	46.6	Halifax, N.S.	Hayes (1926)
Littorina littorea	46.0	Aberystwyth, Wales	Evans (1948)
Gibbula umbilicalis	42.1	Aberystwyth, Wales	Evans (1948)
Nucella lapillus	40.0	Aberystwyth, Wales	Evans (1948)
Mactra solidissima	37.0	St. Andrews, N.B.	Henderson (1929)
Modiolus modiolus	36.3		
Zirfaea crispata	35.5		
Oxystele sinensis	39.6–39.0	False Bay, S. Africa	Broekhuysen (1940)
Cominella cincta	39.4–39.0		
		Mid-Tidal Zone	
Littorina saxatalis	43.4–42.3	St. Andrews, N.B.	Gowanloch and Hayes (1926)
Littorina palliata	42.5–41.8		
Littorina rudis	45.0	Aberystwyth, Wales	Evans (1948)
Patella vulgata	42.8		
Patella depressa	43.3		
Osilinus lineatus	45.8		
Oxystele variegata	42.1–41.5	False Bay, S. Africa	Broekhuysen (1940)
Thais dubia	41.7–41.2		
Oxystele tigrina	40.5–40.0		

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TABLE 1.—*continued*

Species	Lethal temperature	Locality	Author
		Upper Intertidal Zone	
Littorina knysnaensis	48.6–47.9	False Bay, S. Africa	Broekhuysen (1940)
Littorina neritoides	46.3	Aberystwyth, Wales	Evans (1948)
Macoma fusca	42.3	St. Andrews, N.B.	Henderson (1929)
Mytilus edulis	40.8		
Mya arenaria	40.6		
		Level Not Stated	
Crassostrea virginica	48.5	St. Andrews, N.B.	Henderson (1929)
Pterotracha coronata	42.3	Naples, Italy	Vernon (1899)
Tethys leporina	40.5		
Octopus vulgaris	36.0		
Cymbulia peroni	35.7		
Thais lapillus	35.5–35	St. Andrews, N.B.	Gowanloch (1926)
Ilyanassa obsoleta	35		

optima are not sharp but range over several degrees and are usually nearer the maximum than the minimum temperatures which life withstands.

Most metabolic processes that have been measured in cold-blooded animals, such as respiration, increase with rise in temperature up to the point where heat death ensues. At the other end of the scale, the minimum temperature at which a reaction can proceed to completion is the effective temperature threshold.

The thermal death point for most terrestrial poikilotherms is around 42° to 45°C; for marine animals it is lower, usually from 30° to 35°C, although for most shore or intertidal animals the lethal temperature is about the same as for terrestrial forms (Table 1).

Semper (1881) said that animals from the North Sea died at 30°C. Some marine animals from the vicinity of Naples survive temperatures up to 42°C, and Mayer (1914) found that *Limulus* has a thermal death point of 46.3°C in Florida and 41°C at Woods Hole. Many organisms are killed by temperatures not far above those to which they are accustomed, and it is not uncommon for heat death to occur in the natural environment. This is particularly true for tropical animals, which normally live at temperatures much nearer their thermal death point than northern forms, whereas some arctic animals may live in water as much as 13° to 16°C below their death points (Mayer, 1914). Many animals accustomed to exposure at low tide may withstand comparatively high temperatures for periods longer than they would be exposed to under natural conditions (Broekhuysen, 1940; Evans, 1948). Marine invertebrates and fishes die from heat at lower temperatures than land animals. High temperatures of water off the coast of Peru, brought by the irregular appearance of the Equatorial Countercurrent, cause terrific mortality (Gunther, 1936). According to Schott (1913) the temperature of this current, El Niño, averages about 25°C,

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which is about 7°C higher than normal waters of that region. Yet the vast destruction of life is exceeded by few if any catastrophes on the earth today. (*See* Chapter 29.)

Death from heat is not a simple effect, and several hypotheses have been advanced to explain the mechanism by which heat may kill an organism. (*See* Heilbrunn, 1952, for an extended discussion of this problem and of temperature in general.) When cells are exposed to heat, the viscosity of the protoplasm increases. This reaction is reversible, up to a point, beyond which it becomes irreversible, and death ensues. In most cases coagulation of the cell protoplasm occurs at the time of heat death, and apparently coagulation is the immediate cause of death. Many organisms, however, die before the protoplasm coagulates, some—*e.g.* certain algae and phyllopods—at temperatures of 18° to 19°C. Similarly many cells may be killed by heat before the enzymes are destroyed; most proteins (including enzymes) will not coagulate at temperatures below 70°C, and the coagulation of protoplasm, which occurs at lower temperatures, is that of a different complex.

There is evidence that increase in water content enhances the susceptibility to heat death, while decrease in water content retards it (Davenport and Castle, 1895). In high salinities or hypertonic solutions marine organisms survive heat better. It is suggested (Heilbrunn, 1924) that the concentration of lipids within the protoplasm is correlated with differences in sensitivity to heat, and it is generally observed that organisms living at lower temperatures have fats with lower melting points than those living at higher temperatures. Northern populations of salmon, for example, have more fluid fats than do those of the same species farther south (Brocklesby and Bailey, 1933). According to Hilditch (1952, p. 181) observations are in harmony with the hypothesis that formation of the less unsaturated from the more unsaturated fatty acids proceeds less far in seeds matured at a lower than at a higher temperature. Coagulation of cell contents by heat is accompanied by vacuolization of the protoplasm, a precipitation reaction apparently dependent upon the release of free calcium in the cell. The cell protoplasm seems to be a complex of protein, lipid, and calcium, and any agent freeing the lipid also frees calcium. If heat released the lipid and thus the calcium, it would have less effect on fats with a high melting point, thus explaining why warm-water organisms, which contain such fats, resist heat better than do cold-water organisms.

Hamano (1951) notes that the oil content of living salmon eggs (*Oncorhynchus keta*) increases when the eggs are treated with various chemicals or heat, up to 20°; he suggests that the increase may come from release of oil from protein lipid and the denaturation of protein. Other workers have noted the release of fat droplets in heated protoplasm (Heilbrunn, 1952, p. 490).

On the other hand, the cause of heat death may lie in the upset or changed relative rates of reaction of a complex of interrelated physical and chemical reactions which are little understood.

The lower temperature, where metabolic activity slows to practically a stop, near 0°C, is not nearly so lethal as heat, and many organisms will recover from cold that has caused near cessation of their activities, if the cold is not protracted. They are not killed by short exposure unless ice crystals form in the tissues and cells. Sudden thawing in many plants may be more injurious than the freezing temperatures, and

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some, such as palms, are much more sensitive to change of temperature than to low temperatures attained gradually (Warming, 1909, p. 23).

Death from cold is as universal in nature as death from heat, and among marine organisms it is particularly prevalent in warm-temperate and subtropical areas, which are subjected to cold waves irregularly. Bangs (1895), Finch (1917), Storey and Gudger (1936), and Miller (1940) have described instances in Florida; Verrill (1901) described one in the Bermuda Islands. Gunter (1941) and Gunter and Hildebrand (1951) discussed occurrences on the Texas Coast. Storey (1937) and Gunter showed that in Florida and Texas death of fishes and other animals during cold spells comes at intervals of about 10 years. Littoral organisms in northern climates may be killed in great numbers by ice in shallow waters and on the beaches in colder years (Blegvad, 1929; Smidt, 1944). Fish, Crustacea, and porpoises are also killed (Johansen, 1929). Porpoises, however, seem to drown under thick ice in enclosed seas from which they cannot escape. The fluctuations of abundance of invertebrate larvae from year to year in Danish waters seems to be due to high mortality of shallow-water species in "severe ice winters" (Thorson, 1946, p. 473).

The resistance of organisms to cold is much more variable than is their resistance to heat. Certain animals, such as rotifers, nematodes, and tardigrades, can, in a desiccated condition, survive several hours of exposure to temperatures as low as −272°C, and a dried lichen has been reported to resume growth after 18 days in liquid nitrogen. In these examples the organisms must be cooled and warmed quickly, to prevent the formation of ice crystals in the protoplasm; the ice crystals not only kill by mechanical effects but by concentration of salts within the cells through the removal of the water (Luyet and Gehenio, 1940). Gels resist freezing much better than do liquids, and it has been postulated that, in organisms where gelation of protoplasmic colloids takes place before ice crystals can be formed, the critical stage is passed, and much lower temperatures can be withstood. For most organisms, attainment of these conditions in nature is impossible. In the examples given, it will be noted that dehydration is the first condition; gelation is enhanced by the dehydration. Dehydration also increases the resistance to heat, as noted above.

Where death from cold is due to formation of ice crystals, high-salt content tends to make organisms cold resistant, recalling the influence of salts on heat death. Most marine organisms die at a few degrees below 0°C, while numbers of them die at even higher temperatures. The organisms killed by cold in the Bermuda Islands and Texas were not subjected to temperatures lower than 7° and 4°C, respectively. Some derangement of metabolic activity seems to be the cause of death in these instances. In fishes and crustaceans it may be such a simple matter as the cessation of breathing movements or of heart beat, and consequent asphyxiation. On the other hand, some sort of protoplasmic breakdown is induced by cold. Pigment granules are broken down, and liquefaction of cortical protoplasm and gelation of the interior takes place. These changes are like responses to stimulation. Stimulation produces death if excessive, and death from both heat and mild cold are similar in that both seem to be the result of a stimulation. In both cases calcium is released from the protoplasm (Heilbrunn, 1952).

Death from cold may result indirectly from inactivation. Gunter (1941) noted that

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shrimp, *Penaeus*, and pistol-shrimp, *Crangon* (= *Alpheus*), were "numbed" and washed up on the beach, where they were revived by the sun, but in the meantime most of them were consumed by gulls. He also observed that large numbers of gastropods, pelecypods, and echinoids were rolled onto the beach by the surf. They revived but could not return to the water.

Within normal limits the absolute temperature seems to have less effect than temperature changes, and these latter effects are greater when the amount of departure and its rate of change from the optimum are greatest.

Most fishes cannot survive a sudden temperature change of more than 6° or 8°C. Some, however, can withstand changes of 30° or 35°C, if the change is gradual (Norman, 1936).

According to Johansen (1929), fishes with higher breeding temperatures suffer much heavier mortality during periods of killing cold than do those which spawn at low temperatures. A similar relationship exists (Storey, 1937) among the fishes of west Florida; their resistance to sudden cold spells is correlated with their distribution as temperate, subtropical, or tropical species. The resistance of animals to cold seems to vary at given stages, and there is some evidence that among marine poikilotherms the resistance to cold varies with size; observations indicating that the young of certain marine animals can withstand cold better than their elders have been made by Hildebrand and Cable (1930), Pearse and Wharton (1938), and Gunter (1947). The work of Rao and Bullock (1954) indicates that this may be a general phenomenon; they have shown that within physiologically normal ranges of temperature Q_{10} for various measures of activity commonly increase with increasing size. Conversely, this would mean that Q_{10} is depressed less with decreasing size. On the other hand, Brett (1952, p. 283) found that smaller sizes of young salmon tend to succumb to induced cold in greater numbers than do larger ones.

ACCLIMATIZATION

Neither optimum nor lethal temperatures are fixed points, even for a given individual, and many animals can be acclimatized to temperatures beyond their usual tolerance by intermittent or continuous exposure to sublethal extremes. In general, young animals have a greater capacity for adjustment to such changes than do their elders and are therefore more easily acclimatized, although they may be more susceptible to extreme conditions (Shelford, 1929, p. 95). Acclimatization to high temperatures can last for some time after the return of the organism to lower temperatures, but there are indications that cold hardiness, at least, is not a continuous phenomenon but must be acquired anew with each season (Uvarov, 1931); work with reactions of insects to supercooling indicates that animals exposed to seasonal lowering of temperatures have a corresponding seasonal variation in their critical supercooling temperature (Allee *et al.*, 1949, p. 101). Probably there is a slow acclimatization of many organisms in temperate zones with the change in seasons. Brett (1944) has shown that the lethal temperatures for certain fishes of Canadian lakes rise as temperatures for the lakes rise in the spring.

The actual process of acclimatization is not well understood, and it remains to be determined whether it occurs at the level of the cell or of the organism as a whole.

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In the work of Loeb and Wasteneys (1912) on *Fundulus*, there is some suggestion that it occurs at the particulate level; they found that resistance to high temperatures in these fish is directly correlated with the amounts of Na, K, and Ca salts of the water, and that a one-fourth molar solution gives maximum protection. This was determined to be a specific, not an osmotic effect. On the other hand, Doudoroff (1945) attributed the death of *Fundulus* (another species) at slowly lethal low temperature to osmoregulatory disturbances, and at rapidly lethal cold to respiratory disturbances of the organism. In earlier work, Sumner and Doudoroff (1938) found indications that acclimatization was independent of metabolism. According to Pearse (1939, p. 47) a poikilotherm removed to a higher temperature increases its metabolism at first but gradually slows down to the previous rate; if removed to a lower temperature, the processes are roughly reversed. Sayle (1928) noted this phenomenon while working on dragonfly nymphs.

Although some marine poikilotherms have been acclimatized to temperature changes under laboratory conditions and many exhibit seasonal differences in optima which would suggest a ready capacity for acclimatization in nature, distribution of the majority of marine organisms in nature can be associated with temperature differences. Acclimatization in nature is apparently a slow process, resulting in physiological species whose optima and breeding seasons correspond with the prevailing temperature conditions of their respective latitudes. Many broadly ranging, essentially eurythermal species are larger in higher latitudes or colder waters, but, possibly, as indicated by recent work (Rao, 1953), the high-latitude members of a species have correspondingly higher metabolic rates at equivalent sizes. This tends to equalize the rate per unit of a cold-water representative and a warm-water member of the species. (*See also* Thorson, 1946, p. 457.) Rao's results, however, may be the result of age differential in that at equivalent sizes high-latitude poikilotherms are in general older than those from lower latitudes. Metabolic rates on total populations of low- and high-latitude organisms must be determined before this question can be answered precisely. Nevertheless, it appears that cold-water organisms are fitted for their environment by an ability to maintain a high metabolic rate at low temperatures. Fox (1936) demonstrated that, when cold- and warm-water echinoderm eggs are kept at the same intermediate temperatures, cleavage is fastest in the cold-water eggs. Orton (1923) first noted that the oxygen consumption of arctic, boreal, Mediterranean, and tropical lamellibranchs was about equal, although the temperatures may be 0°, 8°, 12°, and 30°, respectively. Scholander, Flagg, Walters, and Irving (1953, p. 90) say in reference to oxygen consumption of arctic and tropical aquatic animals,

> The arctic curves are displaced toward cold, and the arctic forms at the normal temperature of their habitat, 0°, have a three to ten times lower metabolic rate than have the tropical forms at a habitat temperature of 30°. If the tropical curves are extrapolated to 0°, they would be lowered by thirty to forty times, and hence there is a very considerable, although not complete, metabolic adaptation in the arctic forms relative to the tropical forms.

The same writers (1952) found that at all temperatures certain arctic lichens respire faster than do tropical members of the same family, and thus seem to be metabolically adapted to cold. However, they found that "in the main bulk," of arctic and tropical lichens O_2 consumption overlaps at all temperatures and shows no clear metabolic

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adaptation to different climates. They concluded that metabolic rates of lichens are highly variable, depending on moisture content and temperature, and that the group has not developed demonstrable adaptations to climatic influences on respiratory rate.

Thus the commonly held idea that life proceeds at a faster pace in tropic seas is probably correct, but the differential is probably not so great as is commonly supposed. Thorson (1946, p. 455) has summarized information showing that certain invertebrate larvae in cold seas develop at about the same rate as their congeners in warm seas. The evidence is somewhat contradictory, however, and varies with the species or group concerned. Collectors of invertebrates who travel to the tropics soon learn that tropical crabs are not the slow-moving beasts they are accustomed to pursuing in northern latitudes. Fox and Wingfield (1937) demonstrated an increase in metabolic rate in colder waters for *Pandalus montagui* but not for *Pandalus borealis*; in general these authors concluded that metabolism was higher in the English representatives of species found farther north, whereas Spärck (1936) and Thorson (1936) found that metabolism was high in northern lamellibranchs.

Bullock (1955) has recently reviewed the question of physiological compensation for temperature changes by poikilotherms. He concluded that in single organisms there are several mechanisms operative at different rates and different levels of organization, involving enzymes, cells, organs, and behavior. He noted that the existence of "temperature" races among eurythermal species has been clearly demonstrated. Some species are at first hyper-responsive to temperature change and then settle down to a steady rate after some hours; others respond slowly. Bullock points out that neglect of consideration of this short-term factor vitiates many comparisons made during dissimilar phases of response to temperature change. He concluded that the wide occurrence of acclimatization and related rate compensations for temperature indicate the large role of the phenomena in ecology and evolution.

TEMPERATURE AND REPRODUCTION

Many organisms have different temperature optima and limits for different processes; for example, Hopkins (1931) has shown that pumping of the oyster's gill ceases at low temperature before opening and closing of the shell ceases. This is particularly true of reproduction, which requires a more critical temperature optimum than the bodily processes, and most marine animals have restricted temperature ranges for breeding. The common American oyster, *Crassostrea virginica*, for example, can feed and grow at temperatures both lower and higher than are required for spawning. Oysters grow annually in the northern parts of their range, but successful spawnings may be as much as 4 years apart.The critical temperature may control some aspect of reproduction other than spawning, as in the case of the European lobster, whose larvae require a minimum temperature of 15°C although the eggs, cleavage stages, and adults will tolerate lower temperature (Appellöf, 1912). Eelgrass, *Zostera marina*, grows well between 10° and 20°C but reproduces only between 15° and 20°C (Setchell, 1922). According to Setchell (1920), marine plants have a wider range than their ability to reproduce would indicate, and live outside their normal temperature zones, where reproduction could take place only during a very short period of the year.

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Runnström (1927) has shown that cleavage stages of most marine invertebrates are more sensitive than larval stages. The distinction between temperature optima for ripening of gametes and their release is pointed out by Thorson (1946, p. 422); in many marine invertebrates these processes are distinct. Loosanoff and Davis (1951) delayed spawning of lamellibranchs by holding them at temperatures high enough to permit gametogenesis but too low to induce spawning. Oysters (*C. virginica*) treated in this manner resorbed the sexual products; in *Venus mercenaria* the gametes remained viable until the next season.

The importance of temperature acting on reproduction as a limiting factor in distribution was suggested by Appellöf (1912) and emphasized by Orton (1920). Appellöf pointed out that arctic and more temperate species lived side by side in the intertidal zone of the Norwegian coast, but spawned at different times of the year, and that the vegetative processes of organisms are less dependent on temperature than are the reproductive. Orton's conclusion that "most animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely, at either the maximum or the minimum temperature of the locality" is sometimes referred to as "Orton's rule" (Thorson, 1946, p. 422). A corollary to this generalization is that the spawning season of a widely distributed organism corresponds with the local temperature conditions. Oysters in Long Island Sound may spawn in temperatures as low as 16°C, while southern oysters require 20°C. Loosanoff and Nomejko (1951) consider this fact as evidence of physiological races. Such conditions are probably common in widely ranging species.

In temperate and higher latitudes reproduction is closely associated with warmer seasons of the year. Rising temperatures in the spring induce development of the gonads in most marine organisms, and actual spawning takes place when a certain temperature level is reached, which varies for different species. Thorson (1946, p. 458) has given an example among the Danish echinoderms. Arctic, boreal, and Mediterranean species spawned in the Öresund in spring, summer, and autumn, respectively. Species of diatoms show different temperature preferences by the different seasons of the year at which they bloom (Gran and Braarud, 1935). Temperature thresholds for spawning are not sharp and may vary a little depending upon the past history of temperature changes. If the warm season is long there may be two spawning peaks. (*Cf.* Hopkins, 1931, on oysters.) Conversely some animals spawn when the temperature drops, and by Orton's rule marine animals can be divided into two groups, those that spawn at rising or maximum temperatures and those that spawn at falling or minimum temperatures. Gunter (1945, p. 96, 176) has shown that spring and summer spawners among the fishes of the Texas Coast outnumber the fall and winter spawners by more than 4 to 1, and among the shrimp and crabs all were spring or summer spawners. Nevertheless, some of the fall and winter spawners, such as the croaker, are extremely abundant, and this group may form an important part of the fauna.

Vatova (1949) grouped the reproductive periods of 97 species of benthic animals of the Adriatic as follows: spring 64, summer 49, autumn 26, winter 18. Some species spawned in two seasons. Vatova (1948) also showed that reproduction of the marine algae off the coast of Istria in the northern Adriatic was predominantly in spring and

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summer. He shows the following species ratios for spring, summer, fall, and winter: 22, 18, 11, 15.

Orton's generalization applies to all shallow-water organisms in temperate seas, so far as is known, but it may not apply to locales of equable temperatures, such as the great depths. It has been recognized that the gradient or extent of temperature change is quite important. A slowly rising or falling temperature induces gonadal development, and then a sharper or more sudden change in the same direction may lead to spawning. For instance Yamamoto (1951) says that spawning in *Pecten yessoensis* is induced only by a sudden rise as little as 0.5°C within the effective temperature range and that the stimulus is most effective at the peak spawning season—, *i.e.*, the time of greatest gonadal development. Spawning seems to be induced by the same direction of temperature change which leads to gonadal development, and thus most spawning seasons do not immediately follow the season of temperature reversal.

Resting stages of diatoms around the poles are viable after being frozen in solid ice, and it has been reported that the vast flowerings in the spring in these waters are started by diatoms released by melting ice. Because of their possession of resting spores and different temperature preferences, temperature does not limit the range of some temperate and cold-water diatoms but instead determines the season at which they grow. Thus polar and subtropical species may grow in the same area at different times of the year, if they have resistant stages that can survive the inclement season. The same situation will come about if "seeds" are brought in by currents at the proper season.

The larvae of animals in arctic and antarctic waters are dependent on the brief periods of phytoplankton production, and the breeding cycle may thus be more closely related to this period of production than to temperature. In Northeast Greenland, 42.5 per cent of the species of bottom invertebrates live within the narrow range of 3.5°C, and, of those possessing planktonic larvae, the larval life corresponds with the period of available phytoplankton which is in turn more dependent upon light than upon temperature conditions (Thorson, 1936). Nevertheless, temperature is usually the most important factor in the breeding of marine organisms. Nelson (1928) said the rate of growth and length of larval life of bivalves was largely determined by temperature. Thorson (1946, p. 452) has given several examples from the literature. Weymouth (1918) said that crabs and salmon grow faster and attain greater size at comparable ages in years when the growing seasons are warmer and longer.

Lack of periodicity in a homothermal environment may be true of a relatively few organisms in the surface layers of the tropics and perhaps of those of the deep seas. The idea that tropical organisms have continuous breeding seasons, long ago suggested by Semper (1881), requires qualification. The work of Yonge (1930) on the Great Barrier Reef showed that many organisms had definite breeding rhythms. The indications are that the majority of tropical animals spawn "either exclusively or most actively in the warmer months" (A. Stephenson, 1934), and Thorson (1946) suggests that breeding seasons of tropical animals are so distributed that their larval stocks as a whole occur in the plankton on a year-round basis.

The variations in spawning intensity in the tropics may coincide with factors other than temperature, such as light, or in some way with the phases of the moon

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or the tidal differences associated with these phases. The famous Palolo worm (*Eunice viridis*) is the best-known example of this type of lunar periodicity. (*See* Chapter 27.)

TEMPERATURE AND PERIODICITY

The cyclic character of the annual life of the temperate and cold zones is intimately related to the temperature conditions. Pearse (1939) said,

> The annual cycle of many species of animals is made up of a series of stages in a characteristic life history or of a characteristic series of periods of rest and activity which are closely correlated with seasonal progression. . . . Long established correlations operate in such a way that seasonal environmental changes serve to stimulate animals to appropriate activities or inactivities, and cyclical physiological changes within animals prepare them to react properly with recurring seasonal events.

The rhythmical changes imposed upon the physiology of animals by light and heat are most conspicuous in such phenomena as sleep, breeding, and hibernation; some of these rhythms are so deeply impressed that they continue after the cause is removed (Borradaile, 1923). The annual migrations and seasonal movements of many marine organisms are as regular as the migration of birds. On the Texas Coast, with its complex of bays and neritic coastal waters on the borderland between temperate and tropical conditions, temperature is the chief factor governing seasonal migration and other seasonal cyclic activities of fishes and motile invertebrates (Gunter, 1945: 1950). In colder climates vast flowerings of diatoms and other plankton come in the spring, and there may be two peaks of abundance in the warm season. However, in the warmer temperate zone there is a tendency toward one annual peak of abundance falling in the winter (Steuer, 1910). Coe (1932) has shown that hydroids and algae grow luxuriantly in the winter in California, while oysters, barnacles, Bryozoa, and other fouling organisms attach and grow fastest in the summer. Gran and Braarud (1935) have shown that the species components of diatom populations change considerably during the year as the temperatures change.

Organisms with short generations undergo great population changes with the seasons. One of the best examples is the commercial shrimp, *Penaeus setiferus*, of the South Atlantic and Gulf coasts of the United States. The rapid summer growth of this animal leads to a sudden increase in the number of large shrimp amounting to millions of pounds, as is clearly evidenced by the rapid onset of the bay-fishing season in the fall and similarly its rapid decline as the shrimp move out to sea. There most of them die, and a very few return to the bays. The little coquina clam, *Donax variabilis*, of the Gulf beaches apparently has a similar annual fluctuation of abundance; it is most numerous in the summer.

Most marine animals in the temperate regions grow more rapidly in the warmer months. Since breeding is also seasonal, this means that various size groups or year classes, as they have been called by the fisheries biologists, make up the population of a species. These year classes can be detected by size alone, but they are also indicated by growth rings or checks in animals with cumulative hard parts, as on mollusk shells or the scales and otoliths of fishes. As animals grow larger they grow more slowly, and thus the year classes tend to overlap more. The same thing happens with all year classes as the tropics are approached, because the breeding season and grow-

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ing season are both increased. If a paleontologist finds a species with distinct and discrete size groups it is a fairly good indication that the organisms grew in a region with distinct seasonal changes. If the same thing is observed in several species the indication is, of course, considerably strengthened.

Some organisms have the growing seasons reversed from north to south. For example, on the Gulf Coast of the United States the common oyster grows fastest and stores glycogen in the winter (Gunter, 1942), while from spring to fall most energies are put into spawning and reproduction. In the Chesapeake Bay and northward, most growth takes place in the summer and fall, and oysters become quiescent or dormant during the winter if the water temperature falls to around 4.5°C, and life goes on at a low ebb, approaching a condition suggestive of the hibernation of terrestrial organisms. Sverdrup, Johnson, and Fleming (1946, p. 770) have pointed out that a cold-water diatom may thrive in the Arctic in summer and in lower latitudes in winter, while the growing season for the warm-water species may shift poleward with the summer.

TEMPERATURE AND DISTRIBUTION

Temperature largely determines the distribution of life on Earth. The body temperatures and vital processes of the vast majority of marine organisms, bathed as they are by water, are affected immediately by change in temperature; and, although the range of temperature is restricted in the oceans, the barriers created by it are extensive. Distributional differences arise because organisms have varying tolerances for maximum and minimum temperatures and different optima as well. Such terms as "boreal," "Lusitanian," "arctic," "Caribbean," etc., are primarily names for temperature conditions. These conventional provinces and temperature zones are discussed in Chapter 13. The distribution of deep-sea animals is discussed in Chapter 22.

The temperature range for many species of marine organisms is relatively narrow. Stenothermal animals may be cold- or warm-limited. Some may be stenothermal for one stage and eurythermal for others. Warm-water stenothermic species are the most numerous in the world seas.

Reef-forming corals will not live where the temperature falls blow 18°–19°C, and all reef formation takes place between the surface minimal isotherm lines (isocrymes) of 20°C. Pruvot (1896) stated that most of the fixed algae are eurythermal and that the principal types are in general cosmopolitan. Conversely, nearly all the marine spermatophytes are stenothermal (Setchell, 1920). Barnacles are exceptionally eurythermic as are many pelecypods. The European oyster, *Ostrea edulis*, can tolerate temperatures from 0° to 20°C. The American oyster, *C. virginica*, is even more eurythermic and survives temperatures from 4° to 34°C on the Gulf Coast. Shallow-water shrimp of the family Peneidae are limited to warmer waters of the seas, while the Pandalidae are limited to cool waters. Littoral organisms, except for seasonal transients, are in general eurythermal.

There are, of course, all gradations between stenothermic and eurythermic organisms and cold- or warm-limited divisions of each. Shelford (1916) found that crustaceans from depths of 55 fathoms could not withstand high temperatures as well as

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their congeners from shoal waters. The underlying causes for these temperature divisions and limitations of life are doubtless physiological.

The relations between temperature and distribution are not simple, as indicated by the overlapping distributions of many organisms. The control in one organism may be affected on the breeding season, in another on the survival of adults or larvae at the extreme; usually the distribution is a result of various combinations.

Orton (1920) says temperature is "of paramount importance in controlling distribution and its influence on breeding is one of the ways this controlling effect is exerted." Species restricted by reproductive stenothermy may live in other areas but must be recruited every year from a spawning center. Huntsman and Reid (1921) and Fish and Johnson (1937) have shown that certain fish, medusa, amphipods, and arrowworms seldom spawn in the Bay of Fundy, and the populations are largely recruited from waters flowing in from the Gulf of Maine. Similarly Bigelow (1926) found a common arrowworm in the Gulf of Maine, which could not breed there but was brought in from the Gulf Stream.

Lest temperature be overemphasized as a distribution factor, attention should be called to the peculiar distribution of the American horseshoe crab, *Limulus*, which is common to abundant throughout a range from Cape Cod to tropical Florida and Yucatan, but is relatively uncommon in the eastern Gulf of Mexico and has been reported only twice west of the Mississippi River. Thus, the animal is rare, or for practical purposes absent, from a large littoral area lying well within its temperature zone.

Both zonation and local distribution change considerably in shallow waters with temperature changes of the seasons in the temperate zones. This is due not only to seasonal variation in the growth of sedentary organisms (Coe, 1932) but to the movements of motile organisms in and out of the bays or to and away from the shallows near shore. Along the northern Gulf Coast of the United States a number of fishes and invertebrates leave the bays and go to the Gulf during the coldest months. Others depart from the shallow Gulf in the fall and are seen only seasonally (Gunter, 1938; 1945; 1950). A very few species, less than 1 per cent, enter the bays only in the cool months; during the warmer months they live in the offshore waters of the Gulf which are cooler at that time of the year. In this connection the catastrophic mortalities caused by cold, and Taylor's (1934) emphasis upon the critical aspect of extreme years should be recalled. Distribution may be influenced more by the recurrence of scattered extremes than by several years of normal temperature.

The surface temperatures of the open ocean change gradually, and temperature barriers are not usually abrupt. Nevertheless, the cold or warm currents in certain places constitute barriers as effective as if they were solid walls. According to Steuer (1910) the Gulf Stream divides the craspedote medusae into two groups. A sudden change in the flow of a current may amount to a catastrophe or greatly change the biota of a region. El Niño, mentioned previously, is an example of a catastrophic change. Since about 1930 cod stocks in northern waters generally have greatly increased owing to large-scale hydrographic changes (Russell, 1942, p. 48).

Plants as well as animals have fairly restricted temperature tolerances. Limitations of range by temperature may be affected by influence on one organ or life process of

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an organism, or by influence on a particular stage in the life history. Apparently the varying tolerances were acquired ages ago and have been largely preserved for given organic groups ever since. Regardless of what the physiological explanations of these tolerances are, their present pattern can be explained only on a basis of the genealogy or past history of the species.

TEMPERATURE AS RELATED TO GROWTH AND FORM

Long ago Möbius observed (*see* Semper, 1881) that mollusks living on the coast of Greenland grew larger than those in the Baltic Sea. It is now known that cold-blooded marine animals grow larger in the northern part of their range. Warming (1909, p. 170) noted that in colder seas individual brown seaweeds are hundreds of feet in length and added: "In tropical seas species are smaller throughout." Rhumbler (1911), Murray and Hjort (1912), and many other naturalists have noted the larger size of northern individuals of the same species, and the larger size of northern representatives of the same genus. This tendency to larger sizes in colder waters is noticeable in related species of copepods as well as within single species (Sverdrup, Johnson, and Fleming, 1946, p. 856). The most precise data on this matter were furnished by Weymouth and his associates (Weymouth and Thompson, 1931; Weymouth, McMillin, and Rich, 1931) who worked on the Pacific cockle and razor clam. Data for such differences in the Virginia oyster were summarized by Butler,

Location	Mean annual temp. 0° C.	Calendar months to grow select oyster			Months in hiber-nation	Average no. of growing months	Oz.-yield per bushel (USFWS statistics)	Oz.-yield per bushel (Biologists' estimate)	Oz.-yield per calendar month	Oz.-yield per growing month
		poor area	best area	average area						
CANADA	6	84	48	66	5	46	–	120	1.8	2.6
LONG ISLAND SOUND	10	80	42	52	4	36	122	120	2.3	3.4
CHESAPEAKE BAY	15	60	18	30	3	24	72	96	3.2	4.0
SOUTH CAROLINA	20	48	18	30	0	30	42	76	2.5	2.5
GULF OF MEXICO	22	48	18	30	0	30	66	72	2.4	2.4

FIGURE 2.—*Physiological characteristics of* Crassostrea virginica *at various localities along the eastern coast of North America*

After Butler (1953)

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(1953) (Fig. 2). Mann (1947, p. 332) says giant size of invertebrates is a characteristic of Antarctic seas and that large size with a correspondingly relatively small surface favors life in cold surroundings. Several species of fishes, which on the Gulf Coast of the United States are too small to be of any value, are utilized commercially in the Middle Atlantic States where they attain greater size (Gunter, 1950). Wimpenny (1941) has discussed this subject in some detail, has summarizing the literature, and discussing some of the exceptions to the general rule.

It is also well known that organisms in colder seas grow more slowly, mature later sexually, and live longer. Slow rate of growth, greater length of life, and larger size in colder waters are somehow connected. Clearly these characteristics are connected with temperature, and, within certain limits, all become more emphasized as temperature of the water drops. This is a fundamental aspect of growth comparable to what happens to populations of bacteria grown under comparable conditions but at different temperatures (Graham-Smith, 1920). Bacteria grown at lower temperatures reach a higher peak of concentration and at a later time than those grown at higher temperatures. Marine Protozoa in cold currents grow to larger size than their relatives from warmer waters (Kofoid, 1930, p. 4). The same thing has been noted in certain copepods (Steuer, 1931). Some Radiolaria increase in size with depth, apparently because of the lowering temperatures (Popofsky, 1908). Whatever the nature of this phenomenon paleontologists can take advantage of it. A pole to equator gradient of decreasing size over widespread horizons would indicate something of the climate of the area examined, might possibly throw light on changes from time to time, and give some indication of comparative temperatures prevailing in the preexisting seas.

Jordan (1891) and others have noted that marine fishes and other animals have structural correlations with temperature. Apparently the observation was first made by A. Gunther in 1862. Hubbs (1926) discussed the growth and development of fishes in warmer and colder waters and summarized the literature on the subject. Growth and morphogenetic differentiation are accelerated or retarded in the same ways and seem to follow parallel courses. In warm waters fishes develop rapidly, but growth and differentiation also come to a stop or are retarded more quickly, probably by attainment of sexual maturity as well as other factors. Therefore, fishes living in cold waters grow to a larger size, mature later sexually, have smaller heads proportionately, and have more vertebrae, cirri, bony plates, and spines than do their congeners in warmer waters. Möbius and Heincke (1883) appreciated this fact when they compared fishes from the deeper colder waters of the sea and those of warmer, brackish waters. Mann (1947, p. 328) suggests that the larger number of vertebrae of Antarctic fishes is due to the fact that ossification comes late, and therefore there is more time for subdivision. Hubbs stated that spiny-rayed fishes with the low-vertebral formula of 10 + 14 all pass through a rapid and abbreviated development. He summarized the literature, which shows that closely related species with different rates of development have varying degrees of final differentiation. This difference in final differentiation, correlated with rate of development, may be brought about by environmental factors or any condition leading to retardation of growth or stunting. It may be related to salinity or other factors.

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Those fishes which pass through a protracted development usually show an extenuation not only of growth, but also of those age differentiations in form which result from the differential rate of growth in various parts of the body. They usually have, for instance, proportionately shorter heads and smaller eyes than related forms (or individuals) of more accelerated development, the normal age changes in the proportions of these parts being carried to a farther degree. . . . The changes seem to occur when the basis of retardation is individual, as well as when it is genetic. Fishes of retarded development frequently show, also, an increased development of those modifications of the skin, such as cirri, bony plates and spines, which appear at a relatively late stage.

This increase in differentiation of form and of dermal structures in the later part of development, under retardation conditions, is not merely proportionate to the extenuation of growth rate; it is evident sooner in reference to general development. Thus not only at the larger sizes attained, but also at comparable sizes, the head and the eye are proportionately reduced. This general phenomenon lines up with the central interpretation that differentiation is affected in the same direction as growth by conditions altering the development rate. In this case the action of differentiation controls (inhibitions) is obviously hastened and accentuated in accelerated development. (Hubbs 1926).

In any case there is ample evidence that a pole to equator gradient of final differentiation (number of segments, increased dermal modifications, and meristic characters in general) exists among fishes, which is correlated with increased size along the temperature gradient. The fishes living in colder waters have more vertebrae, spines, bony plates, etc., and attain larger size. There is every reason to believe that this gradient existed in the past seas when latitudinal differences in climates were extensive. This morphological gradient may be of some value to the paleontologist in evaluating previous environmental conditions.

Just how general the above applies in the plant kingdom is not known. Most organisms have not been studied with this point in mind. Lehenbauer (1914) found that rapid growth of plant seedlings under high temperature is not maintained while slow initial growth at low temperatures is maintained under prolonged exposure.

Hegner (1919) reported that spines of the fresh-water protozoan, *Arcella*, were longer when the animals were raised at high temperatures than when raised at low temperatures. The spines of various marine Protozoa and diatoms are longer in the warmer waters of the tropics than in colder seas. This holds true within a given wide-ranging species and for different species. Similarly, fall and winter generations in the temperate seas have shorter spines than summer generations, and specimens living in cold currents have shorter spines or horns, as in the dinoflagellates, than specimens from warmer waters. Wesenberg-Lund (1910) showed that winter forms of fresh-water Protozoa, rotifers, and Entomostraca are less spinose than summer forms. The rule holds for fresh water as well as the sea. Viscosity of the water is lowered by rising temperature, and the longer spines which develop on the nonmotile unicellular organisms in warm waters keep them afloat better than shorter spines would. Viscosity of water in the open sea is largely a function of temperature. A change from 25° to 0°C will double the viscosity. Therefore, diatoms may sink to the thermocline and no farther, and may bank up there, rather than sink below the photic zone.

ECOLOGICAL GRADIENTS

Older naturalists recognized the similarity between the cold-water biota at the opposite ends of the earth and originated the theory of bipolarity (Chun, 1897). For a time it was thought that many of the species around the north and south poles were identical, although distribution was discontinuous. It is now known that very few species are identical, and these are continuous at the depths, but there are strong parallels or counterparts of genera and families of organisms. There is also a bi-

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polarity of phenomena, such as the mass production of diatoms in the spring. Probably bipolarity developed as a result of parallel evolution of organisms under similar conditions. In any case it is closely connected with temperature of the seas. Ekman (1953 and earlier) points out that bipolarity is not confined to polar biota alone but is quite common with temperate species. He says it is not a taxonomic bipolarity alone and calls attention to other phenomena which constitute a "bipolarity of analogous phenomena."

Hesse *et al.* (1937, p. 159) say

> Large-yolked eggs, with more complete development of the embryo within the egg, and the brood care or ovoviviparity which are associated with such eggs, are by no means confined to cold waters; but the frequency with which these phenomena appear among the most diverse groups in arctic and antarctic seas indicates a convergent association with low temperatures.

It is generally accepted that in the seas life is most abundant in the colder parts of the world. Polar and Temperate ocean waters are much richer in plankton than are tropical waters, and the bottoms of cold oceans have a much more abundant fauna than do those of tropical seas. Warming (1909, p. 170) said the most luxuriant "forests" of brown seaweeds develop in the coldest seas. Murray (1896) said that the organic material in plankton tows is much greater in cold seas than in the tropics. Murray (1908), Johnstone (1911, p. 72), and Pearse (1936, p. 70) said that lower metabolic rate and longer length of life partially explain the greater abundance of life in the colder seas. However, Regan (1929) said the amount of life produced in the tropics in a year's time was greater than in the cold zones, that it was used up faster, and did not reach such peaks as in areas with a short growing season. There is certainly a more rapid turnover of energy in the tropics because of higher temperatures. It is also possible that because of the greater depth of the photic zone there is as much living material per water column in the tropics as in the temperate zone. However, the great fisheries of the world are in the temperate zones, and it is certainly true that there are vast concentrations of one or a few species in the colder seas at certain times, unlike anything known in the tropics.

Möbius recognized that eurythermal animals are much less numerous than are the stenothermal species which can withstand only equable temperatures. Hesse (1913) said that in the North Sea, where the temperatures were low and uniform, the fauna was abundant, but it was scanty where the temperature varied. However, species that can live at equable warm temperatures are much more numerous than those which can live at equable cold temperatures. The numbers of individuals in given species decrease from the temperate to the tropic zones, but the numbers of species becomes much greater. This applies to animals and plants alike as a whole and for most major subdivisions within each kingdom. It also holds both on land and sea. Therefore, another cold to warm gradient is established which can be utilized by the paleontologist concurrently with the decrease in maximum size of marine animals from cold to warmer zones. The numbers of individuals of a given species, within major groups, decrease, while the number of species increases considerably. The numbers of families also increase. Many families of marine animals are found only in the tropics or subtropics. Hesse, Allee, and Schmidt (1937, p. 24) give a table of the genera and species of ascidian genera from the poles to the tropics. There are

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145 species around both poles and 635 in the tropics. Ekman (1953) has given several examples. Wimpenny (1941) has presented similar tables, from various sources, for algae, Coccolithophoridae, sponges, tunicates, Crustacea, and fishes. He has also given tables of fishery yields from various parts of the earth showing inferiority in yield for the tropical area compared with those north and south of it. Copepods, corals, and other groups show the same thing. Ninety species of reef corals occur in Hawaii, but only 10 at the northern limit of their range in the Bermuda Islands. Many families of fishes are found only in the tropics, few have no representatives there, and most families have the majority of their species there. Almost as many species have been reported from the Moluccas as are living in both the fresh and salt waters of Europe. Jordan (1891) found 72 species in one haul of a seine at Key West, Florida, while a week's work in Massachusetts resulted in the tabulation of 48 species. Many observers have noted the uniformity of the plankton in cold seas in contrast to the vast diversity in tropical waters.

Cleve (1900) found 34 species of Atlantic copepods living between temperatures of 20.3° to 27.5°C, 19 between 11.4° and 19.6°C, and 8 between 0° and 11.1°C. Murray (1896) has shown that the number of species of organisms decreases with depth. Chun (1897) stated that cold water is unfavorable to the formation of varieties. The diminution in species from warm to cold zones seems to be one aspect of the impoverishment which occurs when any deviation from the optimum takes place and any physical or chemical factor varies toward the extremes.

Murray (1896) and Chun (1897, p. 35) noted the scarcity of larval invertebrates in the plankton of the Arctic and Antarctic seas. Thorson (1936) has observed that in the waters of East Greenland there is phytoplankton production for only 3 weeks or 6 weeks a year. He says (Thorson, 1950) very few planktotrophic larvae can complete their development in this length of time, which accounts for their scarcity in colder seas. He adds that poor food conditions are characteristic of the continental shelves of the coldest seas over a large part of the year. In the high seas, plankton production is comparatively richer. Nevertheless, whatever the full relations of metabolic rate and temperature to the growth and production of organisms in cold and warm seas, the colder seas are characterized by great density of bottom life and few species.

Thorson (1950) has demonstrated another pole to equator gradient associated with temperature, which should be of particular interest to paleontologists, as he suggests. There are no known planktonic prosobranch larvae in the high Arctic and Antarctic seas, but as the tropics are approached the percentage of species with pelagic larvae increases and in some areas may be as high as 85 per cent. As a general rule species with large eggs and bottom larvae develop a large, coarse apex, while species with planktonic larvae have a delicate, narrowly twisted finely sculptured apex. These can be seen in fossils and may be of importance in studying the temperature gradients of former seas. These statements apply to shelf seas and not to the open oceans (Fig. 3).

Wimpenny (1941) has discussed the cold to warm gradients in the seas and calls attention to the similarity of ecological and physiological polarity. His paper should

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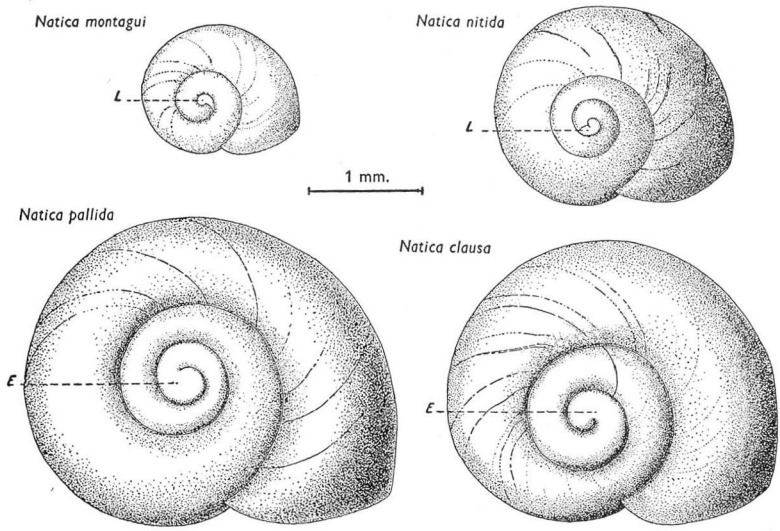

FIGURE 3.—*Sketches showing increase of size in apex of* Natica *shells in species from colder waters*
From Thorson (1950)

be consulted by those interested in additional literature and more extensive discussion of the physiological basis of these phenomena.

The biological differences discussed above are correlated with temperature gradients and extend from the poles to the tropics. However, this general picture is complicated by cold and warm currents in various regions, depth gradients, and the presence of bays and estuaries with salinity gradients which extend at right angles or may even be reverse to that of the temperature. Therefore, care in interpretation should be used where evidence of gradients is found in geological units. It is an opportune fact that depth, current, and salinity will show greater changes in short distances and may thus differentiate themselves from temperature gradients.

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Chapter 9

Oxygen in the Ocean*

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"Circulation is responsible for the aeration of The Deeps, without which all but the uppermost stratum would be a waste more desert than the Sahara" —H. B. Bigelow

INTRODUCTION

In the early investigations of marine biology, many scientists believed that the deeper parts of the ocean must be anaerobic and azoic. However, deeper and deeper probes in the latter half of the nineteenth century showed that life existed and that dissolved oxygen was present to the greatest depths sounded (C. W. Thompson, 1874). As early as 1869, the oxygen content at depths as great as 2090 fathoms had been determined by W. L. Carpenter (1874), the chemist aboard the PORCUPINE; he ventured to predict to the biologists whether their dredge hauls would be "good" or "bad", depending on the proportions of dissolved oxygen and carbon dioxide he found in the water.

Dittmar's analyses of oxygen samples taken on the CHALLENGER expedition in 1873–1876 (Dittmar, 1884) were the first relating to the general distribution in the world oceans. Dittmar was surprised to find surface-oxygen contents showing "negative deficits" from the amounts he computed for saturation, and he noted "very small values for the dissolved oxygen. . . at many places of the ocean bottom [and] . . .occasionally even at moderate depths. . . ." (p. 226). He also observed (p. 225) "Amongst the many deep-sea waters which were analysed for their gas contents, we found none that were quite free from absorbed oxygen, which confirms our conviction that absolute stagnation nowhere exists in the ocean, not even at its greatest depths".

Since the time of the CHALLENGER expedition, investigation of the distribution of dissolved oxygen in the sea has closely attended oceanographic exploration, and at present a body of data exists which is the most extensive for any of the nonconservative, biologically conditioned variables of the marine environment.

Oxygen can be added to the sea only in the upper layers, by absorption of air and, in a layer strictly limited by the depth of light penetration, by photosynthesis. At the surface, oxygen can be lost from the sea by exchanges with the atmosphere, but at all depths it is consumed by the respiration of plants and animals, including the decomposition of organic material by bacteria. Reactions of oxygen with reduced materials such as sulfides, iron[I], manganese[II] and [III], other auto-oxidizable substances, and the consumption of oxygen actuated by enzymes are of limited extent and largely confined to the surface and bottom layers (Thompson, *et al.*, 1934; ZoBell, 1939). The respiratory processes of practically all organisms require the oxidation of organic compounds which are formed only in the upper layers, and so consumption of oxygen at all depths is limited by processes which have occurred in the

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upper, photic zone. Since the rate of molecular diffusion through water is too small to be effective in carrying dissolved matter great distances, replenishment of oxygen to the deeper parts of the ocean can take place only by the circulation of waters oxygenated in the surface layers, which themselves insulate the deeper waters from atmospheric exchanges.

The distribution of oxygen in the oceans of the world is, therefore, the manifestation of processes which (1) add oxygen to the surface layers, (2) consume oxygen by respiratory, chemical, and enzymatic oxidation, and (3) distribute it to all depths (Gaarder, 1927; Wattenberg, 1927; Sverdrup, 1929; Bigelow, 1931; Vaughan, 1940). Its distribution differs from that of the conservative properties of sea water because it is intrinsically involved in the biological processes, which are invariably accompanied by corresponding changes in oxygen, carbon, phosphorus, nitrogen, and the other elements of which protoplasm is composed.

SOLUBILITY OF OCEAN GAS IN SEA WATER

When in equilibrium with 1 normal atmosphere of dry air containing 20.90 per cent oxygen, the solubility of oxygen in sea water decreases with increased temperature and salt content according to the equation

$$1000a = 10.291 - 0.2809t + 0.006009t^2 - 0.0000632t^3 - Cl(0.1161 - 0.003922t + 0.0000631t^2)$$

1000a is the solubility of oxygen in ml at *NTP* in 1 liter of water
t is the Centigrade temperature
Cl is the chlorinity in parts per mille

This relationship was definitively determined by C. J. J. Fox (1909)[1]. Dittmar (1884) investigated the solubility of oxygen in sea water, but his data did not fully show the effect of the salt content (Whipple and Whipple, 1911). In the range of salinity found in most sea water, a temperature change of 1°C corresponds to a solubility change of 0.1 to 0.2 ml/liter.

Whipple and Whipple (1911) were in the process of determining these constants when Fox's data came to them. They abandoned further experiments, since their results at that point agreed with Fox's, and used his data to compute the amount of oxygen dissolved in sea water when in equilibrium with a normal atmosphere saturated with water vapor, expressing the solubilities in parts per million. The amounts of oxygen soluble in sea water in equilibrium with 1 atmosphere (760 mm) of pure oxygen gas have been computed by Sverdrup *et al.* (1942) and by Redfield (1948b) from Fox's (1909) data.[1] The basic data of Fox and the Whipples have been used to construct expanded tables, graphs, and nomograms (Table 1).

"Percentage saturation" is frequently computed using the formula

$$O_2/O_2' \times 100 = O_2\%$$

where O_2 is the observed oxygen content, O_2' is "100% saturation". The term "100% saturation" has no physical meaning in subsurface waters, where there is a hydrostatic head directly proportional to the height of the water column (Rakestraw and Emmel, 1938). Subsurface concentrations corresponding to greater than "100% saturation" are frequently referred to as "supersaturated" but do not necessarily represent a metastable system, as this term ordinarily does in physical chemistry.

The difference between the actual oxygen content and the concentration at "100% saturation"

[1] P. F. Scholander has pointed out to the author that neither 20.90 nor 20.99 per cent oxygen is acceptable for the composition of the atmosphere. The latter figure is quoted by Humphreys (1926), Sverdrup *et al.*, (1942), and other writers. Glueckauf (1951) recommends 20.946 ± 0.002 per cent as the most likely figure for the O_2 content of uncontaminated air, but Scholander states that it is somewhere between 20.93 and 20.95, depending on the method of analysis and on possible real fluctuations in the composition of air. *See also* Hock *et al.* (1952).

Since the writing of the present paper, new oxygen solubility data have been published (Truesdale, G. A., Downing, A. L., and Lowden, G. F., The solubility of oxygen in pure water and sea-water, Jour. Appl. Chem., vol. 5, no. 2, pp. 53–62, 1955) which indicate that the solubility is appreciably lower than Fox reported.

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TABLE 1.—*Representations of oxygen solubility in sea water*

Nature	Expression of salt content	Expression of temperature	Expression of oxygen solubility	Dry air	Saturated air	Reference
Equation and Table	‰ Cl	°C	ml/liter	X		Fox (1909)
Table	ppm Cl	°C	ppm		X	Whipple and Whipple (1911)
Nomogram	‰ Cl	°C	ml/liter	X		Kalle (1939)
Nomogram	‰ Cl	°C	mg-atoms/liter		X	Tully (1949)
Table	‰ S or ‰ Cl	°C	ppm		X	Redfield (1948b)

($O_2' - O_2$) was referred to by Dittmar (1884), Brennecke (1909), and others as the "oxygen deficit", and by Redfield (1942) as the "apparent oxygen utilization". Buch (1929) used the term "biologically uninfluenced" oxygen, O_2^N, and computed it from the observed nitrogen content of the water and its salinity, because he felt these were less subject to *in situ* changes than was temperature. The salinity and the temperature at which this amount of nitrogen just saturated the water, found from Fox's tables, were used to compute what the oxygen content of the water was when it became saturated with both oxygen and nitrogen—*i.e.*, when the oxygen content was still "biologically uninfluenced". Rakestraw and Emmel (1938) redetermined nitrogen-solubility data, accounting for the presence of the small amounts of other inert atmospheric gases, chiefly argon, by improved methods, thus improving the precision of determining the "biologically uninfluenced" oxygen content.

The assumption that all the waters of the oceans have at one time been at the surface and at that time became approximately saturated with the atmospheric gases was made by Dittmar (1884) and has been confirmed by observations that all ocean waters are approximately saturated with nitrogen.[2] Oxygen and nitrogen are subject to the same physical and hydrographic influences, but nitrogen is essentially uninfluenced by biological and chemical changes and thus affords a measure of what the oxygen content would be if unchanged by the latter (Buch, 1929; Rakestraw and Emmel, 1938; Hamm and Thompson, 1941, and others).

Oxygen-solubility relationships are such that, on mixing two masses of water of different temperature, each just saturated with oxygen, the resulting mixture will be "supersaturated" with respect to the equilibrium solubility of oxygen (Rakestraw and Emmel, 1938).

PROCESSES AFFECTING THE DISTRIBUTION OF OXYGEN IN THE OCEANS

EXCHANGES ACROSS THE SEA SURFACE

The difference between the partial pressures of oxygen in sea water and in air will determine the direction of exchange with the atmosphere. Near the surface, local nonequilibrium concentrations may exist in the sea because of biological activity and upwelling, but contact of the surface layers with the atmosphere and vertical mixing tend to eliminate these deficits and excesses. In regions where there is extensive photosynthetic production of oxygen, excess gas will tend to escape into the atmosphere, and, in regions where upwelling brings unsaturated water to the surface, oxygen will tend to be absorbed by the water (Fleming and Revelle, 1939), and a homogeneous surface layer, in equilibrium with the atmosphere, will result. The thickness of this layer will vary with geography, season, climate, and weather (Fig.

[2] D. E. Carritt, in a paper read before the American Society of Limnology and Oceanography Meeting at Gainsville, Florida, September 1954, pointed out that changes in barometric pressure can account for appreciabe fluctuations in the amounts of atmospheric gases that will be in solution when equilibrium is established with the natural atmosphere.

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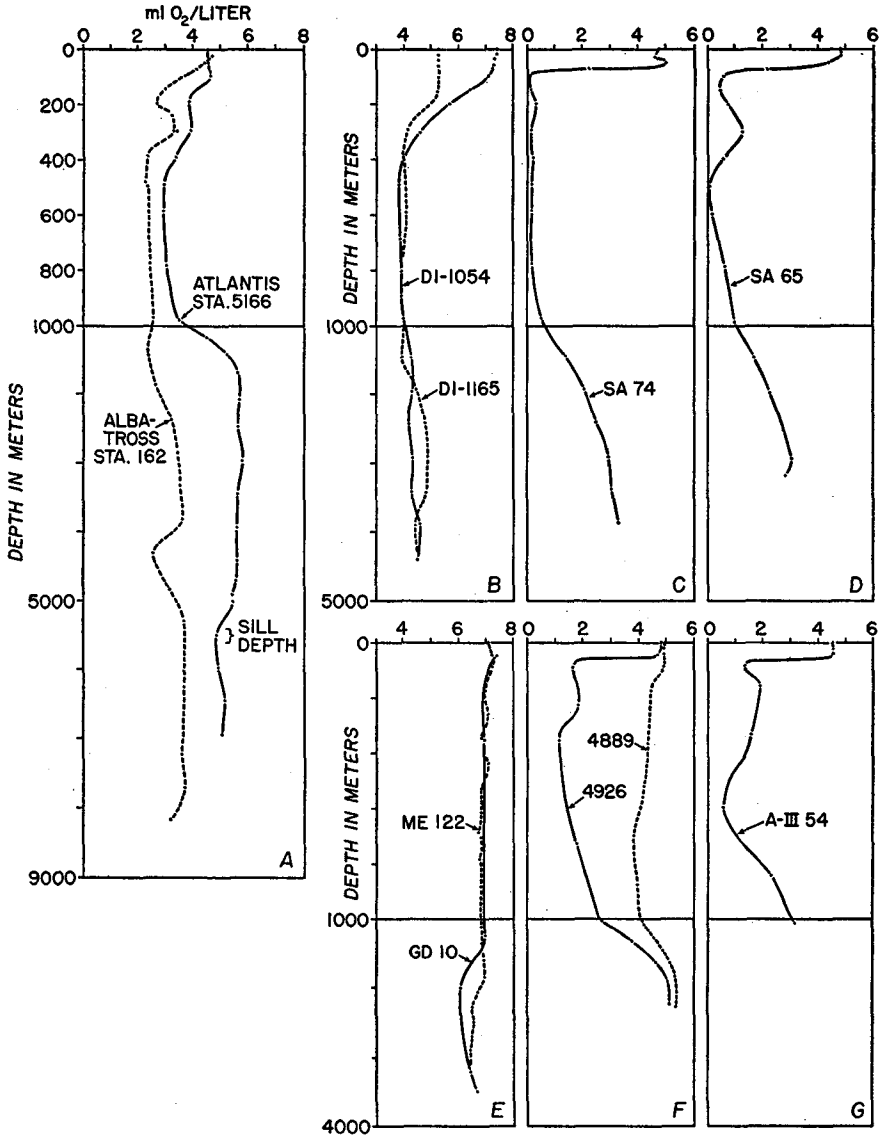

FIGURE 1.—*Representative vertical distributions of oxygen*

A. ALBATROSS station 162 in Mindinao deep. 23 January, 1948. 5°23′N.,127°48′E., data from Bruneau *et al.* (1953), and ATLANTIS station 5166 in the Brownson Deep, 24 February, 1954. 19°55′N., 64°51′W. B. DISCOVERY Station 1054 in Antarctic Convergence. 3 December, 1932. 50°07.8′S, 35° 48.6′N. DISCOVERY station 1165 in Subantarctic Convergence, 24 February, 1932. 41°00′S., 09°30′E. Data from DISCOVERY Committee (1949). C. ALBATROSS Station 74, in eastern tropical Pacific. 22 September, 1947. 11°39′N., 114°15′W. Data from Bruneau, *et al.* (1953). D. ALBATROSS station 65 in eastern tropical Pacific, showing two minima. 16 September, 1947, 6°21′N., 103°42′W., data from Bruneau *et al.*, (1953). E. GODTHAAB station 10, 3 June, 1928, 56°56′N., 51°17′W., and METEOR station 122, 55°03′N., 44°46′W., 9 March, 1935, in North Polar Front. Data from Bulletin Hydrographique for 1929 and 1936. F. ATLANTIS stations 4926 in tropical eastern Atlantic 28 February, 1952, 12°53′N., 22°59′W., and 4889 in southeastern North Atlantic, 4 February, 1952, 29°52′N., 30°12′W. G. ALBATROSS III station 54 showing two minima and lowest concentrations observed in tropical eastern Atlantic. 16 February, 1952, 17°00.5′N., 30°03′W.

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1 *A*, *B*, *F*, and *G*). In most parts of the oceans, the processes of photosynthesis, respiration, upwelling, and vertical mixing are such that very few subsurface concentrations of just 100 per cent saturation are found. Large near-surface oxygen deficits are found in regions of upwelling; these areas in the south Atlantic are shown in Wattenberg's (1939a, Beilage L to LVIII) charts of the percentage of saturation found at several depths. The depth to which equilibrium with the atmosphere is achieved is largely determined by the stability of the water, which in turn determines the ease of vertical mixing, is related to the depth of the seasonal thermocline, and is markedly affected by winds. Seiwell (1934) found that in the western North Atlantic the oxygen content generally begins to decrease at about the same depth as does the temperature. In the latitude of Bermuda the uniform oxygen layer was about 350 m thick, but it was less than 35 m thick off Chesapeake Bay (36°12′N., 73°32′W.). The thickness of the layer corresponded to the depth of the thermocline in both places. Rakestraw and Carritt (1948) found a seasonally fluctuating correspondence between the depth of the oxygen minimum and of the thermocline at stations in the western Atlantic slope water and in the Sargasso Sea. According to Wattenberg (1939a, Beilage LI), the layer of uniform oxygen content is about 50 m deep in the Atlantic south of 50°S., and at 100 m the water in these latitudes is still 90–95 per cent saturated. In many places in the equatorial regions, the surface waters are less than 92.5 per cent saturated, and at 100 m large areas of low-oxygen concentrations occur.

Redfield (1948a) studied the annual cycle of oxygen exchanges across the sea surface in the Gulf of Maine. He assumed that *biological* changes in the oxygen content in ml/liter, ΔQ_x, could be estimated from the equation

$$\Delta Q_x = 28.3\,\Delta PO_4^{\equiv},$$

where ΔPO_4 is the change taking place in the inorganic phosphate in milligram atoms/M^3. Assuming that in the area studied exchanges of oxygen across the sides and lower surface of the water column were negligible, the total change in oxygen content, ΔQ_o, is given by

$$\Delta Q_o = \Delta Q_x + \Delta Q_E,$$

where ΔQ_E is the exchange of oxygen across the sea surface, and can be computed from changes in the dissolved oxygen and phosphate in the water column. If ΔQ_E is negative, it represents the escape of oxygen to the atmosphere; if positive, oxygen has been taken up by the water. Redfield estimated that about 30×10^4 ml of oxygen leaves a square meter of surface of the Gulf of Maine during the spring and summer, and a similar amount re-enters from the atmosphere during the winter months. About two-fifths of the partial-pressure differences bringing about this exchange was attributable to biological activity, the remainder to the effects of temperature on the solubility of oxygen. Redfield computed that pressure-head differences ranged from −0.021 atmospheres in May to 0.103 atmospheres in January. The values given are for $P - p$, in which p is the partial pressure of oxygen in sea water and P the partial pressure of oxygen in a water-saturated atmosphere. Positive values of $P - p$ favor the movement of oxygen from the atmosphere into the water. They were com-

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puted from the equation

$$P - p = P(C_o - C_x)/C_o$$

in which C_x is the oxygen content of the water and C_o the solubility of oxygen in sea water in equilibrium with air saturated with water vapor at the temperature in question. Using these pressure-head differences, he computed that the coefficient of oxygen exchange was about 13×10^6 cc/m^2 per atmosphere per month in winter and 2.8×10^6 in summer. The range in the coefficients reported by Redfield can be attributed to conditions at the sea surface (sea state, stability, etc.), which make the actual amount of surface on a water column of 1 square meter cross section highly variable. Redfield's estimates, based on observations of phosphate and oxygen concentrations in the Gulf of Maine, are of the same order of magnitude as those of Krogh (1910) and Adeney and Becker (Dorsey, 1940; p. 552–555) based on laboratory experiments in which the absorption of oxygen from bubbles was observed. The coefficient reported by Krogh equals 33.5×10^6 cc per month per square meter per atmosphere; that estimated by Dorsey from Adeney and Becker's data is 7.3×10^6.

The general ideas presented by Redfield must apply to the sea as a whole, with oxygen entering the sea surface for most of the year in polar regions and in regions where upwelling brings oxygen-deficient water to the surface, and leaving the sea surface most of the year in the tropics, where photosynthesis and high temperatures favor excesses of oxygen. Seasonally alternating periods of oxygen exchanges in opposite directions would be expected in the temperate zones.

PHOTOSYNTHETIC PRODUCTION OF OXYGEN

In the photic zone the oxygen content may increase appreciably above that found at the surface and in many places reaches values greater than 100 per cent of equilibrium-saturation concentrations (Fig. 2). Rakestraw (1933) found the upper 20–40 meters of the Gulf of Maine were invariably "supersaturated" in August 1932, and values up to 120 per cent of saturation were regularly observed in the spring. At depths down to the *compensation depth* photosynthetic production of oxygen exceeds its respiratory consumption, by definition, and at all greater depths the net change is a loss of oxygen, even though photosynthetic production continues. The penetration of light is probably the most important factor in determining the compensation depth, but temperature, differences in the species of plankton, and nutrient supply are also important. In regions of intense photosynthetic activity the compensation depth will be nearer the surface because of decreased transparency corresponding to the large phytoplankton populations.

Rates of photosynthetic production and respiratory consumption of oxygen and the compensation depth can be determined by suspending transparent and opaque bottles containing sea water and its organisms at various depths in the ocean, and noting changes in the oxygen concentration. Only respiration can occur in the opaque bottles, but both processes can proceed in the transparent bottles; the differences in the changes in oxygen content are a measure of the photosynthetic production.

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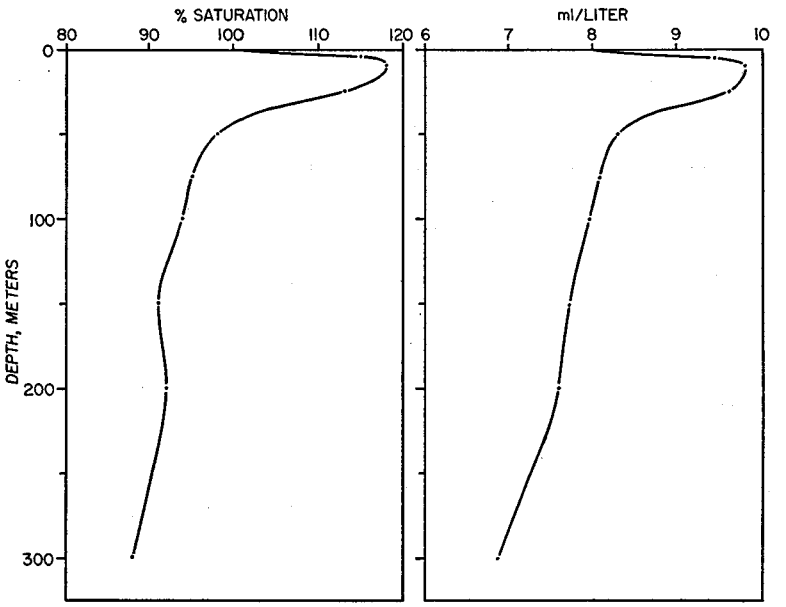

FIGURE 2.—*Representative vertical distribution of oxygen showing greater than 100 per cent saturation* POLARBJØRN Station 20, 14 August, 1932, off East Greenland Coast. Data from Jakhelln (1936).

If

ΔO_l = change in oxygen content in transparent bottle,

ΔO_d = change in oxygen content in dark bottle,

ΔO_p = photosynthetic change in oxygen content,

ΔO_r = respiratory change in oxygen content,

$\Delta O_p = \Delta O_l - \Delta O_r$

and at the compensation depth

$$\Delta O_p = \Delta O_d.$$

Ketchum (1951) has reviewed the depths at which the compensation depth has been found in various parts of the world (Table 2). They range from 0.8 to 2.1 meters in Great South Bay to more than 100 meters in the Sargasso Sea. The latter probably represents an extreme value for the compensation depth but may be typical of those parts of the ocean which correspond to the Sargasso—*i.e.*, the gyrals of the South Atlantic, North Pacific, and South Pacific.

Ketchum (1951) has also reviewed the rates of total organic production estimated by various workers. These can be converted to rates of oxygen production by using Redfield's (1934) or Fleming's (1940) equivalents, from which most of the rates of organic production were originally computed (Table 3).

If natural, mixed plankton is used in these experiments, the respiration of the

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TABLE 2.—*Depths at which the photosynthetic and respiratory rates are equal (compensation depth) at various locations*

Location	Date	Compensation depth (Meters)	Reference
Sargasso Sea	August	100*	Clarke (1936)
Georges Bank	June max.	59**	Clarke (1946)
English Channel	July	45†	Jenkin (1937)
Gulf of Maine	June	24–30*	Clarke and Oster (1934)
Loch Striven	Summer	20–30†	Marshall and Orr (1928)
Passamaquoddy Bay	Summer	17*	Gran and Braarud (1935)
Puget Sound	Summer	10–18*	Gran and Thompson (1930)
Oslo Fjord	March	10*	Gaarder and Gran (1927)
Georges Bank	April min.	9**	Clarke (1946)
Woods Hole Harbor	August	7*	Clarke and Oster (1934)
Loch Striven	March	5†	Marshall and Orr (1928)
Helsingør Sound	Annual range	4.5–7†	Steeman Nielsen (1937)
Great South Bay Long Island	July-August	0.8–2.1†	Unpublished observations

* Exposed for short periods during daylight only

† Exposed for 24-hour period

** Calculated from incident light and transparency

TABLE 3.—*Total oxygen production from various estimates*

Computed from estimates of total organic production from Ketchum (1951).

Location	Production	Reference
English Channel	$72.5–188 \times 10^3$ ml. O/m²/6 mos.	Harvey (1945)
Long Island Sound	$177–1861 \times 10^3$ ml. O/m²/ year	Riley (1941)
Western Atlantic		
28°–38°N.	986×10^3 ml. O/m²/ year	Riley (1941)
38°–41°N.	595×10^3 ml. O/m²/ year	Riley (1941)
28°–41°N.	$260–986 \times 10^3$ ml. O/m²/ year	Riley (1941)
3°–12°N.	517×10^3 ml. O/m²/ year	Seiwell (1935)
Pacific, off S. Cal.	400×10^3 ml. O/m²/ year	Sverdrup and Fleming (1941)
Gulf of Maine	223×10^3 ml. O/m²/ year	Redfield *et al.* (1937)*
Barents Sea	316×10^3 ml. O/m²/ year	Kreps and Verjbinskaya (1932)
Helsingør Sound	82×10^3 ml. O/m²/ year	Steemann Nielsen (1937)

* Calculated for this table using the C:P ratio of 100:2.5

animals is added to that of the plants, so some investigators have used phytoplankton cultures, in order to find the depth at which photosynthesis just balances plant respiration (Jenkin, 1937; and others). In either case, it is assumed that the respiratory rates of both the plants and animals are unaffected by light. Steemann Nielsen (1952) holds that this assumption is not valid and that errors in the light- and dark-bottle method are so great that, where the numbers of organisms and oxygen changes are small, the results are invalidated. However, Ryther and Vaccaro (1954) have com-

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pared rates of biological activity as measured by oxygen changes and as measured by radioactive carbon (C^{14}) uptake by plankton organisms (as advocated by Steemann Nielsen); in actively growing cultures of phytoplankton they found only small differences in the results of the two methods. In regions where phytoplankton populations and productivity are small, there are consistently large differences in the results of the two methods. Ryther (unpublished results) has made observations of productivity in bacteria-free cultures that lead him to conclude that a portion of the photosynthetically bound C^{14} is quickly expelled by the respiration; when photosynthesis is small, this may amount to a large fraction of the total radiocarbon involved. He concludes that the C^{14} method measures *net* photosynthesis, and the oxygen method measures *gross* photosynthesis.

Rates of oxygen changes have been determined directly in very few parts of the world, and such wide variations have been found that it is impossible to estimate the oceanic production or to draw any accurate general conclusions concerning the consumption of oxygen (or total organic production). Riley (1939) found that the mean oxygen production in the northern waters between Cuba and Woods Hole, Massachusetts, was about 0.18 mg per liter per day, about twice that found in the tropical waters. However, he suggests that, because of the greater transparency of the southern waters, the maximum depth of photosynthesis is about three times as great as in the north, and that the total oxygen production in southern waters may equal or exceed that of northern waters.

BIOLOGICAL CONSUMPTION OF OXYGEN

At all depths of the ocean, oxygen is consumed by the respiration of plants and animals, including bacteria. The consumption is limited by the amount of organic matter (except for small amounts reacting with Fe^{II}, Mn^{II}, Mn^{III}, etc.) which can be produced in the water, and in the open ocean is so balanced by ventilating processes that the oxygen supply is never completely exhausted. However, in the Black Sea, threshold fjords, and other arms of the sea, hydrographic conditions are such that the oxygen is completely consumed, and anaerobic metabolism of bacteria produces sulfides. These regions are invariably characterized by hydrographic traps into which disproportionately large amounts of organic material, with its attendant reducing capacity, collect. Nikitin (1931) found that in the Black Sea, at depths greater than about 200 meters, oxygen was absent; hydrogen sulfide was present and increased from 1.48 ml/liter at 300 meters to 6.17 ml/liter at 1500 meters. There is no free circulation of the deep water of the Black Sea; its only connection with the Mediterranean is the shallow Bosporus. Fresh-water tributaries enter the sea, and their waters flow out as a shallow surface layer. During their stay in the region, their inorganic nutrients are consumed by growing plankton organisms. These settle through to the stagnant underlying layers, continually adding organic matter to the deeper parts of the basin. Oxygen consumption far exceeds its supply, and in the absence of oxygen anaerobic bacteria continue to decompose the organic matter with the formation of sulfides. (*See* Chapter 25.)

The direct measurement of rates of oxygen consumption is difficult or impossible in the deep sea. Laboratory experiments, in which the oxygen consumption is observed over a period of time, repre-

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sent static conditions, rather than the dynamic systems of the seas, and more nearly measure the oxygen-consuming potential of a parcel of water than the rate at which oxygen consumption proceeds in nature. Seiwell (1937c) incubated samples of sea water from various depths for 11 days and found that the average daily oxygen consumption was 0.122 cc per liter at 24°C. and 0.0487 cc/liter at 11°C. He realized that these rates were probably much higher than those in nature, and Rakestraw (1947) found that the rates of consumption are higher in the earlier stages of incubation than they are later on. Bacterial growth is accelerated when a surface is presented (Waksmann and Renn, 1936; ZoBell and Anderson, 1936), accounting for the rapid consumption of oxygen in the first few days. Seiwell's work indicated that the amount of oxygen consumed was roughly proportional to the oxygen concentration found at the depth from which the samples were taken.

Rakestraw incubated water samples from the surface, the oxygen minimum layer, and from deep water, at temperatures near those found at the depths from which they were taken. Rates of consumption decreased rapidly with time, and in all cases stopped after 50 days. The highest rates of consumption in waters of subsurface origin, 0.025 ml/liter per day at 8–9°C. for water from the oxygen minimum layer, and 0.035 ml/liter per day at 4–5°C. for deep water, were observed during the first 2 days. Increased temperatures resulted in increased oxygen consumption. The total amounts of oxygen consumed were about 0.5 to 1.0 ml/liter (8–25 per cent of the original oxygen) in the surface samples and 0.15 to 0.4 ml/liter (1–4 per cent of the original) in the subsurface samples. The rapid changer in rates of consumption observed in the early stages of *in vitro* captivity would not be expected in nature, because, to maintain a steady state, such changes have to be balanced by corresponding changes in rates of replenishment, which, in the depths of the ocean, would require improbably large changes in the velocity of water movements.

A quasi-direct estimation of the rate of oxygen consumption was made by Redfield (Rossby, 1936), who observed the changes in oxygen content below 200 meters in a stagnant pool of water below sill depth in the Gulf of Maine. He estimated that the annual oxygen consumption there was 0.36 ml/liter. E. F. Thompson (1939) estimated that the annual consumption of oxygen was 2 ml/liter in the Red Sea.

Rates of biological consumption of oxygen can also be estimated indirectly. One can calculate the oxygen content which will result from physical and hydrographic forces acting on water masses. The difference between this quantity and the amount of oxygen actually present is assumed to be the result of biological activity. If the rate at which the physical and hydrographic changes have taken place can be evaluated, then the rate of biological changes in the oxygen content can be estimated. Physical and hydrographic changes, including mixing and velocities, can be evaluated from the salinity, temperature, and density distribution. In the superficial layers of the sea, current velocities can be estimated with considerable accuracy, either directly or by the application of the theorems of physical oceanography, but, at great depths, reliable estimates of the velocities of water movements cannot now be made with precision.

Sverdrup and Fleming (1941) estimated rates of biological consumption (and production) off the coast of California by an application of the above principles. In the region studied, two water masses, one of northern, one of southern origin and each having characteristic temperature-oxygen and temperature-salinity correlations, enter a region between 32 and 35°N., and mix. The *T-S* and *T-O* correlations were used to compute the proportions of the parent water masses in the mixtures and the oxygen content which should be present if it were unaltered by continuing biological activity. The oxygen concentrations actually observed varied in a systematic way from those expected on the basis of simple mixing along isopycnals; the anomalies were attributed to photosynthesis and biological consumption. The velocities of the water masses were computed; they indicated that, in a water column of 1 sq. cm cross section reaching from a depth of 50 to 700 meters, oxygen was consumed at the rate of 0.11 to 0.22 ml per day, or 0.000169 to 0.000338 ml per liter per day. Other results are summarized in Table 4.

Rates of oxygen consumption in the Atlantic Ocean have been estimated by Riley (1951). He analyzed, statistically, the physical oceanographic observations available from the Atlantic Ocean, and from them computed current velocities and lateral and vertical coefficients of eddy diffusivity. These values were then used to compute the effects of physical processes on the distribution of oxygen, phosphate, and nitrate. Knowing the observed oxygen content, and the effect which physical proc-

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TABLE 4.—*Rates of oxygen consumption off the California Coast*
From Sverdrup and Fleming (1941)

Depth, meters	O_2 consumption
200	1.8 ml/liter/year
400	0.6 ml/liter/year
700	0.05 ml/liter/year
50–700 (range)	3580 milligram atoms O_2/M^2/year

TABLE 5.—*Rates of oxygen consumption in the Atlantic Ocean*
From Riley (1951)

Sigma$_t$	Mean depth (Meters)	O_2 consumption ml/liter/year	Depth range (Meters)	O_2 consumption mg-at/M^3/year
26.5	200	.21	200–1250	3780
26.7	280	.08	1250–4250	145
26.9	370	.050	>4250	33
27.1	510	.055		
27.3	700	.035		
27.5	1000	.013		
27.7	1250	.005		
	1500	.0016		
	2000	.0013		
	2500–4000	.00013		

esses had had on it, he could compute rates of biological changes which had to act to maintain a steady state distribution. These rates were estimated for a series of sigma$_t$ (potential density) surfaces at mid-depths and in a north-south profile in the deep waters. Table 5 presents a summary of these rates of change.

Riley's estimates of rates of consumption are somewhat lower than those of Sverdrup and Fleming (Table 4), but they are of the same order of magnitude. On the other hand, they are much smaller than those made earlier by Seiwell (1934), who computed that the consumption within the oxygen-poor sratum of the western North Atlantic was 0.34 to 0.63 cc per liter per year—*i.e.*, 10–18 per cent of the oxygen present in the minimum layer appeared to be consumed each year. Seiwell's estimates were based on the assumption that maxima and minima observed in the average oxygen content of the layer between the 5° and 10° isotherms were annual. Riley (1951) pointed out that this assumption may not be valid, that Seiwell ignored possible effects of diffusion and transport normal to the profile analyzed, and that it is probably not valid to average the entire layer between the 5° and 10° isotherms. The rates Seiwell computed are about 10 times those computed by Riley (1951) and by Sverdrup and Fleming (1941) at comparable levels.

The apparent oxygen consumption in the oxygen-minimum layer indicates that it is the result of about 100 years' oxidation at the rates Riley calculated. His estimates of minimum rates in the deep water (2500–4000 m) indicate that oxidation has been continuing there for as much as 10,000 years. These estimates can be compared with Kulp's (1953) estimates of the age of ocean waters, made by carbon-14 age dating of the carbonate released from large water samples. Kulp's estimates range from 450 $\pm$ 150 years to 1950 $\pm$ 200 years (Table 6). There are uncertainties in the carbon-14 method, but it promises to be very useful in deducing the speed of deep-ocean circulation. Kulp's estimates and Riley's are not contradictory, but it can only be concluded that, between the oxygen-minimum layer and the bottom, oxygen consumption has continued for between 100 and 10,000 years. Kulp's

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TABLE 6.—*Apparent ages of sea-water samples dated by carbon-14 content*
From Kulp (1953)

Location	Depth (Meters)	Apparent age (Years)
13°35′N.66°35′W.	Surface	Recent
19°24′N.78°33′W.	Surface	Recent
41°00′N.54°35′W.	Surface	Recent
38°42′N.67°54′W.	4,115	450 ± 150
63°46′N.00°26′W.	3,182	500 ± 200
34°56′N.68°14′W.	5,047	1,550 ± 300
35°46′N.69°05′W.	4,641	1,950 ± 200
58°19′N.32°57′W.	1,829	1,600 ± 130
53°53′N.21°06′W.	2,774	1,900 ± 150

figures indicate that the 10,000-year figure (which Riley designates as a maximum age) may be about five times too large.

It is interesting to compare Kulp's first, third, and fourth subsurface samples (Table 6); their locations are not too far apart, and neither are their depths, yet the first is dated at 450 ± 150 years, the latter two at 1550 ± 300 and 1950 ± 200 years, respectively. Salinity, temperature, and oxygen data are not available for these samples; they could be internally consistent if the younger sample represents lower North Atlantic deep water and the older sample the subantarctic bottom water of Wüst (1935, Beilage XXIII).

If Riley's estimates of rates of oxygen consumption are applied to Seiwell's data, an apparent age of the water in the oxygen-minimum layer can be derived. Riley estimated maximal rates (0.055 ml/liter/year) at the σ_t surface 27.1. Seiwell found the oxygen minimum at $\sigma_t = 27.23$, where the apparent oxygen consumption was 2.87 ml/liter (ATLANTIS station 2639, 35°07′N., 66°25′W., Seiwell, 1937b). Combination of these data indicates an apparent age of 52 years. This isentropic surface rises to a depth of 100 meters at about 50°N.—*i.e.*, the water in the minimum zone had traveled at least 15° of latitude (900 nautical miles), and the minimum average drift of the water was 17 nautical miles per year. Seiwell's assumptions led him to estimate that the southerly component of drift was 180 to 360 nautical miles per year.

Riley estimates that 90 per cent of the organic matter produced in the photic zone is consumed in a layer approximately 200 meters thick, and only the remaining 10 per cent is oxidized in the deeper waters. In the deep water, oxygen consumption doubtlessly proceeds very slowly indeed, which would be expected from the low temperatures and the paucity of both living organisms and dead organic matter. Probably wherever excess organic matter is present, biological consumption of oxygen can proceed more rapidly than mixing processes can replenish it. The fact that the deep waters are not anaerobic is further evidence that rates of consumption must be very slow because, to maintain a steady state, these must exactly equal the rate of oxygen replenishment, which can be brought about only by the slow circulation of deep waters. It is probable that rates of consumption depend, in final analysis, on the rates at which organic matter enters the system.

CIRCULATORY AND MIXING PROCESSES

Since the processes by which oxygen can be added to the ocean are confined to the surface layers, it is necessary to examine the processes of advection and diffusion, by which surface waters become distributed into and throughout the deeper layers.

The coefficients of molecular diffusion of oxygen in 1 per cent and 20 per cent sodium chloride are 1.98×10^{-5} and 1.7×10^{-5} cm²/sec respectively (Bruins, 1929).

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Rates of this magnitude are negligible in accounting for transport of oxygen throughout the ocean, which must therefore depend upon the transport of water. This transport can be accomplished by advection, the mass movement of a body of water, or by eddy diffusion, in which transport of solutes is accomplished by mixing across concentration gradients. When mixing occurs across a concentration gradient, dS/dz, the same mixing coefficient, A, applies to all solutes, and the transport, T_s, is the product of this coefficient and the gradient:

$$T_S = A \frac{dS}{dz}$$

Replacement of oxygen to the deeper parts of the oceans (below the main thermocline) is probably brought about by advection, in which cold highly oxygenated water is formed and sinks in the high latitudes and is carried to greater depths and lower latitudes by subsequent lateral and vertical movements. Eddy diffusion along isentropic surfaces may also be important in this transport and is probably predominant above the main thermocline, but it is at present impossible to evaluate the relative importance of advection and diffusion on transport of oxygen. Both oxygen and surface-formed organic material will sink at the high latitudes, and the decomposition of this organic matter, accompanied by oxygen consumption, will proceed within the water mass.

Mixing can take place with the least change in potential energy and entropy along surfaces of equal potential density (isentropic surfaces), and it is generally accepted that, in the absence of vertical mixing, water flows along these surfaces (Montgomery, 1938). Analyses of the distribution of oxygen along isentropic surfaces have been made by Montgomery (1938) and Riley (1951). The former analysis was made as an aid in deducing the circulation in the upper layers of the Atlantic between the equator and 30°N. Riley's analysis enabled him to estimate the rates of biological changes in nonconservative properties. An isentropic analysis of the apparent oxygen utilization in a longitudinal section through the Atlantic from 60°N. to 60°S. was made by Redfield (1942).

These analyses show tongues of characteristic oxygen content extending along isentropic surfaces, with the oxygen content gradually changing in the direction of flow. Redfield's diagrams show a region of maximum oxygen utilization between 50°N. and about 15°S. Between the equator and about 25°N., it is deeper than the main thermocline and nearly concurrent with the salinity minimum which marks the Antarctic Intermediate water, but, south of the equator, the maximum in oxygen utilization lies somewhat above this salinity minimum. In all latitudes, oxygen utilization is maximal between the surfaces $\sigma_t = 27.0$ and 27.25. Montgomery's figures extend no deeper than the surface $\sigma_t = 27.0$, but they clearly show how the lowest oxygen concentrations in the upper layers arise in the eastern tropical Atlantic, extend westward, and are eroded horizontally by mixing along isentropic surfaces.

The distribution of oxygen in a detailed section across the Gulf Stream (Fig. 3) shows that, in the upper layers, the waters of the Stream contain up to 2.5 ml/liter less oxygen than do adjacent waters of the same density, but this oxygen-poor water

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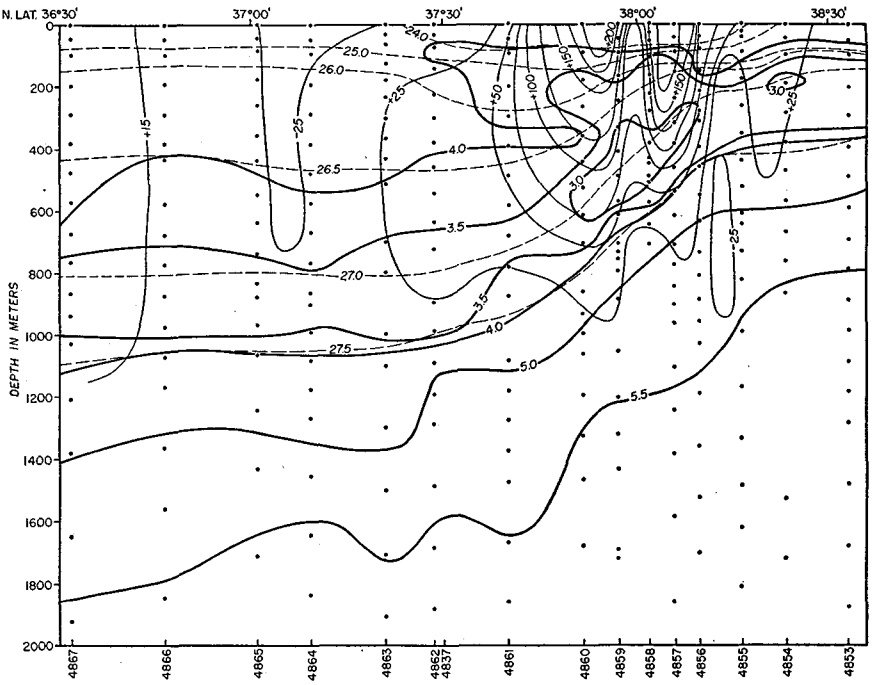

FIGURE 3.—*Oxygen, ml/liter, σ_t, and velocity in cm/sec., in a detailed section across the Gulf Stream*

Oxygen range, <3.5 to >5.5 ml/liter, σ_t range <24.0 to >27.5, velocity range −25 to +200 cm/sec. The figure shows oxygen concentrations of less than 4.0 ml/l at densities less than 26.5 in the region of high current velocities, but not in regions outside the main body of the Gulf Stream—*i.e.*, where velocities are less than about 25 cm/sec. Current velocity data from Worthington (1953).

is in the process of spreading out and mixing, along σ_t surfaces, with the waters on either side. An unpublished section extending south from the tail of the Grand Banks across the Gulf Stream system indicates that oxygen-poor waters are still present, but in smaller amounts, having been reoxygenated by mixing both quasi-horizontally along σ_t surfaces and vertically.

The ease of vertical mixing is inversely related to the stability of the water column, which is nearly proportional to the vertical rate of change in density. The depth to which vertical mixing is effective in the surface layers is reflected in the thickness of the surface layer of homogeneous oxygen content and the depth of the seasonal thermocline. Evaluation of the magnitude of vertical-mixing processes in deeper waters is a difficult problem, but according to Riley (1951) vertical transport is more important than lateral transport in the replenishment of oxygen to the deep parts of the ocean.

The importance of stability to the distribution of oxygen has been shown by Wattenberg (1938, Beilage I). In the southern Atlantic, the oxygen content in the core of the minimum layer decreases as the stability increases—*i.e.*, it tends to retain its low-oxygen concentration best when the stability is great and vertical mixing requires more energy. Wattenberg has also shown (1938, Beilage II) that the depth

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at which the oxygen minimum occurs is great where the stability is small. This is most apparent in the southern convergences.

In this connection, Montgomery (1939) states that the potential-density layers reaching the sea surface in regions of strong convergence may be expected to be thicker (less stable) than those reaching the surface in regions of weak or negative convergence. He concluded, from studying METEOR data, that in certain cases layers of relatively low stability can be attributed to strong convergence at their intersection with the surface, and that these layers have high-oxygen content.

Horizontal and vertical mixing effects are reflected in the shape of the low-oxygen zones extending westward from the west coast of Africa and the Gulf of Panama. Formed near the coasts in dynamic systems flowing generally westward, vertical mixing tends to decrease their thickness, while mixing along isentropic surfaces tends to decrease their latitudinal extent. The zones become thinner, more oxygenated, and cover less and less latitude as they extend westward. Figure 4 shows the shape of the oxygen minimum zone, at whatever depth it occurred, as observed in the Atlantic by ATLANTIS and ALBATROSS III during January to April and in December 1952, and demonstrates the effect of mixing along the westward course of these

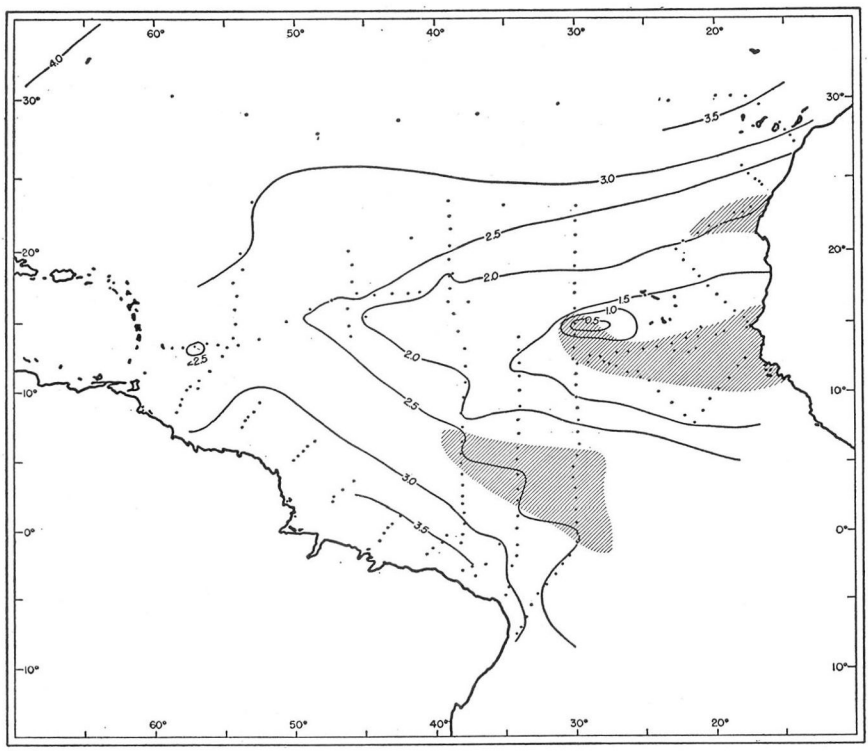

FIGURE 4.—*Minimum oxygen content (ml/liter) at whatever depth it occurred, in the Atlantic Ocean*

As observed by the ATLANTIS and ALBATROSS III January–April and December 1952. Double minima were found in the shaded areas.

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waters. These effects are also shown in Montgomery's (1938) charts of the distribution of oxygen along isentropic surfaces. Along the surface $\sigma_t = 27.0$, oxygen concentrations of less than 2 ml/liter are found in a region covering about 20° of latitude at 20°W., but at 40°W. they extend over only 2° or 3° of latitude, and at about 48°W. they disappear. The zone becomes thinner and covers less latitude with increasing distance westward. Examination of data from the oxygen-poor zone in the tropical Pacific shows a similar erosion of the minimum zone by lateral and vertical mixing processes.

Riley (1951) has attempted to assess transport and mixing rates and the rates of biological change in oxygen content necessary to balance them and maintain a steady state distribution. In the steady state

$$AX + K'Z - V + R = 0$$

where AX and $K'Z$ are the net rates of increase caused by lateral and vertical diffusion, respectively, V is the net rate of increase caused by both lateral and vertical advection, and R is the net rate of increase caused by biological change. Riley's statistical values of these rates of change of oxygen in the upper layers are shown in Table 7.

Negative values for the effect of vertical sheer and a maximum (negative) value of advection are found at $\sigma_t = 27.3$—*i.e.*, near the statistical value of the density at the oxygen minimum (Seiwell, 1937b) and show the tendency of vertical mixing and advection to erode the oxygen-minimum zone.

Riley's analysis of the deep and bottom waters was simplified to consideration of a north-south vertical profile, so that only one component of horizontal velocity was involved. With the exception of one value (0.25×10^{-4} cm/sec at the 3500–4000 meter depth at 45°–54°S.) vertical velocity ranges from .15 (downward) through zero to $-.15$ (upward) $\times 10^{-4}$ cm/sec at depths greater than 1000–1500 meters (Riley, 1951, Table XIV). Coefficients of vertical eddy diffusivity were approximated by Riley (1951, Table XVII), and represent results of an important attempt to establish the order of magnitude of the effects of the various physical and biological processes on oxygen in the ocean. The scarcity of data makes it difficult to determine the reli-

TABLE 7.—*Statistical values of net rates of diffusive, advective, and biological change in oxygen in the upper layers of the Atlantic Ocean*

From Riley (1951)

σ_t	AX	K'Z	V	R
26.5	9.4	13.5	−44.4	−67.3
26.7	2.7	9.9	−12.6	−25.2
26.9	2.0	10.9	−3.5	−16.4
27.1	1.7	6.1	−9.3	−17.1
27.3	.3	−8.1	−19.2	−11.4
27.5	.3	−.4	−4.3	−4.2
27.7	.2	.1	−1.0	−1.3

Values are ml/liter $\times 10^{-10}$ per second.

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ability of the estimates, but no direct methods are available for measuring these quantities in the deep oceans, and Riley has attempted to estimate them indirectly from the spatial distributions of salinity, temperature, and the concentrations of oxygen and other nonconservative elements, which have been observed.

It should be emphasized that the assumption of a steady state may not be valid, especially in deep waters. Worthington (1954) has presented preliminary evidence of possible secular changes in the oxygen concentration of the North Atlantic Deep water which supports the hypothesis that deep-water formation is catastrophic in nature—the very opposite to a steady-state model. Worthington's studies indicate that there has been a decline of about 0.3 ml/liter in the over-all oxygen content of the North Atlantic Deep water in the past 2–3 decades. That this is a real decline and not attributable to systematic errors in the oxygen determinations is attested by the fact that comparative data for the Mediterranean show no comparable decrease in the oxygen content there. This decline represents an annual loss of 0.015 ml/liter and, upon extrapolation to fully saturated water, leads to the date 1810 for the formation of this water mass. The decade 1810–1820 was one of catastrophically low temperatures in the high latitudes, and Worthington proposes that a vast mass of North Atlantic Deep water was formed at that time. This implies that a large mass of the deep water is essentially stagnant, and it could be assumed that it will become anaerobic, unless replaced by a future catastrophe or mixed away by slow convective processes. This also introduces the corollary possibility that large areas of deep-ocean waters may have been anaerobic in the past, but we know of no evidence to support or refute this possibility.

RELATIONSHIPS BETWEEN OXYGEN CONTENT AND PHYSICAL PROPERTIES OF SEA WATER

In the study of the oceans it is useful to identify or characterize water masses by correlations between their conservative properties. The temperature-salinity correlation (Helland-Hansen, 1916) is one of the most useful and most uniform characteristics. However, nonconservative properties change, *in situ*, by biochemical processes, altering correlations between non-conservative and conservative properties without mixing. On the other hand, a non-conservative property may distinguish one water mass from another in which the conservative properties are quite similar, or may help in the study of dynamic relationships within a single water mass.

Rossby (1936) used the oxygen-salinity correlation as a quasi-conservative property of the Gulf Stream; he found it more useful than the salinity-temperature correlation in studying exchanges between the stream and the surrounding waters (Fig. 5). The salinity-temperature correlation was too conservative to distinguish between the waters of the Gulf Stream on one hand and of the Sargasso Sea and Western Atlantic Slope water on the other. Although the oxygen-salinity correlation changed along the course of the stream, it was characteristic and distinctive in sections normal to the stream.

A study of the oxygen-density (σ_t) correlation in the waters of the western North Atlantic, particularly in the Gulf Stream system, has been made by Redfield and the author (Figs. 3, 6). In a near-surface layer, the oxygen content of the Gulf Stream

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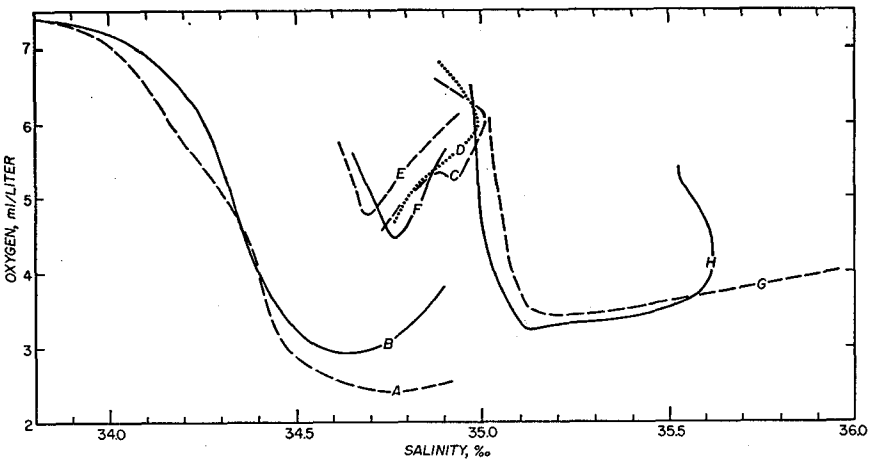

FIGURE 5.—*Characteristic oxygen-salinity correlations*, S = f(O_2)
A. Core of Subantarctic Intermediate Water, Eastern Atlantic
B. Core of Subantarctic Intermediate Water, Western Atlantic
C. Core of Intermediate Deep Water, Eastern Atlantic
D. Core of Intermediate Deep Water, Western Atlantic
E. Antarctic Bottom Water, Eastern Atlantic Basin
F. Antarctic Bottom Water, Western Atlantic Basin
A, B, C, D, E and F redrawn from Wüst (1935)
G. North Atlantic Slope Water
H. Western Sargasso Sea
G and H redrawn from Rossby (1936)

is as much as 2.5 ml/liter lower than that of adjacent Sargasso Sea waters of the same density, in the σ_t range 24.0 to 26.5 (Fig. 6 c). At greater densities, the waters are indistinguishable from those of the Sargasso Sea. Three detailed cross sections of the Gulf Stream have been made and analyzed; these show oxygen-low waters centered at about the maximum current velocities in the stream (Fig. 3). It is indicated that the waters of the Gulf Stream left their origins in the Caribbean and equatorial Atlantic regions with a characteristically low-oxygen content, which is persistent at least as far as the tail of the Grand Banks. This correlation with density seems particularly useful because horizontal mixing can take place most readily along isopycnals.

Other workers have used correlations between the oxygen content and other conservative properties. Jacobsen (1929) plotted percentage saturation against salinity, but, since percentage saturation depends on salinity as well as temperature, it does not appear to be suitable as a characteristic diagram (Montgomery, 1938). Oxygen content was plotted against salinity by Wüst (Fig. 5) to show the correlation between these properties in several water masses of the Atlantic. Seiwell (1937a, Fig. 8) found that at one station which was occupied for 60 hours, the oxygen-salinity correlation behaved essentially as if oxygen were a conservative property at all depths greater than 100 meters. Dietrich (1937) plotted oxygen against temperature (Fig. 7) and showed that the oxygen content varied as much as 2.4 ml/liter at about 13°C. in 12

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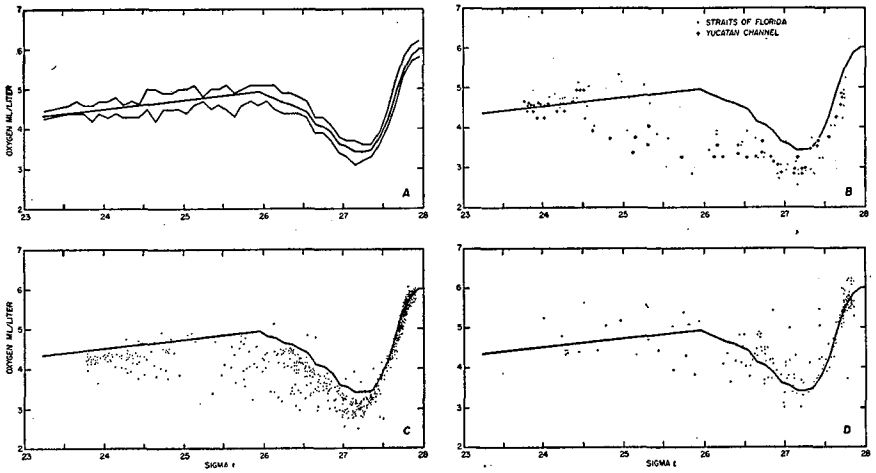

FIGURE 6.—*Oxygen-σ_t correlations, $\sigma_t = f(O_2)$, in A, the Western Sargasso Sea; B, the Yucatan Channe and Straits of Florida; C the Gulf Stream system between 36° and 39° N., and D southeast of the Grand Banks, between 39° and 45° N., and 45° to 50°W.*

The correlation in A is from all observations in the Sargasso Sea between 30 and 40°N latitude. The envelope contains half of all observations made in this area. Between σ_t values of 23.1 and 25.95 the correlation (heavy line) is the least-squares regression; at greater values, the arithmetic mean of all observations. In B, C, and D, the correlation shown in A is repeated. The lower oxygen content of the samples having σ_t values between about 24 and 26.5 is characteristic of the southern waters, but water of these same characteristics was observed in the Gulf Stream system southeast of the Grand Banks.

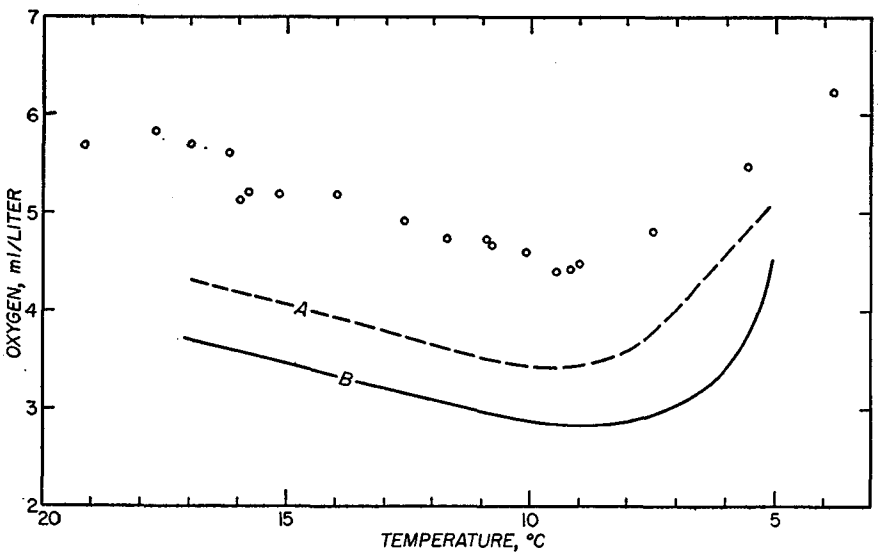

FIGURE 7.—*Characteristic oxygen-temperature correlations, $T = f(O_2)$*

A, Western North Atlantic and B, Western Caribbean Sea and Florida Strait, redrawn from Dietrich (1937). Circles are values observed at DANA station 1369, 12 June, 1922, near the Azores, 35° 44'N., 29°33'W., data from Schmidt (1929).

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stations between Chesapeake Bay and Bermuda, but at the oxygen minimum, which uniformly occurred very close to 10°C., it varied only about 0.6 ml/liter. Between Bermuda and the Azores, the minimum was found at about the same temperature, but at all temperatures the water contained less oxygen than in the Chesapeake Bay-Bermuda section. In stations through the Caribbean to the Straits of Florida, the oxygen at any one temperature decreased as much as 0.4 ml/liter along this course. Other diagrams by Dietrich show the lowest oxygen at a given temperature in the waters south and east of Bermuda and in the Caribbean and Gulf Stream, with the Sargasso waters immediately adjacent to the latter containing considerably more oxygen. Oxygen was plotted against density by Riley (1951) to enable him to determine the characteristic oxygen content of the Atlantic at discrete σ_t surfaces of areas bounded by parallels and meridians with their centers 1000 kilometers apart (Riley 1951, Fig. 11). Miyake (1948) used oxygen-chlorinity correlations to evaluate the effect of the mixing of two water masses on the diurnal variation in the oxygen content of shallow waters.

In addition to these characteristic correlations, Seiwell (1937b) established statistically that in the western North Atlantic the oxygen minimum occurred at that depth where σ_t was 27.23. Sverdrup and Fleming (1941) noted that this was near the density at which the minimum was found, on the average, off the California coast but declined to comment on any possible significance in this relatively close agreement. The main oxygen minimum is also found near this density in most of the central Indian Ocean (data of Bruneau *et al.*, 1953).

Seiwell (1937b) also studied the value of the salinity anomaly at the depth of the oxygen minimum in the western North Atlantic. According to Helland-Hansen (1930) the normal temperature-salinity relationship for the northern North Atlantic is

$$S_t‰ = 34.737 + 0.038t + 0.0029t^2$$

and the salinity anomaly is

$$SA = 100(S‰ - S_t‰).$$

Seiwell used these equations to compute the mean salinity anomaly at the depth of the oxygen minimum; he found a systematic distribution of these values in the western North Atlantic. He attributed high negative anomalies (*i.e.*, salinities lower than normal) to waters of subantarctic origin; these were associated with low minimum oxygen contents. A tongue of high positive anomalies was attributed to waters of Mediteranean origin, and these had relatively high oxygen contents in the minimum layer.

RELATIONSHIPS BETWEEN BIOLOGICAL CHANGES IN DISSOLVED OXYGEN AND OTHER CHEMICAL CONSTITUENTS

The rates at which biological changes in the oxygen content of sea water take place were discussed in an earlier section. Physiologically, these changes are accompanied by concurrent changes in the other elements which constitute living matter. Oxygen is involved in the photosynthetic formation and respiratory decomposition of carbo-

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hydrate, as represented by the simple reversible equation

$$CO_2 + H_2O \underset{\text{respiration}}{\overset{\text{photosynthesis}}{\rightleftharpoons}} CH_2O + O_2.$$

However, the bodies of plants and animals do not consist exclusively of carbohydrate. Nitrogen, phosphorus, sodium, calcium, potassium, iron, chlorine, sulfur, and other elements (especially silicon in the marine environment) are also involved in the processes of formation and decomposition of living tissue. It follows that the above equation should be accompanied by a series of equations showing the fixation and release of nitrogen, phosphorus, and the other elements in definite proportions to the amount of oxygen released and consumed. These proportions will depend upon the composition of the living matter.

Redfield's (1934) study of the proportions in which phosphate and nitrate occur in sea water revealed that these two elements are found in statistically definite proportions one to another, suggesting that the deep water contains the products of the complete oxidation of varying amounts of organic matter of similar composition. Further studies showed a close correspondence between the ratios in which changes in the concentrations of nitrogen and phosphorus take place in sea water and the ratios in which they occur in plankton organisms. Redfield was also able to show statistically significant correlations between changes in total carbon dioxide, the amount of oxygen consumed, and the concentrations of phosphate and nitrate. He concluded that carbon dioxide, phosphate, nitrate, and oxygen are bound and released in statistically definite proportions during the formation and decomposition of organic matter in the sea.

The ratios reported by Redfield were O:C:N:P = 239:140:20:1 by atoms. This O:C ratio is smaller than the theoretical 2:1 ratio involved in the formation of carbohydrate, which Gilson (1937) suggested should be increased by about 20 per cent to allow for the oxidation and reduction of nitrogen. On the other hand, investigations by Sargent and Hindman (1943) indicated that, during the active photosynthetic period, the correspondence between moles of CO_2 absorbed and O_2 evolved was not significantly different from 1. Redfield pointed out that the available estimates of changes in the total carbon-dioxide content of sea water were not very precise.

Cooper (1938) showed that the phosphate figures used by Redfield should be corrected for the analytical error known as the salt effect. Sverdrup *et al.* (1942, p. 236) applied the salt-effect correction and, using the ratio O:C = 2:1, settled on the ratios O:C:N:P = 212:106:16:1 by atoms or 109:41:7.2:1 by weight. These relationships are shown schematically in Figure 8.

Deviations (other than statistical) from these ratios would be expected and are found. In surface waters, particularly near shore, land drainage and other features can appreciably affect the composition. Variations in the composition of plankton populations will affect the ratios of the elements in their decomposition products, and nitrogen and phosphorus compounds are not necessarily released in the same ratio in which they are found in the whole organism. Phosphate is released by living zooplankton (Gardiner, 1937), and nitrogen is excreted rapidly by copepods fed on

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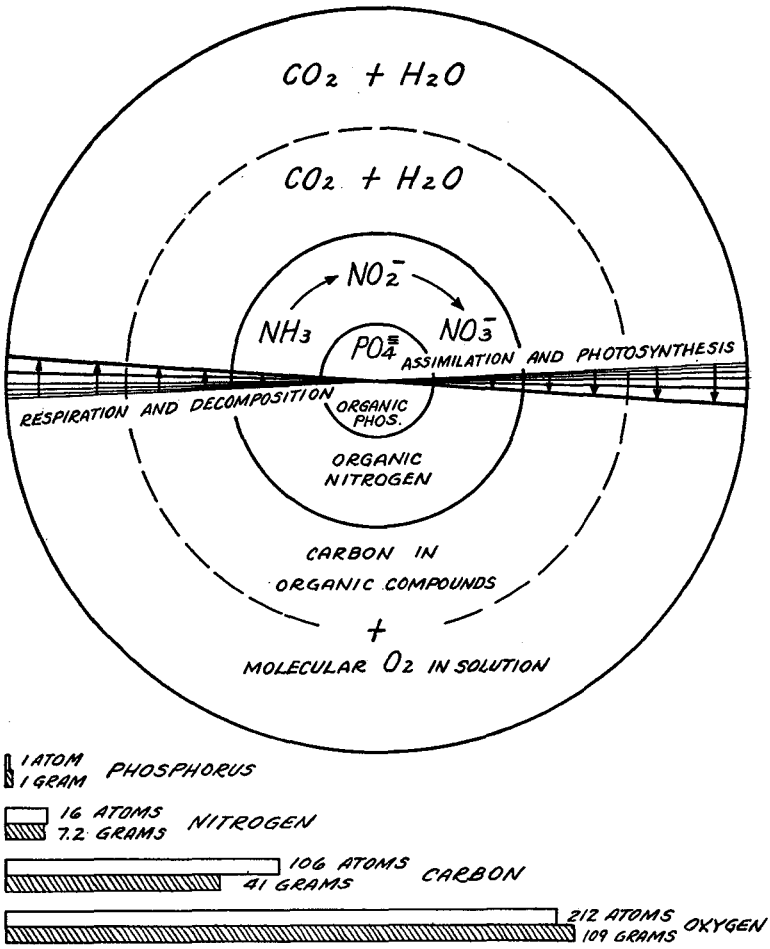

FIGURE 8.—*Representation of the average proportions in which oxygen, carbon, nitrogen, and phosphorus are bound and released by biological processes in the sea*

diatoms (Fuller, 1937). There are doubtlessly other mechanisms by which nitrate or phosphate are released to the water without involving oxygen and carbon dioxide in the statistically normal ratios; refractory compounds may retain one or the other of these elements in bound form, and local concentrations of phosphate may be out of proportion to the concentration of nitrate or the accompanying oxygen consumption. It is probable that in the deeper parts of the ocean, however, oxidation goes essentially to completion and only minute quantities of relatively stable organic compounds are present in the water at any one time. It is here that the ratios hold most reliably.

Even in deep waters, major deviations between the phosphate or nitrate concentrations and the apparent oxygen consumption are found. Redfield (1934) found this true of deep waters having their origins in the convergences in high latitudes. These deviations are the result of the fact that these waters are fully oxygenated when they

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sink from the surface of the sea, but contain appreciable quantities of inorganic nitrate and phosphate, contrary to the situation in most saturated surface waters, in which virtually all the phosphorus and nitrogen are bound in organic compounds. The former circumstance leads to subsurface water containing larger amounts of nitrate and phosphate than would be computed from the apparent oxygen consumption. Redfield (1942) referred to these excesses as "preformed" and computed that the surface waters from 20° to 60°N. contained over 1 milligram atom per cubic meter of preformed phosphate, assuming the relationship

$$O_2(ml/liter) = 0.373\ mga\ P/M^3.$$

This relationship yields negative values in the upper layers from 48°N to 33°S., however, and Riley (1951) pointed out that this can only mean that Redfield over-rated the phosphate regeneration ratio.

Riley (1951) computed a series of nitrogen and phosphorus oxidative ratios for different levels in the Atlantic Ocean. These ratios are highly variable, but they indicate that the O:P ratio is large in the neighborhood of the oxygen-minimum layer. However, the average ratio he computed for the water column between σ_t 26.5 and the bottom is O:P = 255:1 compared with the ratio O:P = 239:1 which Redfield used and the ratio 212:1 which Sverdrup *et al.* (1942) settled on. The numbers empirically arrived at by Riley and Redfield both tend to substantiate Gilson's (1937) factor of 20 per cent additional oxygen needed to oxidize nitrogen compounds, which would require a ratio of O:P = 264:1 by atoms.

The ratios in which oxygen, carbon dioxide, phosphate, and nitrogen are bound and released correspond, statistically and approximately, to the chemical law of combining proportions and enable one to make quasi-stoichiometric computations relating these variables. Oxygen and carbon dioxide are radically changed by exchanges with the atmosphere, but this is not the case with phosphate and nitrate. Thus it is possible, by observing changes in phosphate and nitrate, to assess the extent of biological changes in the oxygen and carbon-dioxide content; and to distinguish them from changes attributable to exchanges with the atmosphere; these principles were used by Redfield (1942) to estimate the exchanges of oxygen across the sea surface, as discussed in a previous section.

Ecologically, these biochemical relationships between dissolved oxygen and the nutrient salts should be more useful, in describing changes in the environment, than a consideration of dissolved oxygen alone. The world-wide distribution of dissolved oxygen is better known than is the distribution of the other nonconservative properties, and, although in most parts of the world ocean the concentration of dissolved oxygen is not important as a factor in limiting the growth of populations, it is functionally linked to the concentrations of nitrate and phosphate, which may become limiting factors.

ORIGIN OF THE OXYGEN-MINIMUM ZONE

The widespread occurrence of minimum concentrations of oxygen at intermediate depths is probably the most striking feature of the distribution of oxygen. Although these minima have counterparts in maximum concentrations of phosphate and ni-

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trate at intermediate (usually somewhat greater) depths, the oxygen feature has received much attention in attempts to explain its *raisons d'etre*. Many oceanographers, beginning with J. P. Jacobsen (1916) and including Wattenberg (1929; 1938; 1939b), Le Danois (1934), Wüst (1935), and Seiwell (1937b; 1937d; 1937e) have offered explanations. These were examined on theoretical bases by Sverdrup (1938), who, with Seiwell, distinguished two basic explanatory concepts. The first, proposed by Jacobsen and held to by Wüst and Dietrich (1936) and supported by Parr (1939), was that the minima (and maxima) are dynamically conditioned by circulatory processes; the intermediate oxygen minima characterize nearly resting boundary layers between different branches of the deep-sea circulation (Wüst), and at the oxygen minimum the replenishment of oxygen by mixing and circulatory processes is at a minimum. Le Danois referred to the very poorly oxygenated zones of the Atlantic and Pacific as fossil waters, implying essentially no circulation. The second concept, held mainly by Seiwell, proposed that the oxygen minimum zone is conditioned chiefly biochemically and represents the depth at which the specific gravity relationships between sea water and sinking detritus are such that the detritus accumulates at intermediate depths, resulting in excessive oxygen consumption at these levels.

Seiwell (1937b) and Sverdrup (1938) point out that in the Gulf Stream System the oxygen-minimum zone does not coincide with a minimum in the mixing and horizontal replenishment processes, and Sverdrup shows that the dynamic explanation requires that (1) the consumption of oxygen must be independent of the amount of oxygen-consuming organic matter, or (2) the amount of oxygen-consuming matter must be at a minimum at the depth of the minimum. The first condition appears to be ruled out on general grounds, and the second seems inconsistent with observations on the distribution of organic matter in the sea, including the recently reported extensive observations of the particle distribution in the ocean made by Jerlov (1953). Sverdrup states other conditions under which the dynamic explanation may be valid: (1) if the amount of oxygen-consuming matter is independent of depth while the oxygen consumption decreases with decreasing oxygen content, or (2) if the consumption is independent of the amount of organic matter but decreases with decreasing oxygen content. The latter condition of both these alternatives is at least tentatively ruled out by ZoBell's (1940) observations that the oxygen tension (in the range 0.31 to 12.74 ml/liter) had little effect on the rate of oxidation of organic matter in sea water by bacteria, and it appears fairly general that within wide limits the oxygen tension has little direct bearing on rates of oxygen consumption by most aquatic organisms.

Another serious discrepancy in the dynamic explanation of the oxygen minimum is its failure to include an explanation of the related phosphate and nitrate maxima. In most parts of the world, these lie somewhat deeper than the oxygen minimum, although this depth difference diminishes if one considers not the minimum-oxygen concentration but the maximum in apparent oxygen consumption (Redfield, 1942) and accounts for the "preformed" phosphate. The phosphate and nitrate maxima are clearly of biochemical origin, since they are not related to the resupply of oxygen

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by processes of aeration, nor can their concentration be independent of the amounts of organic, oxygen-consuming material originally present.

Rakestraw, Rudd, and Dole (1951) have observed that, at one station in the Pacific, the ratio of the two oxygen isotopes, O^{18}/O^{16}, reached a maximum value coincident with the minimum in the oxygen content, and that at all depths to 2870 meters there was a close correspondence between the rise in the isotope ratio and the decline in oxygen percentage. They conclude that O^{16} must be metabolically consumed preferentially over O^{18}. It is difficult to conceive that physical or hydrographic processes—*i.e.*, mixing and flow—could alter this ratio, but it is well known that isotope ratios can be altered by biological processes.

Seiwell and Seiwell (1938) conducted laboratory experiments on the sinking rates of plankton organisms, but their emphasis on the specific-gravity relationships between sinking detritus and sea water appears to have been misplaced. For one thing, it emphasizes relationships between the oxygen minimum and conditions in the surface layers directly above, and for another Parr (1939) seriously criticized their conclusion that sinking particles will asymptotically approach a depth at which differences between their density and the density of the surrounding medium disappear, and sinking stops. Parr's criticism is largely based on the Seiwells' failure to recognize that the density of sinking particles must increase as the particles sink, so that sinking must continue to the bottom.

On the other hand, Sverdrup (1938) showed that Seiwell's theory fails if the oxygen consumption is intrinsically independent of the oxygen content. It is difficult to assume that the oxygen consumption is not independent of the oxygen content, at least within wide ranges of the latter, which forces the conclusion that neither explanation discussed by Sverdrup and Seiwell is wholly satisfactory.

Thompson, Thomas, and Barnes (1934) proposed that the minimum zone in the northeastern Pacific could arise from excessive consumption in the bottom waters in the Gulf of Alaska, which then move southward and are floated on the cold abyssal waters of the Pacific. They postulated that contact with the bottom itself should result in decreased oxygen concentrations, as is demonstrable in many parts of the ocean, and that water thus depleted can move outward and find an equilibrium, intermediate depth. This type of movement appears to have been occurring in the Labrador Sea when sampled by the U. S. C. G. C. General Green (Fig. 9; Soule, 1940, Fig. 55), and Thompson and Barkey (1938) found evidence that waters deoxygenated by the bottom are found at intermediate levels in certain fjords on the western Canadian Coast.

The analysis by Redfield (1942) is enlightening and introduces a new concept: within the depths of the Atlantic Ocean, the oxygen minimum occurs in that layer of water which bore maximal amounts of organic, oxygen-consuming material at the time of its sinking in high latitudes. The density of this water is such that it moves at intermediate depths, and, upon the oxidation of its organic burden, its oxygen content drops well below that of waters above or below it. This explanation does not require that the oxygen minima coincide either with minimum rates of oxygen replenishment or with maximum rates of oxygen consumption, and it is free of assump-

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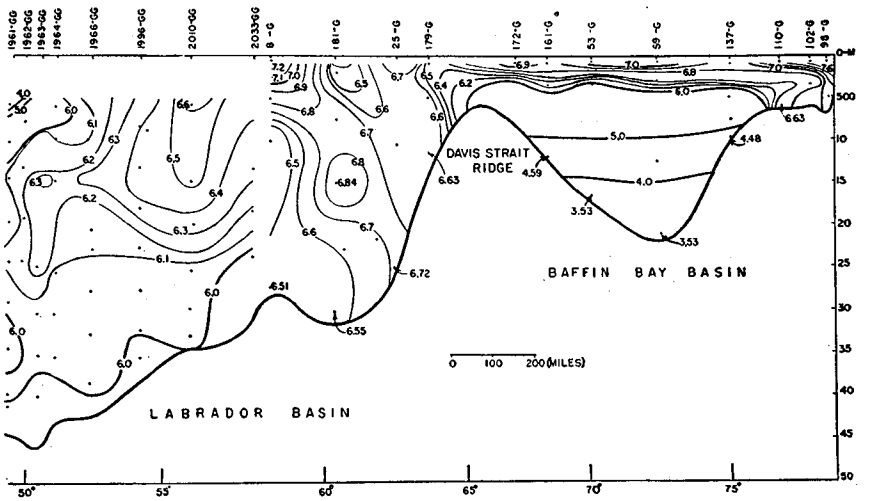

FIGURE 9.—*Oxygen profile,* (ml/liter), *Labrador Sea to Baffin Bay*
After Smith, Soule, and Mosby (1937, Fig. 148).

tions concerning the vertical distribution of current velocities. However, Riley (1951) showed that the rates of oxygen consumption do pass through maxima along isentropic surfaces nearly coincident with the average density at which Seiwell found the oxygen minimum in the western North Atlantic. To maintain a steady-state distribution, this requires that the rate of supply of oxygen-consuming organic matter must also pass through maxima at these levels.

Redfield's analysis involves the zone of maximum apparent oxygen utilization, which lies deeper than the zone of minimum-oxygen content because the lighter, warmer water originally contained less oxygen, and a given oxygen utilization reduces its oxygen content to a lower value. The remaining discrepancy between the depth of maximum-oxygen utilization and maximum phosphate can be attributed to preformed phosphate.

It might be argued that if Parr's (1939) criticism of the Seiwells' views on specific-gravity relationships is correct, then there is no reason to believe that the intermediate layers would retain their organic burden. However, it is reasonable to assume that a large fraction of the oxygen consumption occurs rather rapidly, and also that an early step in the decomposition of particulate matter is the formation of soluble organic compounds not subject to sinking. Redfield, Smith, and Ketchum (1937) found that not more than 6 per cent of the total phosphorus in the Gulf of Maine was bound in particulate matter, although up to 22 per cent of it was present in soluble organic compounds.

On the basis of Redfield's analysis, one can distinguish between the oxygen-minimum zone attributable to waters sunk in high latitudes and the oxygen consumed in the shallower layers of the tropical Atlantic. The latter appears as another minimum zone superimposed on the deeper minimum zone. In large parts of the Atlantic, Indian, and Pacific oceans, the superimposed, lenticulate zones show up as two minima or as inflections in the oxygen-depth curves (Fig. 3). The overlying zones appar-

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ently owe their origin to more or less local introduction of large amounts of organic matter into the upper layers, which in the Atlantic and Pacific is consequent to upwelling along the West African and American coasts. Redfield's analysis clearly relates the oxygen-minimum layer to areas where organic productivity is known to be high and also clearly explains the great differences in the depths at which the oxygen minimum is found in various parts of the oceans.

Comparisons of the Atlantic and Pacific make it obvious that the Pacific is more deficient in oxygen than is the Atlantic. This is true not only of the oxygen-minimum zone but of all the subsurface waters of the Pacific. Many authors, including Schmidt (1925), H. Thomsen (1931), Moberg (1930), and Sverdrup *et al.* (1942), have attributed the very low concentrations of oxygen in the oxygen-minimum zone of the Pacific to its "greater staleness" or to the deflection of aerated polar waters westward at intermediate latitudes, leaving the tropical eastern Pacific a region of very slow and ineffective ventilation. Sverdrup *et al.* (1942, p. 240–241, 754–755) also attribute the higher nitrate and phosphate and lower oxygen content of the Pacific to its slow circulation, which permits the further decomposition of its organic matter.

These explanations do not seem adequate to account for the generally greater oxygen deficit of the Pacific, although it partially explains the location and shape of the minimum zone. Oxidative processes probably go essentially to completion in deep-ocean waters, and, although rates of replenishment of oxygen are important in the equilibrium, steady-state distribution which exists, the amount of oxygen consumed in a body of water is stoichiometrically limited by the amount of reducing compounds introduced into it. Rakestraw's (1947) experiments prove this point fairly conclusively; oxygen consumption stopped after 50 days, but excesses of dissolved oxygen were still present after 2 years, although his bottled samples represented a perfectly static, nonventilated system. It is accepted that phosphate and nitrate concentrations are usually the limiting factors in phytoplankton productivity, and the Pacific is richer in these nutrients than is the Atlantic, making the potential for organic productivity of the Pacific greater. There are no integrated averages for the phosphate concentration or for the apparent oxygen utilization in the oceans, but the highest phosphate concentrations in the Atlantic are about 2 microgram atoms per liter, while in the Pacific up to 3.5 microgram atoms per liter are found (Sverdrup *et al.*, 1942, p. 240). The oxygen consumption corresponding to 0.5 microgram atoms per liter of phosphate is close to 1 ml/liter, so one might expect the Pacific to contain up to 3 ml/liter less oxygen than the Atlantic. This conclusion is based on the biochemical relationships between oxygen consumption and phosphate release alone and is free of any comparisons of circulatory rates.

OXYGEN CONCENTRATION AND POPULATIONS OF THE SEA

The oxygen content of the aqueous environment contrasts markedly with that of the atmosphere. In the lower layers of the atmosphere, oxygen constitutes about 200 ml/liter, with great uniformity, but the maximum in sea water is about 9 ml/liter and ranges between this concentration and nil. It might seem that such extreme variations in an environmental factor would have an important effect on the distribution of species and population densities, but most marine organisms are physiologically better adapted to wide variations in oxygen tension than are many land

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organisms. Although there are wide variations in the respiratory requirements of marine organisms, the literature reveals no simple relationships between these requirements, the distribution of organisms, and population densities.

In general, the literature indicates that, in most aquatic organisms, respiratory consumption of oxygen is essentially independent of the oxygen tension down to some lower limit of the latter. Below this limit, the respiratory consumption may decrease with decreasing oxygen tension, until the tension becomes so low that the organism can no longer survive. Thus, most organisms can withstand large variations in oxygen tension, and only at some low level are the variations reflected in the respiratory rate or survival (Von Ledebuhr, 1939).

ZoBell (1940) found that the *in vitro* rate of respiration by bacteria in sea water was not influenced by varying the oxygen tension between 0.34 and 12.74 ml/liter, but below 0.3 ml/liter the respiratory rate decreased. However, if oxidizable organic matter were present, the bacteria could remove the last detectable trace of dissolved oxygen. A wide variety of observations concerning the oxygen requirements of higher aquatic organisms has been made (reviewed by Bishop, 1950), from which the conclusions in the above paragraph can be drawn.

Under completely anaerobic conditions, only obligate and facultative anaerobic bacteria can live, and their respiration is marked by the production of hydrogen sulfide. In the oxygen-minimum zone of the eastern tropical Pacific, the oxygen content becomes so low that it is scarcely detectable by the Winkler method, but hydrogen sulfide is not present, and oxygen is probably present in minute traces. The region appears to be in a state of delicate balance between oxygen-consuming and replenishing processes. Vaughan (1934) suggested that this region might be of interest in studying the effect of oxygen depletion on the distribution of organisms. Unfortunately, very little study of the vertical distribution of organisms in this region has been published. Graham (1941) sampled the plankton and oxygen content of the upper 100 meters during the CARNEGIE cruise from San Francisco to Samoa, and his data indicate that an abundance of organisms is associated with low-oxygen concentrations in this region. However, this reflects the high oxygen-consuming organic content of the water, and the data show nothing concerning the occurrence of living organisms in the oxygen-poor layer itself. Thompson, Thomas, and Barnes (1934) report that Guberlet and Miller found a scarcity of plankton between 500 and 1000 meters, although very rich hauls were made between 400 and 500 meters, these facts cannot be clearly related to the distribution of oxygen, however. Wooster (1952) reports large catches of lantern and hatchet fish, euphausiids, and squid from waters containing from 0.5 to less than 0.1 ml/liter of oxygen, suggesting that these animals can and do live for at least part of the time in waters containing only a few per cent of the saturation value of oxygen. It would be of great interest to ascertain whether these animals are respiring aerobically while in this low-oxygen zone, since respiration by such large populations as indicated would conceivably affect the oxygen concentration in the zone.

Vertical migrations of copepod populations are well known (Russell, 1925, and subsequent papers; Clarke, 1934a, 1934b; Nicholls, 1933; and others), and many observations of the vertical diurnal migration of the scattering layer have been made

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in recent years (Hersey and Moore, 1948; Moore, 1950; and others). The oxygen gradients through which these migrations take organisms do not appear to deter their movements. Clarke (1934a) observed copepod migrations and oxygen at a station in the Gulf of Maine where the animals must have passed through oxygen gradients of up to 1.7 ml/liter. Hersey and Moore observed euphausiid movements between 20 and 400 meters off Bermuda, corresponding to oxygen changes of about 0.5 ml/liter. At a station occupied in the Mediterranean in May 1948, the scattering layer migrated from about 183 meters and 4.6 ml/liter of oxygen to some 400 meters (Moore, 1950), where the oxygen content was 4.2 ml/liter. Moore also reports a vertical migration of the scattering layer from 150 to 400 fathoms on entering the Gulf Stream from colder water. At this location, the depth difference involved an oxygen difference of at least 2.0–2.5 ml/liter. Moore concluded that the same species was involved in the layer at the different depths.

It appears that in most parts of the ocean the oxygen content is not a primary factor in limiting life and growth, except where sulfides develop under completely anaerobic conditions. When this occurs, bacterial metabolism continues, but combined oxygen, in the form of sulfate, nitrate, and other oxidized substances, or oxidized forms of metal ions, especially ferric iron, constitute the sources of energy.

The abundance of plants and animals decreases with depth, but not in the same way as the oxygen content, and there is no evidence that the abundance increases with depth below the oxygen minimum. On the contrary, the decreased populations can more readily be accounted for in terms of decreased temperature, light, food, and other environmental necessities than in terms of oxygen supply and demand.

OXYGEN CONTENT OF BOTTOM WATERS

The bottom water-sea floor interface forms a zone of particular interest to zoologists, bacteriologists, and especially geologists. The effect of the oxygen content of the bottom waters on this environment is of considerable interest to all three groups. Detritus settles into the region and there serves as food for bottom fauna or is incorporated into the bottom sediments. Oxidative processes leading to the decomposition of organic material will in large degree depend on the oxygen content of the water and in turn will consume the dissolved oxygen. Thus, changes in the amount and composition of organic materials entering this area will be related to the amount of oxygen present. Organic compounds arriving at the ocean floor can be assumed to be those relatively resistant to oxidation, but this will depend on many factors, among which their composition, the rate of sedimentation, the oxygen content, and the temperature of the water will be important.

Within the interstitial waters of bottom sediments, the oxygen may soon be consumed (ZoBell, 1939), leading to reducing conditions, limiting life to anaerobic bacteria, and greatly reducing rates of further decomposition of organic materials. In the overlying water, the amount of oxygen will depend upon the state of balance between the rates at which organic materials arrive and are oxidized and the rate of resupply of oxygen. Where the latter is slow and the former rapid, the anaerobic conditions established in the sediments may extend well upward into the overlying water as they do in the Black Sea and other stagnating areas. However, in most parts

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of the open ocean, the bottom waters are not anaerobic, although they may contain less oxygen than waters directly above. This conclusion is based on the widespread occurrence of benthic animals and on some observations of the oxygen content of near-bottom waters. Wattenberg (1927; 1938) observed depletion of oxygen in near-bottom waters in the Atlantic during the METEOR (1925–1927) Atlantic Expedition, and it was observed by the 1947–1948 Swedish Deep-Sea Expedition (Bruneau *et al.*,

TABLE 8.—*Temperature, salinity, oxygen, and phosphate of near-bottom deep waters in the Indian Ocean*
Data from Bruneau *et al.* (1953)

Station	Position	Depth (Meters)	Distance From Bottom (Meters)	T°C	S‰	O_2ml/L	$PO_4^{\equiv}$, μga/L
205	4°47′S88°18′E	4999	43	1.37	34.73	4.29	2.55
			14	—	34.73	3.52	2.55
207	0°01′S88°18′E	4486	40	1.40	34.73	4.08	2.65
			11	1.40	34.74	3.69	2.55
211	4°36′N82°36′E	4133	41	1.34	34.71	3.89	2.49
			12	—	34.76	3.38	2.49
213	4°12′N77°78′E	3120	49	1.48	34.75	3.64	3.23
			24	1.86	—	—	—
			13	—	—	—	—
			7	—	34.95	0.87	2.13
216	0°04′N74°53′E	4268–4286	4215*	1.37	34.73	4.12	3.39
			4241*	1.33	—	4.09	3.59
			4258*	—	34.75	3.59	3.42
220	1°22′S70°28′E	3885	50	—	34.73	3.97	3.30
			25	1.58	"	4.01	3.20
			19	1.67	34.75	4.03	3.13
			14	1.66	34.75	3.99	3.10
			8	—	"	3.68	3.04
223	1°19′S66°16′E	4344	50	1.51	34.73	4.09	3.13
			25	—	"	"	3.23
			19	1.53	"	4.07	3.04
			13	—	34.74	4.07	3.04
			7	1.55	34.73	3.66	2.65
225	1°22′S62°38′E	4658	50	—	34.71	—	—
			23	1.35	34.71	4.22	3.46
			17	—	34.69	4.26	3.46
			12	1.32	—	4.16	3.46
235	7°14′N52°49′E	5073	97	1.30	34.71	4.28	3.23
			23	—	"	4.25	3.20
			18	1.36	34.69	4.27	3.17
			12	—	"	4.22	3.07
			7	1.38	34.83	3.40	3.07
240	10°23′N52°22′E	3703	50	1.52	34.76	3.91	3.33
			25	—	—	3.86	3.33
			19	1.54	34.75	3.89	3.17
			14	—	34.74	3.88	3.00
			8	1.55	34.74	3.68	3.13

* Sample depths.

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1953) in the Indian Ocean. Van Riel (1943) found rapid declines in the oxygen content at 30 meters from the bottom in several of the basins of the Dutch East Indies; he further noted that there were systematic patterns in the magnitude of these near-bottom decreases.

Table 8 shows the temperature, salinity, oxygen, and phosphate contents of near-bottom deep waters observed in the Indian Ocean, during the 1947–1948 Swedish-Deep-Sea Expedition (Bruneau *et al.*, 1953). Special techniques were used to extend their sampling to within 7 meters of the bottom. At all these stations, there were appreciable decreases in the oxygen content in the bottom 50 meters, which in most cases amounted to about 0.5 ml/liter. In several cases, this decrease in oxygen was accompanied by an increase in temperature of a few hundredths of a degree C. and a decrease in inorganic phosphate. These low-oxygen concentrations in a very thin bottom layer must result from the accumulation of detritus sinking to the bottom layer, an effect which shows itself in a more exaggerated way in the accumulation of relatively stable organic materials in bottom sediments. Brouardel and Fage (1954) report sampling oxygen at different levels near the bottom, using a special device which captures samples at five successive levels adjacent to the bottom; the authors are uncertain as to the exact strata from which their samples are taken, but they appear to come from the bottom 10 meters of water. In this layer the oxygen content decreased an average of 0.1 mg/liter (0.07 ml/liter) between the second and third stage from the bottom, and 0.3 mg/liter (0.27 ml/liter) between the water adjacent to the bottom and the next stage above. These observations were made off Morocco in less than 500 meters of water.

There is considerable opinion and some evidence that the oxygen content of the waters above the sediments is important in determining their organic content (Fleming and Revelle, 1939). Correns (1939) states that the relatively high oxygen content of the deep water of the Atlantic is not favorable to the preservation of organic substances, and Trask (1939) states that the decomposition of organic matter depends mainly on the supply of oxygen. Although Kuenen (1942) found no correlation between the organic nitrogen content of sediments in the Dutch East Indies and the oxygen content of the bottom waters, a good correlation between these functions is demonstrable in the northwestern Gulf of Mexico (Richards and Redfield, 1954). Figures 10 and 11 show the location of the maximum organic content of these sediments, redrawn from Trask (1953), and the minimum oxygen content of the bottom waters drawn from observations made by the ATLANTIS in 1935 (Conseil Permanent Internat., 1936). The zones of maximum organic content and minimum oxygen content coincide, and both roughly parallel the 100-fathom isobath. This zone represents the area where the oxygen-minimum layer impinges on the bottom (sides) of the basin of the Gulf of Mexico, and is consequently the zone of the lowest oxidation diffusion gradient.

The extreme case, in which the bottom waters are anaerobic, is again represented by the Black Sea, threshold fjords, and other stagnant regions in which the organic content of the bottom sediments is unusually high.

The oxygen content of the water has another, although indirect, bearing on the composition of bottom sediments. Because of the inverse relationship between oxygen

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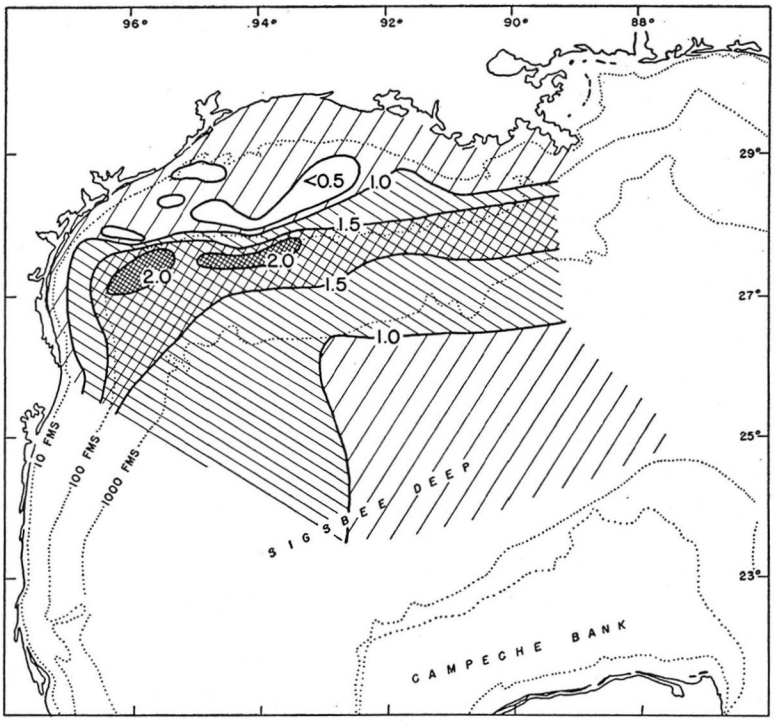

FIGURE 10.—*Organic content of sediments of Northwestern Gulf of Mexico*
From Trask (1953). Numbers represent per cent of organic matter, estimated as 1.8 times the carbon content.

consumption and carbon-dioxide release, low-oxygen values are associated with high total carbon dioxide and low pH values. This in turn increases the solubility of calcium carbonate. The oxygen content of the bottom waters of the Pacific decreases northward, and so does the calcium-carbonate content of the bottom sediments (Trask, 1937). In general, the calcium-carbonate content of Atlantic marine sediments is greater than that of Pacific marine sediments, in agreement with the generally higher oxygen content of Atlantic than of Pacific deep waters.

DISTRIBUTION OF OXYGEN IN THE OCEANS

ANTARCTIC CIRCUMPOLAR OCEAN

The Antarctic Circumpolar Ocean is an important area in which oxygenated surface waters sink and spread northward. Two areas of convergence exist: the Subtropical Convergence, found at about 40°S., and the Antarctic Convergence, between 50 and 60°S. The area between these convergences is the Subantarctic region. Between the Antarctic Convergence and the Antarctic Continent is the Antarctic region, where winter cooling and freezing yield highly oxygenated, cold, saline water. In the Weddell Sea, the Antarctic region south of the western Atlantic, the oxygen content is more than 7 ml/liter in the surface water, but upon sinking it mixes with water entering the area from the northwest through the Drake Passage. The latter

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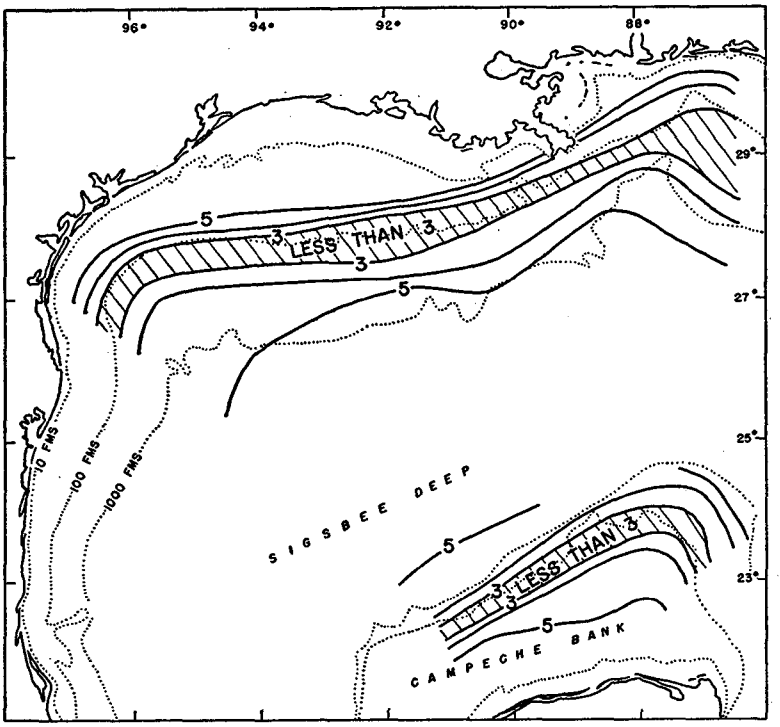

FIGURE 11.—*Oxygen content,* ml/liter, *of waters overlying the bottom, northwestern Gulf of Mexico*
Data from Bulletin Hydrographique for 1936

water contains at most 4.2 ml/liter (in the subsurface layers), and the mixture at the bottom of the Weddell Sea contains about 5.5 ml/liter (Mosby, 1935; Deacon, 1937). This mixture contributes to the Antarctic Bottom water, which fills the bottom layers of the Atlantic to 20°N. The minimum-oxygen content of the Weddell Sea, approximately 5.0 ml/liter, is found at an intermediate depth of about 1000 meters. The circumpolar circulation carries this water eastward around the Antarctic continent, and in general the oxygen content gradually diminishes along its course. Deacon's section from Cape Leeuwin, Australia, to the Antarctic Continent (Deacon, 1937, Pl. XXI) shows this water at about half its circumpolar distance from its source in the Weddell Sea. At this longitude the oxygen minimum, less than 4.0 ml/liter, is found at about 600 meters in the Antarctic region, but at 41°S. it is less than 3.4 ml/liter at 2000 meters.

The water sinking at the Antarctic Convergence forms the low-salinity Antarctic Intermediate water, which flows[3] northward into all the oceans at depths between 800 and 1200 meters. Upon sinking, this water is relatively highly oxygenated and is apparent in the Western Atlantic as an oxygen maximum nearly to the equator; however, consumption within the water mass decreases its content from about 7 ml/liter at 60°S. to less than 4 ml/liter near the equator. On the other hand, the

[3] This "flow" may occur either as a mass movement of a body of water or by the transfer of solutes by eddy diffusion along isentropic surfaces.

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TABLE 9.—*Features of the oxygen distribution in the Atlantic Ocean*
After Wattenberg (1938)

Geographical latitude	60° S	50° S	40° S	30° S	20° S	10° S	0°	10° N	20° N	30° N	40° N	50°
WESTERN SECTION												
Upper layer, O_2CC/liter	7.5	7.1	5.9	5.2	4.6	4.6	4.3	4.4	4.9	5.0	4.8	5.6
Depth of boundary:												
Upper layer/intermediate layer ($60\%O_2$ line) (Meters)	400	700	1100	1300	900	200	250	150	550	700	850	350
Intermediate layer (O_2 min.)												
O_2CC/liter	5.2	4.1	4.1	4.4	4.3	2.3	2.9	2.7	3.2	3.8	3.4	3.5
$O_2\%$	64	54	54	59	58	37	45	40	48	56	52	53
Depth of boundary:												
Intermediate layer/bottom layer	—*	2600	1900	1550	1300	1250	1250	1400	1100	1000	1050	500
Bottom layer (O_2 max.)												
O_2CC/liter	5.2	5.2	5.7	5.7	5.8	5.7	5.6	5.8	5.9	6.0	6.2	6.6
$O_2\%$	67	67	71	76	78	75	76	79	80	82	84	89
EASTERN SECTION												
Upper layer, O_2CC/liter	7.6	7.2	6.2	5.4	5.4	4.9	4.5	4.4	4.9	5.8	5.8	6.1
Depth of boundary:												
Upper layer/intermediate layer ($60\%O_2$ line) (Meters)	200	400	1200	1120	100	50	50	100	200	1000	—*	—*
Intermediate layer (O_2 min.)												
O_2CC/liter	4.5	4.0	4.1	4.3	3.1	0.7	1.7	1.7	1.5	3.7	4.1	4.7
$O_2\%$	56	53	55	57	44	10	27	25	25	60	65	71
Depth of boundary:												
Intermediate layer/bottom layer (Meters)	950	2100	1900	1700	1450	1400	1500	1500	1500	1100	—*	—*
Bottom layer (O_2 max.)												
O_2CC/liter	5.6	4.9	5.0	5.1	5.3	5.2	5.3	5.4	5.3	?	?	6.4
$O_2\%$	69	61	67	69	70	70	70	71	71	?	?	86

tropical and subtropical oxygen minima are found in the nucleus of the Subantarctic Intermediate layer (Schumacher, 1932).

THE ATLANTIC AND ITS ADJACENT SEAS

The distribution of oxygen in the South Atlantic has been classically described by Wattenberg (1938), and a detailed study of the distribution in the Northeastern Atlantic has been made by Gaarder (1927). The oxygen distribution in the western basin of the North Atlantic and the Caribbean has been reported by Seiwell (1934; 1937b; 1937d; 1937e). Earlier contributions were made by Brennecke (1909), J. P. Jacobsen (1916; 1929), and others, and many other papers touch on the distribution of oxygen in various parts of the Atlantic.

The concentrations of oxygen found in the surface waters of the Atlantic are largely a function of the temperature and latitude; they diminish from about 7 ml/liter in high latitudes to about 4 ml/liter in the tropics. Major anomalies occur where upwelling brings oxygen-poor water into the surface layers. The minimum layer is in the upper 1200 meters, finds its greatest depth about 40°N. and 40°S., and rises to about 500 meters near the equator and at 60°N. and 60°S.; the lowest concentrations in the minimum layer are found near the equator in the eastern part of the ocean. Most of the Atlantic contains more than 5 ml/liter of oxygen at depths greater than 2000 meters, and in general there is more oxygen in the northern deep water than in the southern deep water. The general features of this distribution were summarized by Wattenberg (1938; 1939a) (Table 9).

It is of interest to compare the longitudinal sections in the western, central, and eastern Atlantic reported by Wattenberg (1939a) with the average distribution of oxygen computed by Riley (1951) (Tables 9, 10). Wattenberg's sections are composites of observations by the METEOR, ARMAUER HANSEN, DANA, DISCOVERY, ATLANTIS, and GODTHAAB, and Riley's table shows values averaged by latitude for

TABLE 10.—*Average distribution of oxygen (ml/liter) in the deep water of the Atlantic*
From Riley (1951)

Latitude	1000	1500	2000	2500	3000	3500	4000	4500
54–63°N.	5.96	6.26	6.44	—	—	—	—	—
45–54	5.80	6.32	6.36	6.30	6.24	6.22	—	—
36–45	6.16	6.38	6.34	6.16	6.14	6.16	6.23	—
27–36	4.20	5.80	6.02	6.02	6.07	6.13	6.18	6.20
18–27	3.68	5.18	5.55	5.69	5.70	5.67	5.57	5.48
9–18	3.12	4.83	5.47	5.54	5.54	5.52	5.48	5.42
0–9	3.35	4.88	5.42	5.50	5.48	5.45	5.40	5.37
0–9°S.	3.67	4.94	5.40	5.45	5.42	5.38	5.30	5.07
9–18	3.67	4.80	5.35	5.45	5.42	5.30	5.19	5.07
18–27	4.18	4.60	5.34	5.46	5.48	5.42	5.27	5.07
27–36	4.78	4.42	4.94	5.42	5.50	5.43	5.19	5.08
36–45	5.10	4.38	4.78	4.96	4.95	4.89	4.81	4.70
45–54	4.13	4.40	4.52	4.52	4.56	4.74	4.94	5.08
54–63°S.	4.46	4.62	4.80	4.85	4.88	4.92	5.00	5.12

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observations deeper than 1000 meters. The correspondence is best between Riley's averaged section and Wattenberg's central section, as would be expected. Generally, the eastern section contains less oxygen than the average, except in the south. The central section is slightly higher in oxygen toward the south, slightly lower toward the north, than Riley's "average" section. Practically all the western section contains more oxygen than the average (Wattenberg, 1927).

The oxygen-minimum zone in the Atlantic may be considered to be composed of two components. The first is deeper lying, and represents water which sank at high latitudes; this component is therefore oriented north and south. It is thickest at about 4°S. but there it is not so strikingly low in oxygen as it is in the equatorial region. The other component is oriented east to west in the equatorial region and owes its origin to the more local oxidation of organic products which result from the nutrient enrichment brought about by upwelling off the west coast of Africa. These two components cross and merge in the eastern tropical Atlantic, but in much of the region they are distinguishable by "double minima" or inflections in the oxygen-depth curves (Fig. 1, F and G).

The general pattern of oxygen distribution described above is modified by additions of Mediterranean water to the Atlantic and by the circulation through the Caribbean and Cayman seas, Gulf of Mexico, and Gulf Stream system.

THE CARIBBEAN

The Caribbean is characterized by a series of basins and sills which restrict the inflow of water from the North Atlantic below a depth of 1000 meters. Equatorial surface water and some Antarctic Intermediate water enters the Caribbean over this sill.

In the Venezuela Basin in the central Caribbean, the oxygen content is greater than 4.8 ml/liter at all depths below 1500 meters and increases to more than 5 ml/liter at the bottom (3600 to 3800 meters), indicating a relatively rapid renewal of these waters (Seiwell, 1938). The minimum occurs at 400–600 meters, where it is less than 3 ml/liter in the southern part of the section. The oxygen content of the western part of the Caribbean basin is somewhat less than in the eastern section and decreases in the direction of flow. Farther west, in the Cayman Basin, the oxygen content is a little higher than that of the Caribbean Basin because of the entrance of oxygen-rich water through the Windward Passage (Rakestraw and Smith, 1937; Seiwell, 1938; Sverdrup *et al.*, 1942).

The influx of waters relatively rich in oxygen to the Cayman Basin through the Windward Passage is interesting in connection with the oxygen content of the Gulf Stream system and the Sargasso Sea and demonstrates that the Sargasso is a source of subsurface oxygen.

Water moves through the Caribbean and the Cayman seas, Yucatan Channel, Gulf of Mexico, and Straits of Florida into the high-velocity Florida Current-Gulf Stream System. Sill depths in the Yucatan Channel and Straits of Florida limit this circulation to the upper layers. The upper layers of the Florida Current and the Gulf Stream contain less oxygen than adjacent slope or Sargasso Sea water of the same density (σ_t). This effect is confined to an upper layer, above the minimum zone (Fig.

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3), and has been detected as far northeast as the tail of the Grand Banks. This oxygen-deficient layer owes its existence to its relatively recent origin in the equatorial region. On progressing downstream from the Straits of Florida, these waters are reoxygenated by vertical turbulence and by lateral mixing into the adjacent areas. The density at which the oxygen minimum is found is essentially the same for both Gulf Stream and Sargasso waters.

MEDITERRANEAN AND BLACK SEAS

In the Mediterranean, evaporation exceeds precipitation and run-off (Sverdrup *et al.*, 1942), and surface waters sink to the bottom (perhaps intermittently, according to Nielsen, 1912) renewing the deep-water oxygen. The oxygen content of the western Mediterranean was relatively high at all depths when observed by the DANA in April and June 1930. The minimum zone was poorly developed, and with one exception concentrations were greater than 4.0 ml/liter at all depths. East of Sicily the minimum zone was more markedly developed than in the western Mediterranean, although farther east the oxygen decreased constantly to the bottom and showed no intermediate minimum. In this region and in the minimum zone in the western part of the eastern section the oxygen content drops below 4.0 but not below 3.5 ml/liter.

The Black Sea is a special case in which the deep waters become anaerobic, and hydrogen sulfide is produced, but, because of the small water exchange through the Bosphorus, the Sea of Marmora, and the Dardanelles, Black Sea water has little or no effect on the Mediterranean.

Mediterranean waters flow into the Atlantic through the deeper parts of the Straits of Gibraltar, forming a characteristic water mass which can be detected over wide areas of the Atlantic by a salinity maximum at intermediate depths. In the straits, warm and saline Mediterranean water mixes with incurrent Atlantic water, yielding a mixture of about 37.00 ‰ salt at 13°C., containing about 4.5 ml/liter oxygen. According to Wüst (1935), Mediterranean water outside the Straits of Gibraltar was observed to have a temperature of 11.9°, a salinity of 36.5 ‰, and a σ_t of 27.78. In the eastern Atlantic, this water is centered at 1000 meters depth at 40°N. latitude, where it has an oxygen content a little less than 4.5 ml/liter, slightly more than the waters immediately north or south of it. Wüst (1935) traces this water in the eastern Atlantic from 20°N. to 51°N. by its salinity, but it is no longer apparent in his central Atlantic section. However, Seiwell (1937b) attributed high positive salinity anomalies at the depth of the oxygen minimum in the region west of 40°W. and between 25° and 35°N. to water of Mediterranean origin.

THE ARCTIC MEDITERRANEAN SEA

This region includes the Norwegian, North, Baltic, Barents, and North Polar seas and is bounded on the south by the Iceland-Greenland ridge, the Faeroe Islands-Iceland Ridge, and the Wyville Thomson Ridge which runs between the Orkney and the Faeroe islands. It is an important source of oxygenated waters, formed by sinking in the Norwegian Sea in the winter time (Knudsen, 1899; Nansen, 1906; 1912; Nielsen, 1907; J. P. Jacobsen, 1916).

In general, the Arctic Mediterranean is oxygen rich at all depths, but low con-

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centrations are found in coastal areas where the circulation is limited, and Sverdrup (1929) observed low values near the bottom on the North Siberian Shelf. Very high oxygen contents, largely attributable to photosynthesis, were observed in surface waters off the East Greenland coast by Jakhelln (1936) and may well contribute to the ventilation of underlying Atlantic and Irminger sea waters (Fig. 2). In seven stations occupied by the submarine NAUTILIS north of Spitzbergen (Sverdrup, 1933, Fig. 43), the water at all but one station contained more than 6.6 ml/liter at all depths less than 100 meters. The minimum zone, containing between 6.4 and 6.6 ml/liter, lay between 1000 and 3000 meters, and values between 6.6 and 6.8 ml/liter were found at greater depths.

LABRADOR SEA

The Labrador Sea is another important region of convergence and sinking. Sections through this sea and Baffin Bay have been made by the GODTHAAB (Fig. 1, E) (Conseil Permanent Internat., Bulletin Hydrographique, 1929) and U. S. C. G. C. GENERAL GREEN (Fig. 9) (Smith, Soule, and Mosby, 1937). The region is the source of much of the North Atlantic Intermediate water, which, like the Antarctic Intermediate water, is characterized by a salinity minimum. Water containing about 7 ml/liter oxygen sinks in the Labrador Sea (Wüst, 1935; Wattenberg, 1938). Soule (1940) has discussed the formation of bottom water in this region, which contains about 6.4 ml/liter. Low-oxygen concentrations develop in the poorly circulating deep water of Baffin Bay (Fig. 9), and water containing about 5 ml/liter can flow across the Davis Strait ridge into the Labrador Sea, where it has been observed as an oxygen-minimum layer (at 2200–2500 meters) separating the intermediate and deep waters. Upon mixing with Labrador Sea water having an oxygen content of 6.9 ml/liter, it forms deep water containing about 6.4 ml/liter (Soule, 1940), which then flows southward. At 30°N. it forms the middle Atlantic deep water, at 2300 meters depth, and its oxygen content has decreased to about 6 ml/liter; at the equator it is at about the same depth and contains about 5.75 ml/liter. At about 30°S., it deepens to 3000 meters and then begins to shoal, and at about 50°S. it contains about 4.5 ml/liter at a depth slightly greater than 2000 meters. This water apparently then rises to join waters which again sink in the southern convergences.

Bottom Arctic water of high-oxygen content is traced by Wüst (1935) as far south as 20°N. in the Western Atlantic, where it has 5.75 ml/liter at 4000 meters. Farther south, it is replaced in the bottom by subantarctic waters. At 20°S., this water of northern origin is found shoaler, containing a little more than 5.5 ml/liter at 3000 meters depth.

SARGASSO SEA

The Sargasso Sea is a source of oxygen for the shallow layers of the North Atlantic. In March, mixing and aeration produce an isothermal surface layer extending to a maximum depth in this season. In the following warm season, a sharp thermocline develops above these waters and isolates them from the atmosphere.[4] The waters thus oxygenated spread out over the area, retaining their oxygen for an undeter-

[4] The author is indebted to Mr. L. Valentine Worthington for this information.

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mined time and distance. Presumably it is water of this genre that enters the Caribbean through the Windward Passage.

INDIAN OCEAN AND THE RED SEA

The Red Sea is a source of warm, highly saline, oxygen-poor water traceable into the northwestern Indian Ocean, although its exchanges of water through the Suez Canal are too small to be of any significance to the Mediterranean. According to Vercelli (1925) and E. F. Thompson (1939), north-northwest winds prevail in summer, and surface waters flow from the Red Sea to the Gulf of Aden, Indian Ocean waters flow into the Red Sea at intermediate depths, and bottom, highly saline waters flow from the Red Sea to the Gulf of Aden. Opposite winds prevail in winter, so that the deeper Red Sea waters are discharged into the Indian Ocean while surface waters enter the Red Sea from the Gulf of Aden. At the end of winter, the deep oxygen content of the Red Sea is only a little more than 2 ml/liter (E. F. Thompson, 1939), while at the end of summer it is less than 1 ml/liter. Oxygen-poor Red Sea water appears in the Indian Ocean at 8°N. in the section of Clowes and Deacon (1935, Fig. 1), where the layer between 300 and 1000 meters deep contains less than 0.8 ml/liter, but at 11°S. the minimum concentration, 2.0 ml/liter, is at 1200 meters.

Antarctic Intermediate water enters the Indian Ocean from its southern boundary which, oceanographically, is the Subtropical Convergence. Clowes and Deacon (1935) show Antarctic Intermediate water, with about 3.6 ml oxygen/liter, entering the western Indian Ocean from the south at about 1500 meters, extending northward at shoaler depths, and gradually diminishing in oxygen content from south to north. The deep water in the southern part of this section, which parallels the east African Coast, is of Atlantic origin, according to them, but it contains only about 4.4 ml/liter of oxygen, which is 0.5–0.75 ml/liter less than Wattenberg (1938) found at these latitudes and depths in the eastern Atlantic. Clowes and Deacon suggest that the Atlantic water is influenced by Indian deep water from the north. Off the East African coast, the deep-water oxygen decreases northward from about 4.4 ml/liter at 40°S. to about 3.6 ml/liter at 10°N. In the east-west direction, the deep water oxygen content is uniformly around 4 ml/liter between 10°S. and 9°N. (Fig. 193 in Sverdrup, *et al.*, 1942, and ALBATROSS observations), but at about 88°E. it decreases in the northward direction to less than 3.0 ml/liter at 4°36′N. Eastward from 11°S., and 88°E., it decreases slightly, but contains 4.64 ml/liter in 5877 meters at 109°10′E.

The observations of the DANA and the Swedish Deep-Sea Expedition (Bruneau *et al.*, 1953) show that the oxygen-minimum zone of the Indian Ocean is centered at about 5°N. and is most pronounced between 52° and 77°E. This central location (in the east-west direction) is in marked contrast to the location of the minimum zones of the Atlantic and Pacific, probably because relatively highly oxygenated waters enter from the western Pacific, a phenomenon which has no counterpart in the Atlantic and Pacific.

On approaching this minimum core from the south and east, the ALBATROSS observed the minimum concentration of 1.76 ml/liter at 568 meters south of Java. At about the same latitude (11°S.) and at 88°E. the same minimum concentration was found at 768 meters. In their section to the north along 88°E., minimum concentra-

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tions gradually decreased, and overlying minima were found at depths ranging from about 150 to about 500 meters. Double minima occurred along the remainder of their westward course to at least 56°E. At the stations where double minima were found, the lower of them occurred at a density close to $\sigma_t = 27.3$ and at depths slightly less than 800 meters. This deeper oxygen-poor layer was observed from 11°S. to 7°N. at 88°E. and extended southwestward to a point south of the equator at 54°49′E. West of the latter point, the zone ends or curves northward, because at DISCOVERY station 1584 at 49°E. and about 1°S. the minimum was 3.6 ml/liter at 1500 meters, but the ALBATROSS found 0.53 ml/liter at 763 meters ($\sigma_t = 27.26$) at 10°23′N. and 52°22′E. The minimum concentration in the lower oxygen-poor layer, 0.45 ml/liter, was found at 7°14′N., 52°49′E., at a depth of 790 meters and a σ_t of 27.29. This deep oxygen-poor layer was not observed in the Gulf of Aden, where the minimum was found at 143 meters ($\sigma_t = 26.11$), contained 0.24 ml/liter, and was presumably of Red Sea or local origin.

The depth and density at which the shallower minimum layer was found ranged from 148 meters ($\sigma_t = 25.75$) at 52°E. to 389 meters ($\sigma_t = 26.9$) at 82°36′E. The lowest concentration in it, 0.48 ml/liter, occurred at 77°28′E.

In contrast to the Atlantic and Pacific, there is no supply of oxygen-rich waters of far northern origin in the Indian Ocean, and water entering the system from the east tends to shift the overlying minimum zone of local origin westward.

THE PACIFIC

The outstanding feature of the Pacific Ocean is the large wedge-shaped area of very low oxygen extending at intermediate depths westward from the Gulf of Panama, where it was first observed by Schmidt (1925) that the minimum-oxygen content was much smaller and much shallower than on the other side of the Isthmus of Panama in the Atlantic. H. Thomsen (1931) showed that this very low minimum zone extended far to the west. Data now available make it apparent that this zone has a counterpart in the southern hemisphere, and that two oxygen-low tongues extend westward from the Americas. Lowest concentrations are found at about 15°N. and 10°S., with somewhat higher concentrations at corresponding depths (down to around 1000 meters) in the intervening zone. A similar feature is apparent in the oxygen distribution in the eastern Atlantic. Not only is the oxygen content of the minimum zone lower, but the whole subsurface water mass of the Pacific is generally lower in oxygen than is the Atlantic. Possible causes of this have been discussed.

The far southern Pacific was investigated by the DISCOVERY (Deacon, 1937, Pls. 33, 36, 39, 42; and others); four DISCOVERY sections cover the area from about 45° to nearly 65°S., from New Zealand to the southern tip of South America and include parts of the circumpolar Antarctic Ocean. In the northern part of the section from New Zealand to the Ross Sea, minimum-oxygen concentrations of about 3.5 ml/liter are found at 1300 to 2000 meters; a deeper maximum, containing a little more than 4.0 ml/liter, is centered at about 3000 meters, and below this the oxygen decreases to slightly less than 4 ml/liter in the deepest waters. At the southern end, the lowest concentrations, less than 4.0 ml/liter, are found at depths of 600–900 meters, and 4.5 to 4.75 ml/liter is found at the bottom. In Deacon's section from the ice edge

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to 41°03'S., 126°04'W., the oxygen content decreases from south to north, and the depth of the oxygen minimum slopes steeply downward in this same direction; at about 65°S. it is at about 600 meters and contains 3.60 ml/liter, but at 40°S. it is at 3000 meters and contains 3.25 ml/liter. The surface concentrations decrease from about 6.9 ml/liter at about 63°S. to 5.9 ml/liter at 40°S. In the section from 41°03'S., 126°04'W., to the Antarctic Shelf and in the section from the end of the latter section to the western end of the Straits of Magellan, southern surface values reach 7.5 and 7.0 ml/liter, respectively, the depth at which the minimum is found increases sharply to the north, and the northern parts of the sections contain generally less oxygen than do the southern ends.

Few other data are available on the oxygen distribution in the Southern Pacific. Conditions just off the coast of Peru were investigated by the WILLIAM SCORESBY (DISCOVERY Committee, 1949). Schott constructed a longitudinal section (Schott, 1935, Fig. 50) from data of the DISCOVERY, DANA, and CARNEGIE, but only two CARNEGIE stations between the track of the DANA and the areas investigated by the DISCOVERY were available to him. However, this section shows two zones of very low oxygen, centered at about 4°S. and 12°N., lying less than 500 meters deep with somewhat higher oxygen concentrations at equal depths in the intermediate latitudes. A fairly detailed section was constructed from DANA observations by Sverdrup *et al.* (1942, Fig. 206) extending from about 48°S. to 10°S. at about 180° Long., and a new section from 10°N. to 15°S. along 85°W. has been made available to the author by the kindness of Dr. Warren Wooster of the Scripps Institution of Oceanography). There are practically no data available east of the 180th meridian between 20° and 40°S.

The southern end of the section drawn from DANA data (Sverdrup *el al.*, 1942, Fig. 206) is just east of New Zealand. A deep minimum occurs at about 2000 meters and gradually decreases in depth and oxygen content northward to about 1800 meters and 3 ml/liter at 14°S. At about 38°S., a shallower minimum appears, containing between 4.0 and 4.5 ml/liter, centered at about 500 meters. The oxygen of this layer increases to between 4.5 and 5.0 ml/liter in 350 meters at 30°S., and then decreases northward. At about 15°S., an abrupt decrease in the oxygen content of the layer above 1000 meters takes place, and the two minimum layers containing less than 3 ml/liter tend to merge and in the north end of this section at about 10°S. extend from about 350 meters to more than 2000 meters. At 4000 meters the oxygen content decreases from more than 4.0 ml/liter at the south to less than 3.5 ml/liter at the north. According to Sverdrup *et al.*, the intermediate oxygen maximum lies a few hundred meters above the Antarctic Intermediate water, marked by a salinity minimum.

Schott's section (Schott, 1935, Fig. 50) shows, at 30°S., two minima, one at about 400 meters, the other at about 1500 meters. Probably the lower one can be related to Antarctic deep or bottom water, and the other appears to lie slightly above the core of the Antarctic Intermediate water. There is a distinct tendency for the oxygen content of the deep water to decrease northward.

It can be reasoned by analogy that the oxygen distribution off the western coast of South America should be similar to that off the West African Coast, and it is known

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that active upwelling occurs along the Peruvian coast although it may not involve especially deep-water masses (Sverdrup, 1930; Gunther, 1936; Sears, 1954). Five sections extending 100–200 miles out from the Peruvian coast were occupied by the WILLIAM SCORESBY between about 16° and 4°S. There is essentially no continental shelf in this region, so these sections lie in deep water. At about 16°S. there is a region about 100 miles offshore in which low-oxygen values (less than 1.0 ml/liter) extend to great depths; at 2500 meters the oxygen in this zone was 1.09 ml/liter, but both inshore and farther offshore higher values were observed at this same depth; this low-oxygen mass is still apparent at 12°S., where less than 0.25 ml/liter was observed at 2500 meters, and even at 5°S. there is a suggestion that the deep water 100 miles offshore contains less oxygen than farther offshore or closer inshore. In all the sections, less than 0.25 ml/liter appears at depths of 200–400 meters. The section at 12°S. has the largest zone of these low-oxygen concentrations, which extend from 100 to 400 or 500 meters, but in the three sections farther north, at 7°S., 5°S., and 4°S., concentrations under 0.27 ml/liter probably do not extend over more than 100 meters of depth. The minimum values are not appreciably lower than at the equator (CARNEGIE Station 41, 1°37′S., 86°58′W.) (Fleming *et al.*, 1945), where 0.29 ml/liter was found at about the same depth (323 meters). However, the SCORESBY sections are short and doubtlessly reflect local coastal conditions.

A section from 10°N. to 15°S. along 85°W., occupied by the Scripps Institution of Oceanography, shows a large oxygen-poor area containing less than 0.25 ml/liter extending from about 2°S. to the southern end of the section, and a similar zone extending from about 3°N. to the northern end. The southern zone has its maximum thickness, extending from about 150 to 600 meters, at 8°–9°S. The section does not extend far enough south to permit determination of where the most intensely deoxygenated water lies, but a section published by Sverdrup *et al.* (1942, Fig. 207) indicates that the oxygen-poorest water is centered at about 12° in the northern hemisphere. In the section in the southern hemisphere, the 2.0 ml/liter isoxy line slopes downward to the north from 1400 meters at 15°S., but in the corresponding section in the northern hemisphere this line is found regularly at 2100–2500 meters.

The now-classic observations of the DANA (Thomsen, 1937) and CARNEGIE (Moberg, 1930; Graham and Moberg, 1944; Fleming *et al.*, 1945) have recently been supplemented by the Swedish Deep-Sea Expedition (1947–1948) (Bruneau *et al.*, 1953) and the U. S. Fish and Wildlife Service operating out of Hawaii (Cromwell, 1951). The DANA section from Panama to New Caledonia (Thomsen, 1931) clearly shows the oxygen-minimum zone extending westward from the Gulf of Panama, gradually dissipating with increased westing. Concentrations under 0.10 ml/liter were found at 300–500 meters in the Gulf of Panama, but, at about 144°W., no values less than 2 ml/liter were found in the entire water column. Between 145°W. and 150°W., the oxygen content increases rather abruptly to the west at depths less than 1000 meters, more gradually at greater depths. At DANA Station 3570 (148°W.) minima at 400–500 meters and at 1200–1500 meters were separated by a maximum at 1000 meters. At about 174°E., the upper layers contained more than 5 ml/liter to a depth of 800 meters, below which concentrations decreased to a minimum of

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about 3.16 ml/liter at 2500 meters. At all depths concentrations increased westward, but only at great depths (4000 meters or more) did the water contain as much as 4 ml/liter.

Sverdrup *et al.* (1942) have constructed a section showing the oxygen content a few hundred miles from the coast of Central America and North America, extending from the equator to about 50°N. (Sverdrup *et al.*, 1942, Fig. 207). This shows the most intensely de-oxygenated zone, in which the oxygen content is practically nil, extending from about 100 to nearly 1000 meters between 10°N. to 22°N. The deep water in this section contains a little more than 3 ml/liter, and at 2000 meters the oxygen content is uniformly less than 2 ml/liter. At about 120°W. in these latitudes and depths, the oxygen content drops to less than 0.25 ml/liter between about 100 and 600–800 meters. At 7°S., 2.0 ml/liter is found at about 1000 meters, but this concentration occurs in 2400 meters at 25°N.

Three sections occupied by the Swedish Deep-Sea Expedition extend in a zig-zag course from Panama to 2°44′S., 92°46′W., thence to 17°46′N., 126°51′W., and then to 03°0′S., 136°20′W. The first section shows concentrations under 0.5 ml/liter between 250 and 500 meters at the south and between 250 and 700 meters at the north. The low-oxygen zone is thicker and contains lower concentrations at the northern part. In the second section, these low values extend to depths of 1000 meters (compare with the section of Sverdrup *et al.*, 1942, Fig. 207) at about 18°N., but only to 500 meters at its southern end. Much of the northern part of this minimum zone contains less than 0.1 ml/liter and is near the core of the low-oxygen zone of the Pacific. Less than 0.1 ml/liter is found only at the northernmost station in the third section (about 15°33′N.), and the minimum zone is again thinner and more oxygenated at the southern end. CARNEGIE's section V extends from San Francisco to Samoa. Concentrations less than 0.1 ml/liter are found centered at about 12°N. and extend north of 16°N and south to about 9°N. The oxygen content of the upper layers increases markedly toward San Francisco, and the layer containing less than 0.5 ml/liter thins and deepens to the northeast, although less than 0.3 ml/liter is found at around 700 meters all the way to the San Francisco end. Southwest of the minimum zone, the oxygen content increases more rapidly than northeast of it; at about 5°S. and 152°W. the whole water column contains at least 1.0 ml/liter. At Station 157 (1°48′S., 152°22′W.), the column showed three minima: one contains less than 1.0 ml/liter at 100–250 meters; a second, at 500 meters, contains less than 1.0 ml/liter in a layer more than 100 meters thick; and a deeper bubble contains less than 2.0 ml/liter centered at about 2250 meters. The oxygen content between 500 and 3500 meters increases rather sharply toward the Southwest. Beyond 6°S. and 155°W., the minimum occurs at about 450 meters and contains slightly less than 2 ml/liter.

Two north-south sections from around 22°N. to 10°S. have been reported by Cromwell of the U. S. Fish and Wildlife Service. These sections (Cromwell, 1951, Figs. 14, 15) extend only to 1000 meters depth but are in great detail. They alternate with two nearly parallel sections occupied by the Swedish Deep-Sea Expedition. The easternmost of these four sections is at about 150°W., the westernmost extends to about 175°W. They show the gradual erosion of the de-oxygenated zone which orig-

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inated farther eastward. Minimum concentrations occur regularly at about 12°N., and concentrations less than 0.5 ml/liter are found only in the northern parts of the sections.

The oxygen content of two sections in the southwestern North Pacific has been reported by Ito (1930). One section extends from the equator to 34°N. at about 145°E., the other from 127°E. to 161°E. at about 7°N. The first shows the oxygen minimum, with concentrations between 1.0 and 2.0 ml/liter, 800–1000 meters deep at 20°–25°N. This appears to be the residue of the core of the low-oxygen zone of the Pacific. However, along 7°N., a large zone of these low concentrations is found between 250 and 1000 meters as far west as 154°E. West of 140°E., there is a distinct increase in the oxygen content of the water column, which Ito relates to the western limit of the prevailing northeast winds. The oxygen at 250 to 1000 meters increases steadily to about 130°E., west of which it again decreases. The eastern part of this section should be in the North Equatorial Current (Sverdrup *et al.*, 1942, Chart VII), but the currents in the westward part of the section set southward. In the north-south section, the currents north of 20°N. set northeast, east, and southeast and presumably introduce waters of the Kuroshio into the section. These appear as a relatively highly oxygenated zone containing more than 3 ml/liter as far down as 800 meters. Between 10° and 20°N., this section crosses the North Equatorial Current, which contains less oxygen than the more northern part.

THE JAPAN SEA

This adjacent sea of the Pacific has been widely studied by the Japanese, and Uda (1934) has reported on a detailed survey of its oxygen content made in May and June 1932, when it contained more than 5 ml/liter to a depth of 1000 meters. No intermediate oxygen minimum was present, and, below 200 meters in the warm-water area and below 400 meters in the cold-water area, the oxygen content was essentially constant at all depths. Vertical distribution of temperature and salinity has this same uniform characteristic, and there is apparently active vertical mixing in the region.

THE DUTCH EAST INDIES

The oxygen content of the waters of the Dutch East Indies was studied by Van Riel (1943), on the SNELLIUS 1929–1930 expedition. The area covered by this expedition extended from 12°S. to 10°N. and from 112° to 134°E. This region, with its many islands and complicated topography, has an oxygen distribution subject to many local influences. In general, the deep-water oxygen content of the East Indian Archipelago reflects the circulation of the waters. In many cases, heavier waters enter deep basins across threshold sills and carry their characteristic oxygen content to the bottom. The Morotai Basin is a typical case. Pacific waters having an oxygen content of 3.0 to 3.1 ml/liter flow over the Snellius Ridge entrance sill into the basin, where the oxygen content is 3.0–3.1 at all depths between 2600 and 3800 meters. In contrast, concentrations increase to more than 3.4 ml/liter at corresponding depths on the Pacific side of the ridge. A similar situation was found in the Boeroe Basin (Van Riel, 1943, Fig. 11), in which the remarkably uniform oxygen content shows that there must be very little *in situ* consumption—*i.e.*, the oxygen content of the

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TABLE 11.—*Oxygen content of deep waters of the East Indian Archipelago*
Compiled from Van Riel (1943)

Regions Where Deep O_2 Content Decreases Appreciably

Region	Content at bottom	Source	Entering water	
			Depth, m.	O_2
Batjan Basin	2.63	Ternate Trough	2600	2.8–3.0
Sawoe Basin	1.8	Wetar Basin	2100	2.0
Aroe Basin	2.25	Ceram Sea	1600	2.4–2.5
Kaoe Bay	O_2 nil 0.3 ml/1 H_2S	Pacific Ocean	50	4.0

Regions Where Deep O_2 Content is Essentially That of Entering Waters

Region	Content at bottom	Source	Entering water	
			Depth, m.	O_2
Celebes Sea	2.14	Sangihe Trough	1400	2.2
Sangihe Trough	2.73	Pacific Ocean	2000	2.7
Morotai Basin	3.06	Pacific Ocean	2400	3.0–3.1
Ternate Trough	3.04	Morotai Basin	3000	3.0
Boeroe Basin	2.5–2.6	Batjan Basin	2000	2.51–2.57
Banda Sea	2.4–2.5	Batjan Basin	3200	2.5
Halmahera Basin	2.9	Pacific Ocean	700–940	2.9
Aroe Basin	2.3	Timor Trough	1400	2.2–2.4

O_2 contents in ml/liter.

water is established before its entry into the basin. Circulatory processes must be sufficiently rapid and oxygen consumption sufficiently slow or sufficiently complete that no appreciable consumption takes place during the stay of these waters in the basin.

Other basins in this region represent regions of reduced oxygen content and stagnation in the bottom waters. In Kaoe Bay, oxygen disappears at around 400 meters, and appreciable concentrations of hydrogen sulfide were found in the bottom 100 meters. Decreases in the oxygen content (below sill depth) were also observed in the Batjan (Van Riel, 1943, Fig. 8), Sawoe, and Aroe basins.

The oxygen distribution in the deep waters of some of the basins of this region is summarized in Table 11, compiled from Van Riel's data.

THE NORTHEAST PACIFIC, BERING STRAIT, AND BERING SEA

The oxygen distribution in the northeast Pacific, Bering Strait, and Bering Sea has been studied by T. G. Thompson and his coworkers. Their data (Barnes and Thompson, 1938) extending from 54°N. in the Aleutians through the eastern part of the Bering Sea and Straits into the Chukchi Sea show that shallow waters of this generally shallow region are highly oxygenated and well mixed from surface to bottom. Between Dutch Harbor and about 56°N., the waters are deeper but still on the

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eastern shelf area and show no well-developed minimum zone, decreasing rather steadily from 6–7 ml/liter at the surface to 3.5–4.5 ml/liter at 400 meters.

Thompson, Thomas, and Barnes (1934) reported on the oxygen content of the waters off the coast of Washington, Vancouver Island, the North Pacific (south of the Aleutian Ridge), and the Bering Sea. Except in the Bering Sea, there is a well-developed intermediate oxygen minimum zone in this region; its depth tends to increase from north to south. Just south of the Aleutian Ridge it occurred at 800 meters, but off the coast of Washington and Vancouver Island it was found at 1000–1100 meters at several stations. Minimum concentrations increased northward, from about 2.2 ml/liter off the Washington coast to about 6.7 ml/liter in the Bering Sea. In the Gulf of Alaska off Cape Spencer (57°39′N.) the intermediate minimum zone was absent, and concentrations decreased steadily to 4.2 ml/liter in the bottom water at 1900 meters. Hamm and Thompson (1941) found the minimum concentration, 2.46 ml/liter, at 1000 meters, beyond the continental shelf off the coast of Washington (48°24′N., 127°02′W.), but at a station west of the Queen Charlotte Islands (54°10′N., 134°10′W.) the oxygen content decreased steadily with depth to 2.91 ml/liter at 1100 meters.

Vast areas of the Pacific Ocean remain unexplored in so far as the oxygen content is concerned. The evidence leads Sverdrup *et al.* (1942) to assume that the tongue of low oxygen extending westward in the northern equatorial Pacific has a counterpart in the southern equatorial region. The section constructed by Schott (1935, Fig. 50) and the high populations encountered on the drift of the KON TIKI (Heyerdahl, 1950) indicate such a zone is present in these southern latitudes; this view is strengthened by the WILLIAM SCORESBY observations off the Peruvian coasts and is confirmed, for the eastern part of the ocean, by recent observations.

APPENDIX: DETERMINATION OF DISSOLVED OXYGEN

Oxygen determination: The introduction, in 1888, of the Winkler titrimetric method for the determination of dissolved oxygen offered a real stimulus to the observation of this quantity in the oceans. Prior to its first extensive oceanographic use aboard the PLANET (Brennecke, 1909) oxygen was determined gasometrically by a variety of methods. Except for special researches, such as those of Hamm and Thompson (1941), these methods have only historical interest. The Winkler method, in several modified forms, is now used universally in oceanography.

A need for improvement in methodology, in keeping with the high speed and continuously recording methods of oceanography, has developed in recent years. Micro or semimicro methods would be desirable for use in conjunction with the Spilhaus-Miller sea sampler (Spilhaus and Miller, 1948). Semimicro methods based on the Winkler method have been tried with varying degrees of success (Thompson and Miller, 1928; Van Dam, 1934; Harper, 1953). A method in which the concentration of the iodine solution is measured colorimetrically instead of by titration has been described by Austin (1950), but the author has had indifferent success with it at sea, chiefly because of difficulties in achieving the required niceties of technique aboard ship. A microcolorimetric method, in which a solution of reduced indigo carmine is partially oxidized by the oxygen in the test sample, has recently been described by Loomis (1954).

Polarographic and amperometric methods appear to have little advantage for shipboard use, unless they can be made continuously operating, either along a ship's course at a fixed depth or with depth at a fixed location, as the salinity-temperature-depth recorder (Jacobson, 1948) operates. Advances along this line have been made, and Ippen, Yoseph, and Posthill (1951) have described a method for continuously recording the oxygen content in water during aeration processes, using a dropping mercury electrode in water of low turbulence, or a rotating platinum electrode in a system

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of higher turbulence. It appears that the latter might be useful in a flowing system. Other aspects of this subject have been discussed by Olson, Brackett, and Crickard (1949), by Manning (1940), and by Giguère and Lauzier (1945).

THE WINKLER METHOD: This method employs the oxidation of manganous hydroxide, by dissolved oxygen, to give tetravalent manganese. Upon acidification in the presence of iodide ion, free iodine (or I_3^- ion) is formed equivalent to the amount of dissolved oxygen:

$$Mn^{++} + 2OH^- \rightarrow Mn(OH)_2$$

$$2\ Mn(OH)_2 + O_2 \rightarrow 2\ MnO(OH)_2$$

$$Mn(OH)_2 + 2H^+ \rightarrow Mn^{++} + 2H_2O$$

$$MnO(OH)_2 + 4H^+ + 3I^- \rightarrow Mn^{++} + I_3^- + 3H_2O$$

The complex iodine-iodide ion (I_3^-) thus released is then titrated against thiosulfate solution, using starch as an indicator:

$$I_3^- + 2S_2O_3^{=} \rightarrow 3I^- + S_4O_6^{=}.$$

The water samples are drawn from the sampling device, in the absence of air, as soon as they are brought on board. The sample bottles are filled and kept stoppered. With the least practicable delay, solutions of manganous salt and of basic iodide are added, the bottle again stoppered, shaken, and the precipitate allowed to settle. Later, the mixture is acidified, and the liberated iodine is titrated.

The method has been reviewed in more detail by Bjerrum (1904), Jacobsen and Knudsen (1921), Helland-Hansen (1923), Thompson and Robinson (1932; 1939) and others. Thompson and Robinson (1939), Ohle (1953), H. Barnes (1953), and others have discussed sources of error and their prevention. T. G. Thompson (unpublished notes) has estimated that in nearly saturated samples the error in a determined value is about 0.002 mg atom or 0.02 ml/liter of sea water.

A committee of the Association d'Océanographie Physique on Chemical Methods and Units consisting of Bjørn Helland-Hansen, J. P. Jacobsen, and T. G. Thompson (Helland-Hansen *et al.*, 1948) has recommended that the oxygen content be reported as the amount, in milligram atoms, dissolved in an amount of sea water that at 20° has the volume of 1 liter, or in ml at NTP dissolved in a similar amount of water. Because the large majority of data is reported in the latter units, they have been most generally used in this paper. The molecular volume of O_2 is 22.393 liters, its atomic weight is 16.00. Therefore, the atomic volume of oxygen is 11.1965 liters, and the units can be interconverted as follows:

$$11.1965 \times \text{milligram atom/liter} = \text{ml/liter}$$

or

$$\text{ml/liter} \div 11.1965 = \text{milligram atoms/liter.}$$

The factor for the conversion from cubic centimeters to milliliters is 0.999972, and the two units have been used interchangeably in this discussion.

To convert oxygen concentrations to parts per million:

$$11.1965 \text{ mg-a/liter} = 1 \text{ ml/liter} = 0.179144 \text{ grams/liter}$$

$$= 179.144 \text{ grams/1000 liters}$$

If the density of the solution is 1.0, this equals parts per million. If the density is other than 1.0, divide by the density to get parts per million.

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Chapter 10

Carbonates and Carbon Dioxide*

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INTRODUCTION

Carbon dioxide and calcium play fundamental roles in the metabolism of living creatures. Photosynthetic transformations of carbon dioxide and water into organic compounds, together with the subsequent reoxidation of these compounds and their derivatives, are the basic biological mechanisms for the storage and utilization of solar energy. In many living systems the quantity of carbon dioxide controls the hydrogen ion concentration. In the tissues and body of marine invertebrates the presence of calcium stabilizes intercellular matrices and mucous coverings; in its absence the constituent cells of most invertebrate tissues fall apart. Calcium is essential for the normal activity of the neuro-muscular system, for amoeboid and ciliary movement, chromatopore activity, the clotting of the body fluids, and the control of permeability (Robertson, 1941).

Calcium and carbon dioxide are major components of organic hard parts. For this reason they are of particular importance to the geologist and paleontologist, not only because of the high percentage of limestone in sedimentary rocks, but because carbonate structures are the principal remains of the animals and plants that lived during the geologic past.

Calcium carbonate customarily occurs in two crystal forms in the sea. Calcite, crystallizing in the rhombohedral class of the hexagonal system, is usually the most abundant form in cold environments, while aragonite, the orthorhombic form, is most common in warm tropical seas. The two closely related elements, magnesium and strontium, are often associated with calcium in marine carbonates.

Under marine conditions, certain classes of organisms tend to take up magnesium carbonate in solid solution in the calcite lattice; roughly speaking, the more primitive types often take up the most magnesium. No mineral form of pure or hydrated $MgCO_3$ is found under marine conditions, but the double carbonate, $CaMg(CO_3)_2$, dolomite, develops as a diagenetic mineral. This "dolomitization" may be due in part to the metasomatic replacement of calcium in metastable high-magnesium calcite, under particular chemical and thermodynamic conditions.

The mineral aragonite is also metastable, so that under certain conditions it tends to recrystallize as calcite. Aragonite usually carries strontium carbonate in small amounts in solid solution.

Since different phylogenetic types coexist in the same region, and seasonal variations in temperature occur at the same ecologic station, modern carbonate sediments

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(especially in warm-water areas) are often a complex mineralogical mixture. They may contain low-magnesium calcite, high-magnesium calcite, together with aragonite, either high or low in strontium. Such mixtures are found today in varied neritic environments, from biohermal suites and lagoonal facies to littoral deposits such as beach rock, and in calcarenites of eolian dunes derived from beaches. In deep-water environments low magnesium-calcite predominates, and the incidence of mixing is greatly reduced.

The carbonate minerals are formed either by organic activity or by inorganic precipitation in the marine realm. Modern studies of these minerals are having a profound effect on the geologist's understanding of past environments, notably the critical problems of paleoclimatology and paleoecology. Because of the complex relationships among different groups of organisms and the composition of their calcareous skeletons, and the variations in this composition related to environmental conditions, the paleoecologist is equipped with a sensitive apparatus for testing the temperature, atmospheric conditions, depth of water, and other features of ancient environments.

If Clarke's (1924) calculations for the quantities of calcium and magnesium in the ocean today, and those being transported into it, be accepted, we have the following broad picture of their "geoeconomy": There are about 5.5×10^{14} metric tons of calcium in the ocean, against 17×10^{14} tons of magnesium. Annual additions from the land, in solution by rivers, are 526×10^{6} tons for calcium and 93×10^{6} tons for magnesium. Thus, at the present rate the amount of calcium in the sea would be doubled in a million years. Calcium carbonate is apparently saturated or supersatured in the open ocean, so that any addition must be compensated for by an equivalent figure for extraction. It is apparent also that if there were not a vigorous removal of magnesium, the amount in the ocean would be doubled within some 18 million years at the present rate of inflow. Much of the removal may be absorption and exchange in clay minerals rather than in carbonates.

It has been calculated that the Ca/Mg ratio in modern carbonate sediments is around 40:1 (Chilingar, 1956), whereas Daly (1910, p. 165) calculated that the Ca/Mg ratio for Precambrian carbonate rocks was only about 4:1. Thus the figures for the present geoeconomy of the carbonates cannot be taken as fixed for geologic time. Additions of less than 500 milligrams per liter of magnesium as the carbonate or bicarbonate will eventually saturate the oceans with magnesium carbonate. Although certain self-stabilizing factors have undoubtedly played a part, cyclic oscillations of solution and precipitation may have occurred; the supply of significant salts has possibly varied according to orogenic activity and the stage of weathering of land masses, and rates of withdrawal have varied, depending on organic activity, the mean temperature of the sea water, and the relative width of shallow seas, which is closely connected with eustatic rise and fall of sea level (Fairbridge, 1955).

Determination of the fundamental characteristics of the present ecologic scene is a necessary first step for the study of the complex problems of carbonate paleoecology.

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PLANETARY EQUILIBRIUM OF CALCIUM AND CARBON DIOXIDE

PARTITION AMONG GEOSPHERES

Very large quantities of calcium and carbon dioxide have passed through the ocean and the atmosphere and now exist in the sediments. The calcium deposited from solution is largely in carbonates, and the carbon is in carbonates or organic carbon. Much smaller amounts of these substances are dissolved in the hydrosphere. The amounts of carbon in the biosphere and the atmosphere are an order of magnitude smaller still. Table 1 summarizes recent estimates of the amounts of carbon in the sedimentary rocks, the hydrosphere, atmosphere, and biosphere. Seventy three per cent of the carbon exists as sedimentary carbonates, nearly 27 per cent as organic carbon in the sediments, and only 0.16 per cent is in the ocean, atmosphere, and biosphere.

The partition of carbon among geospheres depends on a complex mechanism. Among the variables are the temperature and chlorinity of the ocean, the solubility of calcium carbonate and carbon dioxide in sea water, the rate of production of carbon dioxide by volcanoes; the rate of passage of carbon dioxide across the air-sea boundary; the rates of weathering of carbonate sediments and noncarbonate rocks; and the rate and character of various organic processes, including photosynthesis, respira-

TABLE 1.—*Carbon and carbon dioxide in sedimentary rocks, hydrosphere, atmosphere, and biosphere*

	Total on earth	Amount per unit area*	Reference
All quantities computed as CO_2	10^{20} gms	gm cm^{-2}	
$CO_3^=$ in sediments	670	13100	Rubey (1951)
Organic carbon in sediments	250	4900	Rubey (1951)
CO_2 in atmosphere	0.0235	0.46	Hutchinson (1954)
$CO_2 + H_2CO_3$ in ocean	0.008	0.22	See Note (1)
HCO_3^- in ocean	1.147	31.8	See Note (1)
$CO_3^=$ in ocean	0.142	3.95	See Note (1)
Total in ocean	1.297	36.0	See Note (1)
Dead organic matter on land	0.0260	1.73	Rubey (1951)
Living organic matter on land	0.003	0.20	See Note (2)
Dead organic matter in oceans	0.100	2.78	Sverdrup *et al.* (1942)
Living organic matter in oceans	0.0003	0.008	Sverdrup *et al.* (1942)

* CO_2 in sediments and atmosphere given in gm cm^{-2} of earth's surface; CO_2 in ocean and on land given in gm cm^{-2} of ocean and land surface respectively. Gm cm^{-2} means grams per square cm.

Note 1. Carbon dioxide components in sea water assumed in equilibrium with CO_2 partial pressure $= 3 \times 10^{-4}$ atmosphere; chlorinity = 20‰; temperature = 10°C; alkalinity $= 2.46 \times 10^{-3}$ meq/L. Under these conditions, pH = 8.18. Volume of ocean $= 1.37 \times 10^{24}$ cm^3. This is probably an underestimate, because the water below the thermocline contains CO_2 provided by oxidation of organic matter, and the average temperature of the ocean is somewhat less than 10°C.

Note 2. Living organic matter on land estimated from assays of standing timber in the world's forests. Thirty percent of land surface is relatively thick forest, averaging about 5,000 board feet per acre of commercial size timber or 0.26 gm CO^2/cm^2 of forest. Assuming that total living matter in forests is twice the amount of timber, and that other components of the biosphere are ⅓ of total gives 0.0034×10^{20} gms.

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TABLE 2.—*Fluxes of carbon dioxide in the atmosphere, hydrosphere, and biosphere*

	Total on* earth, 10^{15} gms yr^{-1}	Amt. per unit area, mg cm^{-2} yr^{-1}	Reference
Consumption of fossil fuels—CO_2 produced	9.1	1.6	Revelle and Suess (1956)
$CO_3^=$ weathering products added to ocean by rivers (as CO_2)			
(1) by production of carbonates from silicates	0.125 ± 0.065	0.035 ± 0.02	Conway (1942) Hutchinson (1954)
(2) by solution of sedimentary carbonate	0.90 ± 0.45	0.25 ± 0.13	Conway (1942) Hutchinson (1954)
Total	1.03 ± 0.52	0.29 ± 0.15	Clarke (1924)
Photosynthesis on land—CO_2 consumed	73 ± 18	55 ± 14	Hutchinson (1954)
Photosynthesis in ocean—CO_2 consumed	462 ± 303	128 ± 84	Riley (1944)
Computed average rate of volcanic production of CO_2 during the last 3×10^9 yrs.	0.03	0.006	Hutchinson (1954)
Exchange between atmosphere and ocean, across sea surface	210 ± 130	58 ± 36	Revelle and Suess (1956)

* 10^{15} gms yr^{-1} means 1 billion metric tons per year.
mg cm^{-2} yr^{-1} means 1 milligram per square centimeter per year.

tion, building of calcareous skeletons, decomposition of dead organic matter, man's consumption of fossil fuels, and his transformations of the land surface. Some important carbon dioxide flux rates are listed in Table 2. Comparison of Tables 1 and 2 shows that the amount of carbon dioxide consumed each year in photosynthesis on land is $\frac{1}{32}$ of the total amount in the atmosphere, while photosynthesis by marine plants uses about $\frac{1}{2800}$ of the total amount of carbon dioxide in the ocean. At the present rate of consumption of fossil fuels, an amount of carbon dioxide equal to the total now present in the atmosphere will be produced in 260 years.

EXCHANGE OF CARBON DIOXIDE BETWEEN ATMOSPHERE AND OCEAN

The ocean, with its much higher carbon-dioxide content, should act as a reservoir for the atmosphere and the land, but the rates of exchange and the factors determining the equilibrium point are by no means clear. Photosynthesis results in a continuous removal of carbon dioxide from the surface waters over most of the ocean, because some of the organic matter produced by marine plants settles in detrital form to the depths before it is reoxidized. Hence, if the waters were not in motion there would generally be a flux of carbon dioxide from the air to the sea. But the north-south motion of the surface waters must be considered. In such currents as the Gulf Stream and the Kuroshio, the waters are cooled as they move to higher latitudes, and their ability to hold carbon dioxide increases, so that as a result both of cooling and of photosynthesis the flux of gas is still from the air to the sea. In currents off the west coasts of continents, however, the surface waters are warmed as they move toward the equator, and carbon dioxide-rich waters upwell

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from the depths. In the absence of photosynthesis there would be a flux of carbon dioxide from the sea to the air. But these are regions of rapid photosynthesis, and the direction of the net movement of carbon dioxide across the air-sea boundary is not known.

The principal regions in which carbon dioxide passes from the ocean to the atmosphere may be in high latitudes during occasional periods when convection occurs between the surface waters and the carbon dioxide-rich deep waters. Remarkably low values of atmospheric CO_2 (about .015 vol %) were found by Buch (1939) above the sea surface off Spitzbergen, in summer, indicating that even in high latitudes the direction of carbon-dioxide flux is often from the air to the sea.

Account must also be taken of the seasonal and diurnal changes in the waters near the surface In mid-latitudes of the northern hemisphere (30°–50°N.) during late summer, the temperature in the upper 100 meters averages about 7° warmer than in the winter months (Sverdrup, Johnson, and Fleming, 1942, p. 130–131). The solubility of carbon dioxide decreases as the water is warmed; other things being equal there should be a net flux of carbon dioxide from the ocean to the atmosphere, during the spring and summer months, of about 1 mg cm^{-2}, and an equal net flux in the reverse direction during fall and winter. But the rate of photosynthesis also increases during spring and summer, and consequently the "standing crop" of organic matter in phytoplankton and zooplankton increases at the expense of the carbon dioxide dissolved in the water. From data given by Sverdrup, Johnson, and Fleming (1942, p. 928–940) the difference in standing crop between summer and winter in middle and high latitudes can be computed. It is roughly equivalent to 10 mg cm^{-2} of dissolved carbon dioxide. Thus, if equilibrium were attained and no precipitation of calcium carbonate occurred, there would be a net flux of about 9 mg cm^{-2} from the atmosphere to the ocean during spring and summer, and a somewhat smaller reverse flow during fall and winter. (The difference results from the settling of organic matter out of the surface layers into the deep waters.)

In the open sea, similar reversals in the net flux of carbon dioxide occur between day and night. The amount of carbon dioxide produced by animal and plant respiration at night is of the order of 0.5 mg cm^{-2}, roughly equal to the carbon dioxide consumed by photosynthesis in the daytime. The diurnal change in temperature is at most only a few tenths of a degree, so that the amount of carbon dioxide that can be held in the water column varies by only a few hundredths of a milligram per square centimeter. Consequently, the net flux must be from sea to air at night and from air to sea in the daytime. In small, semi-isolated water bodies such as tide pools, the diurnal temperature change may be greater than 10°, and the corresponding change in carbon-dioxide solubility between day and night may overbalance the effects of respiration and photosynthesis. The net flux of carbon dioxide is then opposite to that of the open sea, from air to sea at night and from sea to air in the daytime.

So far we have discussed the direction, and upper limits for the magnitude, of the net fluxes of carbon dioxide between the atmosphere and the ocean. The *rate of exchange* of carbon dioxide between the two great earth fluids should be larger than the net flux. The magnitude of this exchange rate has recently been estimated by Revelle and Suess (1957) on the basis of carbon 14 measurements by Suess (1954; 1955), Rafter (1955), and Hayes, Anderson, and Arnold (1955).

In marine materials from near the ocean surface, the ratios of the stable isotopes, C^{12} and C^{13}, to the radioactive isotope, C^{14}, differ from those in land plants in such a way that the apparent average age of the C^{14} in the surface waters, when compared to that in the atmosphere, is about 400 years. From this it can be computed that the average lifetime of a carbon-dioxide molecule in the atmosphere before it is absorbed by the sea is of the order of 10 years. The exact value depends on the choice of assump-

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tions about the rate of mixing between the deep and surface waters of the oceans and the rate of turnover of carbon between the organic matter in soils and the atmosphere. Craig (1957a) has made a detailed study of the exchange rate, based on the rate of cosmic-ray production of C^{14}, and obtains an average atmospheric life of 7 ± 3 years. He has also evaluated the exchange time by considering its dependence on the internal mixing rate in the sea, using a two-layer model for the sea; this procedure also gives an atmospheric life of about 7 years.

The very large and rapidly increasing rate of consumption of fossil fuels by our industrial civilization allows an independent computation. Between 1850 and 1950, the total amount of $C0_2$ produced by combustion of fossil fuels was about 12 per cent of that in the atmosphere. Callendar (1940) and Plass (1956) believed that nearly all this added carbon dioxide has remained in the atmosphere. They suggested that the warmer climates of northern latitudes during the past few decades resulted from the effect of the increase in atmospheric CO_2 on the infra-red radiation balance. Because the C^{14} content of carbon dioxide from fossil fuel must be negligibly small, owing to the geologically short life of this radioactive isotope, the C^{14}/C^{12} ratio in the atmosphere should have decreased by 12 per cent if all the industrially produced carbon dioxide from fossil fuels has remained in the atmosphere. In fact this is not so; measurements by Suess (1955) of the C^{14} content of tree rings grown a few years ago with those grown in the nineteenth century show that the C^{14}/C^{12} ratio has decreased by less than 2 per cent. The average life of an atmospheric carbon-dioxide molecule before it is absorbed in the ocean was calculated by Suess (1953), from his earlier data, to be between 20 and 50 years, on this basis. However, Revelle and Suess (1957), using later analyses, have considered the problem in more detail and conclude that the value is of the order of 10 years. After taking into account the buffer mechanism of sea water, Revelle and Suess conclude that the increase in atmospheric carbon dioxide from industrial fuel consumption during the past 100 years is between 3 and 6 per cent, but they suggest that the accelerating rate of fossil-fuel consumption may lead to an increase of more than 20 per cent within the next 50 years.

The exchange rate is obtained from the reciprocal of the average carbon-dioxide lifetime in the atmosphere. Assuming a possible range for the average lifetime of 7 to 30 years, the exchange lies between 80 and 340×10^{15} gm yr^{-1} (22 to 95 mg $cm^{-2}yr^{-1}$). As might be expected, these exchange rates are higher than the computed upper limits for the net seasonal flux, even in the oceanic regions where seasonal fluctuations of standing crop are most pronounced. But they yield values for the invasion coefficient of carbon dioxide across a stirred liquid surface close to those obtained experimentally by Bohr (1899).

SOLUTION AND DEPOSITION OF CALCIUM CARBONATE

Judging by present-day conditions, if precipitation of calcium carbonate onto the sea floor were not occurring, the dissolved carbonates being poured into the sea by rivers would double the total carbon dioxide of the ocean in 135,000 years. The calcium carried by rivers would double the oceanic calcium content in 1,000,000 years (Clarke, 1924). It is thus certain that at the present time the ocean is approximately saturated with calcium carbonate. The rate of withdrawal of calcium carbonate in marine sediments must be almost exactly equal to the rate at which carbonates are carried to the sea by rivers. This is equivalent to 0.29 mg. $cm^{-2}yr^{-1}$ of CO_2 (Table 2). We may conclude that the average rate of deposition of calcium carbonate on the sea floor is 0.66 gm cm^{-2} per 1000 years. This is close to the estimated average rate of deposition of calcium carbonate in pelagic sediments (Arrhenius, 1952). Probably most of the present deposition of calcium carbonate takes place on the sea floor at moderately great depths (not exceeding about 2500 fms or 4700 m). Below such depths re-solution takes place. The rates of deposition of shallow-water limestones

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may be much more rapid per unit area, but the total area covered by these sediments is small compared to that covered by calcareous pelagic deposits. This is in marked contrast to conditions during some earlier geologic eras.

The larger part of the calcium carbonate now in the sea is probably derived from the solution of limestone on land and transported there by rivers. This is the view of Twenhofel (1929), Conway (1942), Kuenen (1950), Hutchinson (1954), and others; Kuenen believes that, because of the rise of pelagic Foraminifera during the Cretaceous, there has been a gradual transfer of calcium carbonate from the terrigeneous sedimentary cycle into the deep-sea sediments. He suggests that because these sediments are likely to remain permanently on the sea floor the amounts of calcium available for formation of shallow-water limestones are gradually diminishing and will reach a minimum in a few tens of millions of years. There will then be a "lime famine" —the average rate of deposition of calcium carbonate will be reduced to the rate at which new carbonates are produced by the weathering of noncalcareous rocks. At the present time, according to Conway, this is about one-seventh the rate of solution of carbonates on land (Table 2).

ORIGIN OF CARBON NOW ON THE EARTH'S SURFACE

Rubey (1951) believed that throughout geologic time carbon has been added continuously and at a virtually constant rate to the ocean and the atmosphere from the interior of the earth, through volcanoes and volcanic springs. One of Rubey's principal arguments is that the geologic record indicates little change in the amount of carbon dioxide in the ocean at any time in the past. As will be shown, this approximate constancy of the oceanic carbon dioxide is probably a necessary consequence of the equilibrium system.

Urey (1952) suggested that the carbon now on the earth's surface was present at the beginning of the earth's history as atmospheric and oceanic methane, and that carbon dioxide was produced by oxidation of the methane. Such oxidation would take place relatively quickly, and the resulting high CO_2 content of the air and the water would bring about very rapid weathering. Urey's hypothesis therefore implies that there once existed a very large volume of early Pre-cambrian limestone, and that the earliest sedimentary rocks should contain the products of profound chemical weathering. Available geologic evidence does not support this view; it should be remembered, however, that the oldest rocks now exposed may be considerably younger than the first sediments laid down (Ahrens, 1955).

Urey (1952) was among the first to point out that the carbon-dioxide content of the atmosphere and ocean probably is regulated over geologic times by the tendency toward thermodynamic equilibrium between silicates and carbonates and their respective free acids, silica, and carbon dioxide. The atmosphere contains and probably has contained during geologic times considerably more CO_2 than the equilibrium concentration (Hutchinson, 1954), although uncertainties in the thermodynamic data are too great for an accurate quantitative comparison.

In any case; throughout most of geologic time the rate of production of new carbonate by weathering of noncalcareous rocks must have been fixed by the rate of addition of carbon from the interior of the earth. If we neglect the carbon dioxide initially present, together with that derived from

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Urey's postulated methane, and assume that the volcanic carbon is juvenile, then the average rate of release of carbon by volcanoes would be equal to the total carbon in sedimentary rocks, divided by the length of time represented in the geologic record. Assuming further that this time is 3×10^9 years, we see from Tables 1 and 2 that the present rate of volcanic production, based on the estimates of the rate of chemical weathering of noncalcareous rocks given by Conway and by Hutchinson, would be between 2 and 6 times the average rate. The uncertainty is partly due to the inadequacy of hydrologic data on the rates of discharge into the ocean from rivers and ground water.

Borchert (1951) and Hutchinson (1954) consider that only a fraction of the volcanic carbon is juvenile and that most of it has been derived from the decomposition of deeply buried limestone. This implies that the total amount of limestone deposited during geologic time greatly exceeds the amount now present—in other words that there is a geologically dominant cycle of carbon dioxide between sedimentary, metamorphic, and igneous rocks. The average rate of addition of carbon from volcanoes and volcanic springs during the earth's lifetime might then be equal to or even considerably higher than the present rate.

A promising approach to the problems of the rate of inflow and the total quantity of juvenile carbon on the earth's surface at different geologic times has been made by Craig (1953) using the ratios of abundance of the stable isotopes C^{12} and C^{13}. C^{13}/C^{12} ratios in igneous rocks and in land-derived organic carbon average 2.5 per cent lower than in marine limestones. Atmospheric carbon dioxide and marine invertebrate soft parts have intermediate ratios. Much further work is needed on the mechanisms of fractionation and exchange, and on the distribution of these isotopes in materials of different geologic age, before an adequate picture of the origin and history of the carbon dioxide on the earth's surface can be drawn.

POSSIBLE CHANGES IN THE CARBON-DIOXIDE SYSTEM

From the viewpoint of the geologist and paleontologist, it is interesting to consider possible changes in the atmospheric and oceanic carbon-dioxide systems. There is evidence (Emiliani, 1954) that during the Oligocene, for example, the temperature of oceanic deep water averaged about 10.5°C. and that it declined about 8° by the end of the Pliocene. Consequently the average temperature of the ocean was higher than today. This higher average temperature must have been accompanied by a lowering of the solubility of calcium carbonate and carbon dioxide in the sea water. At equilibrium, the alkalinity of sea water—essentially the amount of carbon dioxide balanced against calcium—would have been less than it is today. With the same CO_2 concentration in the water the pH would also have been lower; the free CO_2 content and hence the partial pressure would rise. This rise would be in addition to the increased partial pressure resulting from the higher temperature. Carbon dioxide would be transferred from the ocean to the atmosphere until the partial pressures became equal. But a higher CO_2 content in the atmosphere should increase the rate of chemical weathering of silicates, hence the rate of transport of "new" carbonates by rivers to the sea, the rate of precipitation on the sea floor, and the rate of removal of CO_2 from the ocean-atmosphere system. Other things being equal, equilibrium would finally be attained with an atmospheric CO_2 content and partial pressure about that of the present time, while the alkalinity, pH, and total carbon-dioxide content of the ocean would be somewhat below the present value. A decrease of average oceanic temperature would have an opposite effect. At equilibrium, regardless of the temperature, the rate of formation of new carbonates from silicates would depend only on the amount of carbon dioxide produced by volcanoes and volcanic springs. Similarly, the average rate of deposition of carbonates would depend only on the rates of supply of calcium carbonate by rivers to the ocean.

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TABLE 3.—*Carbon dioxide in atmosphere and ocean for an initial partial pressure of 10^{-1} atmosphere*

	P_{CO_2}, atmospheres	Total CO_2 in atmosphere, 10^{20} gms	CO_2 in sea water, moles/L	Total CO_2 in ocean, 10^{20} gms	Total in ocean and atmosphere, 10^{20} gms
Initial condition	0.1	7.4	0.0056	3.3	10.7
Silicate weathering only, first equilibrium with carbonates	0.029	2.3	0.014	8.4	10.7
Silicate weathering only, final equilibrium with carbonates	0.0003	0.0235	0.0021	1.30	1.32
Silicate and carbonate weathering, first equilibrium with carbonates	0.048	3.6	0.019	11.5	15.1
Silicate and carbonate weathering, final equilibrium with carbonates	0.0003	0.0235	0.0021	1.30	1.32

From the equations and tables given by Sverdrup, Johnson, and Fleming (1942, p. 192–210) and by Harvey (1945) it is possible to compute the initial partition of the carbon dioxide components in the sea and the atmosphere, and the subsequent sequence of events. This is illustrated in Figures 1 and 2.

Let us now consider the effects of a sudden marked increase in the carbon-dioxide content of the ocean and the atmosphere. As an extreme example, suppose that this increase is sufficient to raise the partial pressure of CO_2 to 0.1 atmosphere, about 300 times the present value. This would require an eight-fold increase in carbon dioxide, from 1.32 to 10.7 $\times$ 10^{20} grams (Table 3), equivalent to 5 to 15 million years production from volcanoes and volcanic springs at the estimated present rate.

Initially most of the added carbon dioxide would be in the atmosphere; the total carbon-dioxide content of the oceans would be somewhat more than doubled. The pH would drop from the present value of about 8 to 6.2. Even if no limestones were exposed to weathering (Fig. 1) the rivers would almost immediately begin to carry large quantities of dissolved calcium and carbonates to the sea from the chemical weathering of silicate rocks, and carbonates would also be formed from silicates beneath the sea. The alkalinity and total carbon-dioxide content of the water would then increase, the pH would rise, and there would be a corresponding rise in the carbonate content. Finally, both the alkalinity and the carbonate would become so high that the ion product of calcium times carbonate would equal the saturation value. At this point calcium carbonate would commence to precipitate onto the sea floor, even though the pH would still be only slightly alkaline and more than one unit below the present value. The partial pressure of carbon dioxide in the atmosphere would have decreased by 71 per cent, but the total carbon dioxide in ocean and atmosphere would not have changed from the initial value. Chemical weathering would continue on the land areas, however, and new carbonates would be carried to the sea by rivers and deposited on the sea floor. This would result in a decrease of the total carbon dioxide in the ocean-atmosphere system and therefore a decrease in the partial pressure of CO_2 in the atmosphere, and in the CO_2 and alkalinity of the ocean. The pH and the carbonate content of sea water would continue to increase. Finally, other things equal, an equilibrium might be established close to that of the present day.

Figure 2 illustrates the sequence of events when both carbonate and silicate rocks are exposed. For simplicity it is assumed that initially only carbonates are dissolved, and no weathering of silicates occurs. The total CO_2 in ocean plus atmosphere, and the oceanic alkalinity, carbonate, and pH would increase, while the atmospheric carbon dioxide would diminish, until carbonates began to be precipitated from the ocean. If no chemical weathering of silicates occurred, an equilibrium would be established at a pH of about 7 and an alkalinity more than 6 times the present value. The amount of calcium carbonate being precipitated on the sea floor would be exactly equal to that being dissolved, and there would be no further change in either the oceanic or the atmospheric amounts of carbon dioxide. This is the situation considered by Rubey (1951). But in fact chemical weathering of silicates would occur and free carbon dioxide would be withdrawn from the system. The par-

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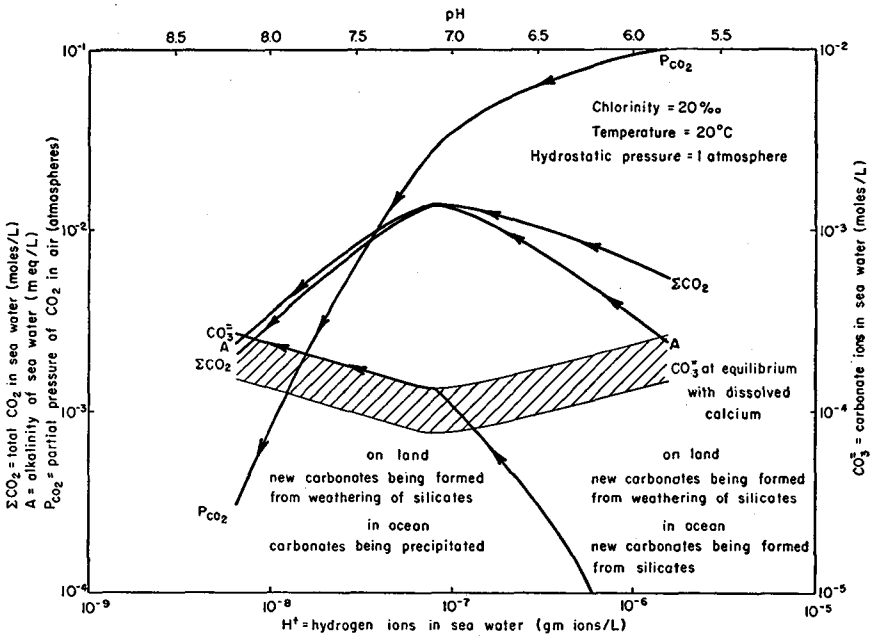

FIGURE 1.—*Changes (with time) of carbon-dioxide equilibrium after a sudden increase in atmospheric and oceanic carbon dioxide*

Only silicate rocks exposed to weathering. Cross-hatched area indicates oceanic carbonate concentration necessary for effective $CaCO_3$ saturation. For additional explanation, *see* text.

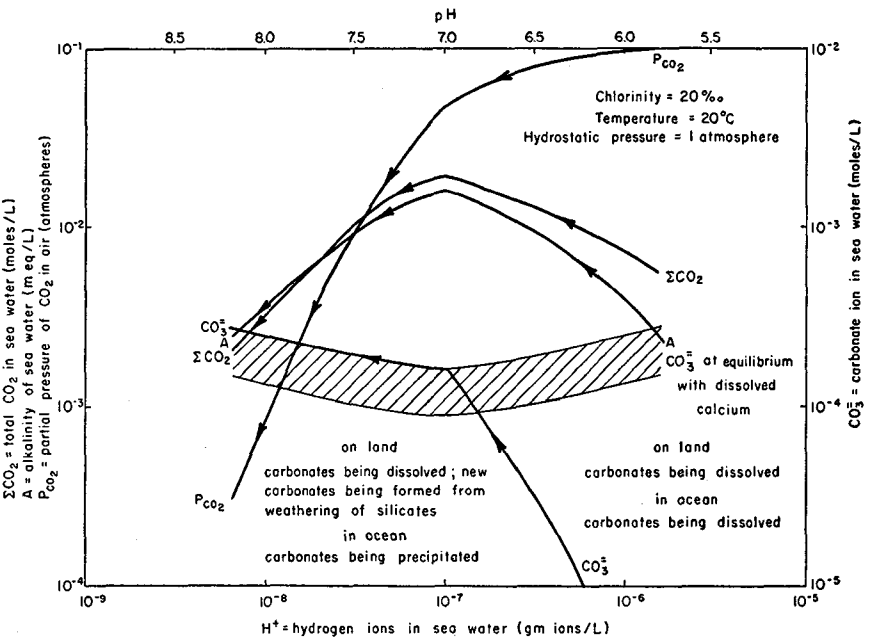

FIGURE 2.—*Changes (with time) of carbon-dioxide equilibrium after a sudden increase in atmospheric and oceanic carbon dioxide*

Same as Figure 1, but with both limestones and silicate rocks exposed to weathering.

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tial pressure of carbon dioxide would decrease, and similarly the alkalinity and total carbon dioxide in the ocean, while the carbonate and pH would increase. A return to present-day equilibrium conditions would be expected.

The times required to re-establish this equilibrium are difficult to compute but would be not more than a few million years and probably much less, because the rate of chemical weathering would be accelerated by the higher acidity of the surface waters on land.

If the rate of inflow of carbon dioxide from volcanoes and volcanic springs remained high for an extended period, however, the equilibrium would be shifted from present-day values. We have already briefly discussed the transient effects of the increased production of carbon dioxide from another source, fossil fuel combustion. In the steady state the carbon-dioxide content of the atmosphere must be such that the rate of production of new carbonates from the weathering of silicates balances the influx of "new" carbon dioxide to the atmosphere. The relationship between the rate of chemical weathering and the atmospheric carbon-dioxide content is unknown. If this relationship is linear, a doubling of the rate of inflow of carbon dioxide would at equilibrium result in a doubling of the atmospheric CO_2 and hence of the partial pressure of free CO_2 in the oceans. The alkalinity would then increase until the effective calcium-carbonate saturation point was reached. It is difficult to compute this increase in alkalinity because the increased carbon-dioxide content of the air would probably bring about a rise by several degrees in average air temperature and hence in the average temperature of the oceans. This would lower the solubility of both calcium carbonate and free carbon dioxide. Computations by Plass (1956) of the effect of carbon dioxide on the infra-red radiation balance indicate that a doubling of the atmospheric CO_2 would raise the average air temperature by 3.6°C. In his computations Plass was forced to neglect other processes accompanying a rise in temperature, such as the increased water-vapor content of the atmosphere and the melting of ice caps and snow cover, which would raise the temperature still further. In any case the required increase in alkalinity would probably be attained after a few tens of thousands of years.

We may thus conclude that over time periods of geological importance the pH of sea water at a given temperature has not varied much from the present value. The alkalinity and total carbon-dioxide content of the ocean may have fluctuated over a wider range, depending on the atmospheric CO_2 content. This is just the reverse of the usual statement that the atmospheric carbon dioxide is regulated by the amount in the sea. The average rate of deposition of calcium carbonate has been determined by the rate at which calcium and bicarbonate are carried to the sea by rivers, but the sites and rates of deposition in different parts of the ocean may have varied widely depending upon average air and sea temperature. These in turn have been at least partly determined by the carbon-dioxide content of the atmosphere which depends on the rate of inflow of volcanic carbon dioxide.

Our discussion has been based on equilibrium considerations. As pointed out by Eriksson and Welander (1956), in a complex multi-component system, such as carbon dioxide, marked oscillations may occur during the transient period preceding equilibrium.

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SOLUBILITY OF CARBONATES IN SEA WATER

PHYSICO-CHEMICAL FACTORS DETERMINING THE SOLUBILITY

So far, we have discussed the system of carbon dioxide and calcium on an ocean-wide basis, and have dealt only with average conditions. From this point of view, the rapid turnover of calcium and carbon dioxide is sufficient proof that on the average the ocean is effectively saturated with calcium carbonate. There is a wide variation in different parts of the ocean, however. Carbonates are accumulating only in certain regions, while in others solution is taking place. Before examining these variations, we must consider the physico-chemical conditions determining the solubility of calcium carbonate.

The apparent solubility product is the product of the measured or "apparent" concentrations of calcium and carbonate ion in a solution at equilibrium with solid calcium carbonate. In normal sea water the apparent solubility product is several hundred times the thermodynamic solubility product in distilled water. Both the apparent and thermodynamic solubility vary with crystal form, temperature, and pressure, while the apparent solubility in a salt solution also varies with the composition and ionic strength of the solution. In sea water the ratios of different salts are virtually constant, hence the ionic strength varies directly with the chlorinity.

EFFECT OF CRYSTAL STRUCTURE

The two principal crystal forms of calcium carbonate are calcite and aragonite. Calcite belongs to the rhombohedral class of the hexagonal system, and aragonite to the orthorhombic system. At ordinary temperatures and pressures calcite is the less soluble. In experiments by Murray and Irvine (1891) aragonite tended to crystallize from sea water above 26°C. under conditions of evaporation, and calcite below that figure. Vaterite is another hexagonal form of calcite, known also as μ-$CaCO_3$ (Johnston, Merwin, and Williamson, 1916), often spherulitic; it is rare in nature, but Dudich (1931) believed he had identified it in arthropod skeletons.

According to Kelley and Anderson (1935) the ratio of the solubility products of calcite to aragonite is given by the following equations:

$$-\ln \frac{K_A}{K_C} = \frac{\Delta F}{RT}$$

where K_A and K_C are the solubility products of aragonite and calcite, respectively, ΔF is the difference in free energy, R the gas constant, and T the absolute temperature. These authors give the following relationships between the free energy and the temperature:

$$\Delta F = -33 - 1.33T \ln T + 0.63T$$

hence at 30°C.,

$$\frac{K_A}{K_C} = 1.59.$$

[1] For an extensive and thorough review of the physical and chemical properties of the various forms of solid calcicm carbonate, *see* Graf and Larson (1955).

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Experiments by Wattenberg (1936) and Hindman (1943) in which calcite was dissolved in sea water give an apparent solubility product for calcium carbonate at 30°C. and a chlorinity of 19 ‰ of 0.5×10^{-6} mol^2 $liter^{-1}$. Smith (1941) found 1×10^{-6} for the solubility product of aragonite in both field and laboratory experiments. A higher value was obtained by Revelle and Fleming (1933) in experiments in which aragonite was precipitated from sea water. Recent measurements by Miyake and Saruhashi (personal communication) confirm Smith's value. The experimental results give a greater difference between calcite and aragonite than that computed from thermodynamic considerations.

EFFECT OF TEMPERATURE AND CHLORINITY

Wattenberg and his coworkers studied the variation of the apparent solubility product of calcium carbonate with temperature and chlorinity (Wattenberg and Timmermann, 1936). Their results are shown in Figure 3. The solubility increases with increasing chlorinity and, unlike most substances, with decreasing temperature. The effect of temperature is intensified by the fact that the carbonate content also varies directly with temperature. The combined relationships are illustrated in Figure 4. Figure 5 shows the temperature relation in terms of total carbon dioxide and hydrogen ion concentration. The total carbon dioxide at equilibrium with the atmosphere increases with decreasing temperature because of the increased solubility of the gas.

From Figures 4 and 5 it is evident that the apparent solubility product of calcite is always much less than the ion product of calcium and carbonate ions when normal sea water near the surface is even approximately at equilibrium with the atmospheric partial pressure of 3×10^{-4} atmospheres. The surface waters are also supersaturated with aragonite except at temperatures below 5° C.

From Figure 5 we may estimate the change in total carbon dioxide required to lower the ion product to the saturation point at any particular temperature in shallow water. When the sea water is not in contact with the atmosphere, this change can be brought about only by biological activity. At a temperature of 20°, for example, an increase of about 10 ml/L is required to give Smith's apparent solubility product for aragonite. This is nearly twice as great as the change in carbon-dioxide content that can normally be brought about by oxidation of organic matter in waters isolated from the surface. Except under anaerobic conditions, such oxidation is limited by the availability of dissolved oxygen, which at saturation at 20° is present only to the extent of about 6 ml/L. Evidently existing physico-chemical data on the solubility of calcium carbonate in sea water are of limited usefulness in evaluating the processes of solution and deposition of calcium carbonate in the sea. Equilibrium in the laboratory is obtained only after some weeks, and in the ocean a considerable degree of supersaturation may perhaps persist indefinitely.

EFFECT OF PRESSURE

Increasing hydrostatic pressure markedly increases the dissociation of carbon dioxide in sea water. At the same time the compression of the water raises the alkalinity and the total carbon dioxide per unit volume. These two processes have op-

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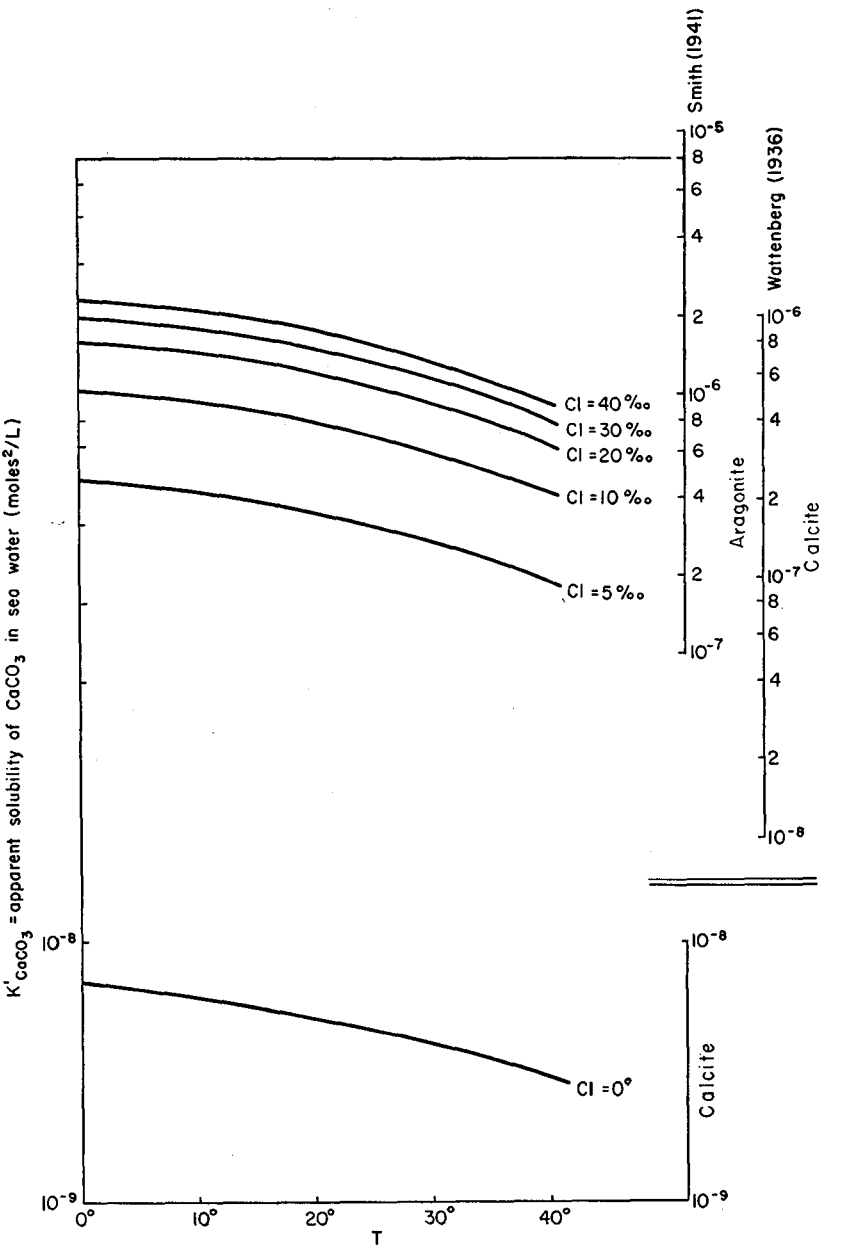

FIGURE 3.—*Variation in solubility products of aragonite and calcite with temperature and chlorinity*

posite effects, with the result that the carbonate concentration tends to remain constant or to decrease somewhat with increasing pressure (Table 4).

Wattenberg (1933) and Revelle (1934) thought that the effect of pressure on the apparent solubility product of calcium carbonate is small. Gibson (1938) questioned

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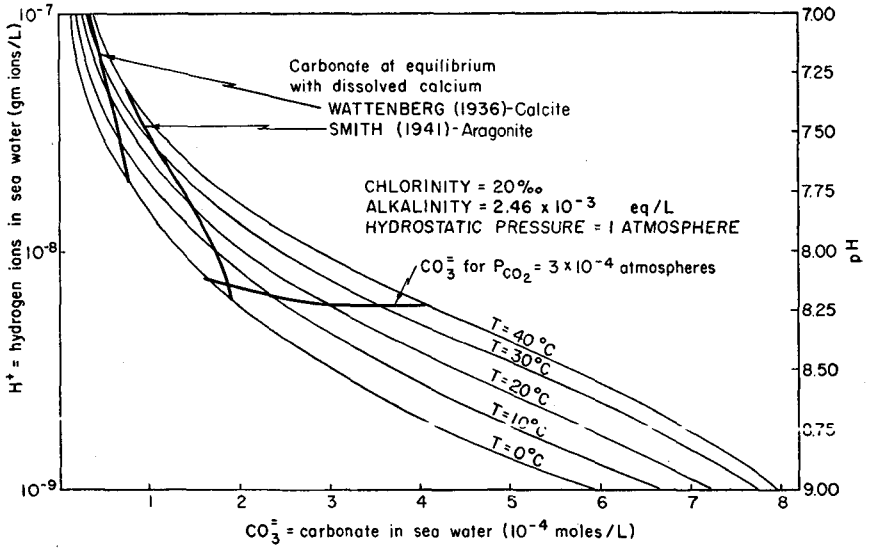

FIGURE 4.—*Carbonate concentration in near-surface open ocean water as a function of hydrogen-ion concentration and temperature*

Also shown are carbonate concentration at equilibrium with present-day atmospheric CO_2 and the concentrations required for saturation with calcite and aragonite.

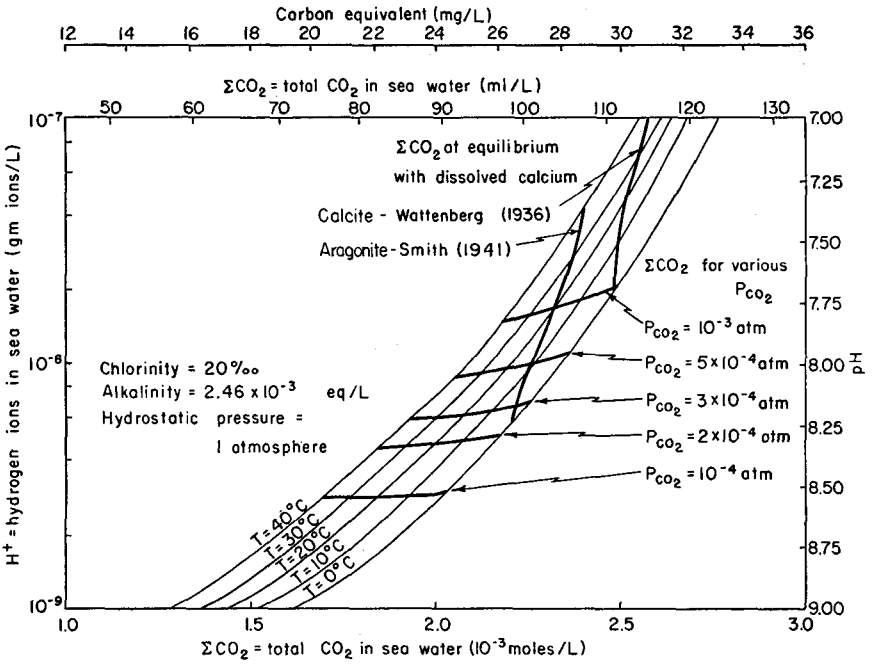

FIGURE 5.—*Total carbon-dioxide concentration in near-surface open ocean water as a function of hydrogen-ion concentration and temperature*

Also shown are the total CO_2 concentrations at equilibrium with different atmospheric partial pressures and amounts required for saturation with calcite and aragonite. Note that, at present atmospheric partial pressure, the water is always supersaturated with calcite, and supersaturated with aragonite at a temperature above 5°C.

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TABLE 4.—*Effects of pressure on carbonate concentration*
From Buch and Gripenberg (1932)

Depth in meters	pH	Alkalinity millimoles/l.	CO_2, millimoles/l	$CO_3^=$ milliequiv./l.
0	8.00	2.40	2.23	0.20
5,000	7.89	2.45	2.27	0.20
10,000	7.78	2.50	2.31	0.20
0	7.60	2.40	2.38	0.09
5,000	7.44	2.45	2.42	0.08
10,000	7.27	2.50	2.48	0.07

this view on the basis of thermodynamic considerations. Owen and Brinkley (1941), using the meager available data on partial molal volumes, compressibilities, and internal pressures in salt solutions, derived a numerical equation for the effect of pressure at 25°C. Based on this equation, values for the ratio of the solubility at a given pressure to the solubility at atmospheric pressure have been computed (Table 5).

Because of the uncertainties of the pressure data and the lack of information on the change of partial molal volumes and compressibilities with temperature, these computations are only of illustrative value. Comparison of Table 5 with Figure 4 shows that, at some depth between 4000 and 5000 meters, normal ocean waters at the presently prevailing temperature are probably undersaturated with calcite.

Wattenberg (1933; 1937) found an increase in the alkalinity-chlorinity ratio at great depths in the Atlantic. A similar but larger increase was found by Revelle (1944) in the deep water of the Pacific. These observations suggest that solution of calcium carbonate takes place at depth in the sea; this conclusion is confirmed by the distribution of calcium carbonate in pelagic deep-sea deposits. (See later under Deep Sea Carbonate Solution.) The solution is undoubtedly partly due to the low temperature and high carbon-dioxide content of the deep water, but the effect of pressure is probably of real importance. Experimental investigations of the effect are greatly needed.

TABLE 5.—*Estimated effect of pressure on solubility products of aragonite and calcite at 25°C from relationships computed by Owen and Brinkley (1941)*

Depth in meters	Ratio of solubility product to solubility product at atmospheric pressure	
	Calcite	Aragonite
0	1.0	1.0
2,000	1.5	1.5
4,000	2.0	1.9
6,000	3.2	3.0
8,000	4.7	4.3
10,000	6.5	5.8

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EFFECT OF OTHER SUBSTANCES ON DEGREE OF SUPERSATURATION AND CRYSTAL FORM

The high degree of supersaturation of calcium carbonate that apparently exists in the sea, the slowness with which saturation equilibrium is obtained in the laboratory, and the fact that aragonite is formed when calcium carbonate is precipitated inorganically from unseeded sea water in laboratory experiments (apparently also under natural conditions in the Bahamas) have not been satisfactorily explained. Some authors have suggested that other substances present in solution may be involved in these phenomena. For example, Reitemeier and Buehrer (1940) demonstrated that minute amounts of sodium hexametaphosphate may prevent the precipitation of calcium carbonate from alkaline solution. In a second paper (Buehrer and Reitemeier, 1940) these authors conclude that the process is an absorption phenomenon in which phosphate enters the lattice and prevents normal growth of the crystals. Johnston, Merwin, and Williamson (1916) believed that the presence of sulfate ion in sea water is responsible for the precipitation of aragonite. On the other hand, Monaghan and Lytle (1956) found that the presence of magnesium ion resulted in precipitation of aragonite from a solution of calcium chloride and sodium carbonate, while the presence of sulfate induced the precipitation of calcite. Their results appear inapplicable to marine carbonate in which magnesium carbonate is always associated with calcite and not with aragonite.

Zeller and Wray (1956) observed that, when $CaCO_3$ is precipitated from $Ca(NO_3)_2$ by addition of Na_2CO_3, aragonite is favored not only by a high pH and temperature and the presence of low Mg^{++}, but also by high Sr^{++}, Ba^{++}, and Pb^{++}. In contrast, calcite is found at lower pH and temperature, in the presence of high concentrations of Mg^{++} and low Sr^{++}, Ba^{++}, and Pb^{++}.

SOLUBILITY OF MAGNESIUM AND STRONTIUM CARBONATES IN SEA WATER

Unlike calcium, the magnesium and strontium carbonates are far below saturation in sea water throughout the entire range of observed pH values and temperature. This may be seen by a comparison of Table 6 and Figure 4.

TABLE 6.—*Solubility and ion products of calcium, magnesium, and strontium carbonates in sea water*
Data from Wattenberg and Timmermann (1938)

Salt	Apparent solubility product Cl = 19‰ T = 20°C	Ion product Cl = 19‰ T = 20°C pH = 8.2
$CaCO_3$ (calcite)	0.5×10^{-6}	2.7×10^{-6}
$MgCO_3\ 3(H_2O)$	310×10^{-6}	14×10^{-6}
$SrCO_3$	0.5×10^{-6}	0.039×10^{-6}

PHYSICO-CHEMICAL CONDITIONS FAVORING PRECIPITATION OR SOLUTION OF CALCIUM CARBONATE

Precipitation of calcium carbonate is thus most likely to occur when: (1) the solubility is low—that is, the water is shallow and the temperature is high or the ionic

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strength low; (2) the concentrations of calcium or carbonate or both are high. A dynamic equilibrium, in which continuing deposition takes place, can exist only when processes tending toward precipitation are continually occurring in a given environment through which sea water is passing.

The most important processes probably are: (1) increase of temperature, which lowers the solubility product of calcium carbonate and also the solubility of carbon dioxide, thus increasing the carbonate ion concentration; (2) evaporation, which increases the calcium concentration and the carbonate alkalinity; (3) movement of supersaturated water into a region where nuclei or catalyzers of precipitation are present; (4) photosynthesis, which lowers the carbon-dioxide content and hence increases the carbonate concentration; (5) bacterial production of ammonia or other weak bases, tending to raise the pH and hence to increase the carbonate concentration; (6) various, largely unknown, processes taking place in the body fluids or tissues of organisms, tending to increase the calcium or carbonate concentrations, to reduce the ionic strength, to produce nuclei, or otherwise to catalyze carbonate precipitation. As we shall see, organic processes are by far the most important cause of marine $CaCO_3$ precipitation.

Two other possible processes should be listed: (7) Upwelling of deep water, in which the alkalinity has been increased by solution of calcium carbonate under pressure, might result in precipitation, because of the reduction in solubility as the pressure is reduced. A sufficient change in pressure is unlikely, however, except in high latitudes where surface temperatures are low and the solubility is high; moreover, the warming of the water and the intense photosynthesis characteristic of upwelling regions would probably mask any pressure effect. (8) Mixing of high-carbonate low-calcium waters with sea water might result in precipitation.

Conversely, cooling or dilution with waters low in calcium and carbonate; CO_2 production by respiration of animals, plants, or bacteria; production of organic acids; or the settling of calcareous particles into deep water all tend to bring about the solution of calcium carbonate.

INORGANIC CARBONATE PRECIPITATION

INORGANIC PRECIPITATION OF ARAGONITE

Euhedral crystals of aragonite and calcite, as evidence of primary, inorganic precipitation, are restricted to relatively small areas in the marine realm. The aragonite deposits are most common today, but since aragonite is metastable similar environments in the past may be marked by recrystallized calcite.

Primary aragonite, if it occurs in Recent sediments, is limited to shallow waters in restricted bays, banks, and lagoons of tropical and subtropical regions, where constant supplies of lime-saturated sea water are abnormally warmed by the sun; a classic example is in the Bahamas. An intertidal environment also showing aragonite is marked by lime induration of beach rock and limestone (often elevated coral) on tropical and subtropical coasts.

The Great Bahama Bank covers about 40,000 square miles west and south of Andros Island in the Bahamas. Over most of its area it is less than 5 meters deep. The inner part of this shallow submarine flat is covered by a fine-grained carbonate mud, known as "drewite", consisting of minute

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particles and needles of aragonite a few microns in length, and small oölites of aragonite. Some shell fragments and Foraminifera tests are present. On the outer bank the sediment consists of a calcareous sand in which the individual grains are rounded and partly recrystallized aggregates of aragonite (Newell *et al.*, 1951; Illing, 1954; Cloud, 1955). The content of $MgCO_3$ in these sediments is probably less than 3 per cent (estimate based on analyses by Smith, 1940). The oölite grains contain about 2.4 per cent $SrCO_3$, and the fine muds nearly as much (H. Lowenstam and E. D. Goldberg, personal communications); thus the ratio of strontium to calcium is about twice that of sea water.

The origin of oölites has concerned geologists for many years; the highly artificial laboratory production by Linck (1903) of these concentrically banded aragonitic spherules has been repeated recently by Monaghan and Lytle (1956). Precipitation from sea water was obtained inorganically (by evaporation); it was also obtained by employing sulfate-reducing bacteria, although favorable conditions for this are restricted.

The question of the fine-grained "drewite" type mud is the greater problem. According to Drew (1911) and others, its formation is controlled by bacteria; according to Black (1933a; 1933b) and others, algae play an important role; however, Vaughan (1917), Thorp (1936), and Smith (1940) and Illing (1954) believed that these widespread deposits are formed inorganically. According to Smith, warm water, supersaturated with calcium carbonate, flows continuously onto the bank from the open Atlantic. Considerable evaporation occurs, raising the chlorinity from about 20 ‰ to as much as 24 ‰, lowering the solubility of CO_2 and increasing the calcium and carbonate contents. The winds agitate the water and stir up the bottom mud, throwing the small aragonite particles into suspension. Some of these serve as nuclei for precipitation of $CaCO_3$. Smith's measurements of the change in carbonate alkalinity of the sea water flowing over the bank indicate that as much as 0.059 grams of $CaCO_3$ are deposited from each liter.

Minute aragonite needles similar to those in the Bahamas have been reported in Recent shallow-water deposits near the Tortugas (Vaughan, 1924); Maiao in the Society Islands (Williams, 1933); outside the barrier reef off the Florida Keys (Ginsburg, 1953a; 1956); in lagoons at Bermuda, and inside the fringing reef at Ochos Rios, Jamaica (Lowenstam, 1955); in the Red Sea (Rusdi Said, 1951); and in the Abrolhos lagoons off Western Australia (Fairbridge, 1948; Spotts, 1952). Experimental evidence for the hypothesis of inorganic precipitation was obtained by Gee, Moberg, Greenberg, and Revelle (1932) and by Revelle and Fleming (1933). These investigators precipitated aragonite needles and spherulites by passing carbon dioxide-free air through filtered sea water. The needles were similar in dimensions and appearance to those from the Bahamas, though perhaps on the average somewhat smaller.

On the other hand, Lowenstam (1955) found that several common species of green, brown, and red algae contain aggregates of easily separated aragonite needles. During photosynthesis, the algae may well precipitate $CaCO_3$ by a mechanism essentially identical to that employed experimentally—namely, by increasing the carbonate concentration through removal of carbon dioxide from the sea water.

Like the experimental precipitates, the algae needles closely resemble in both size and shape those found on the Bahamas banks. According to Lowenstam, the distribution and abundance of needle-secreting algae in the regions where aragonite needles have been reported in the sediments strongly suggest that the needles are of organic origin.

Aragonite needles experimentally precipitated by E. D. Goldberg (Personal communication) and algal aragonite analyzed by Lowenstam (Personal communication) both have strontium contents about twice that of sea water, the same as the Bahama oölites and fine-grained aragonite muds. Measurements by Craig (1954 and personal communication) of the $\delta\ C^{13}/C^{12}$ values (for definition *see* Table 8) of aragonitic algae range from +3.1 to +4.3; oölites from Laguna Madre, Texas, and the Bahamas range from +3.0 to +5.0; and fine muds from Andros Island in the Bahamas from +2.5 to +3.7. It would be of great interest to measure the ratios of carbon isotopes in aragonite needles precipitated experimentally from sea water under different conditions, but it is clear that a definitive means of identifying algal aragonite will be difficult to find.

Numerous workers in coral-reef lagoons (Agassiz, 1894; 1895; Voeltzkow, 1901; Fairbridge, 1948) have noted the "milky" stream of water leaving the lagoon entrances on the ebb tides. It seems

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reasonable to correlate this "milky" water with the aragonitic mud identified on the floors of such lagoons. The change of the lagoon water was observed by Fairbridge one morning in the Houtman's Abrolhos Islands; under perfectly calm conditions (there was no "seeding" by waves stirring up bottom material) the lagoon water, which had been so clear one could see the bottom in more than 10 fathoms, suddenly began to turn milky and within 5 minutes was almost opaque. With the build-up of a breeze and the ebb tide the lagoon was somewhat clearer again by mid-afternoon. The presumed precipitation may have been caused by algal (photosynthetic) reduction in CO_2 pressure or by warming of the surface waters by the sun. The presence of aragonite needles in the mud was determined microscopically and confirmed by X-ray analysis (Spotts, 1952).

A special environment of the warmer seas is the intertidal zone. Here calcareous beach sands tend to become cemented together with great rapidity, generally a few feet beneath the loose surface on the beach. The resultant *beach rock* is a perfect pseudomorph of the original form and location of the beach, and its discovery in ancient rocks is a remarkably useful indicator of a former coast line. Its petrologic characteristics are most distinctive, with poorly sorted, mixed sand grains and cobbles of all sorts, very tightly held together by an aragonite cement that fairly rapidly inverts to calcite (Spotts, 1952; Ginsburg, 1953a; 1953b; Merrin, 1955; Nesteroff, 1955; 1956; Ranson, 1955). The rapidity of the operation is such that mid-twentieth century "artifacts" may be found in it (Fairbridge and Teichert, 1947; Emery *et al.*, 1954, p. 44; Emery and Cox, 1956); along the southern coasts of India there is an annual exploitation of newly formed beach rock for building stone.

The nature of the cementing process has been widely discussed from the time of Darwin, Dana, and Agassiz to the present (Ginsburg, 1953b). Undoubtedly heating and evaporation by the sun's rays must play a major role in this zone of alternate wetting and drying. Special explanations, calling for landward swamps and acid ground water (*e.g.* Field, 1919), fall down on the obvious count that beach rock is almost universal in the warmer regions, even on tiny atoll sand cays and on arid coasts where there is no rainfall; under the microscope the grains show no evidence of solution. Beach rock occurs even in favored but isolated locations in some temperate regions; it is reported as far north as England and as far south as New Zealand.

A process apparently similar to that of beach-rock formation is the intertidal induration of porous limestones in warm latitudes (for example, in the Mediterranean, Crossland, 1907a; in the Red Sea, Crossland, 1907b; in Tahiti, Crossland, 1928, p. 612). Such rocks, perhaps loose and friable away from the shore, may become so indurated that they may ring to a hammer blow (Fairbridge, 1950b). The cementing medium, as with beach rock, is aragonite (Spotts, 1952), and the process seems again to be one of a supersaturated sea water (soaking through every pore space), exposed to heating and evaporation by the sun's rays.

Also related to beach rock and intertidal induration is the formation of superficial pelagosite crusts by the action of spray and evaporation. Pelagosite is generally white, gray, to brownish with a pearly luster, showing in addition to $CaCO_3$ higher $MgCO_3$, $SrCO_3$, $CaSO_4 \cdot 2H_2O$, and SiO_2 than is normal for the substrate. This led to its early description as a distinct mineral "pelagosite" by Tschermak (1878) from specimens collected by Moser on the Adriatic island of Pelagosa. First noted by Darwin on St. Helena, it has been observed on all warm coast lines (Bellini, 1909; Gönner, 1917; Pia, 1933; Fairbridge, 1957).

Processes that may lead to intertidal induration were observed by Fairbridge with the assistance of M. A. Carrigy and J. H. Spotts in May 1951 on the Western Australian coast. In a series of 24-hour surveys of splash pools just above tide limit, it was found that an isolated pool filled by splash at high tide (but not subsequently diluted) warmed with the heat of the sun from 18°C. (open sea) to 24°C. by 3:30 p.m., achieving a rise in pH from 8.2 to 9.4; the pH dropped to 9 at 7:30 p.m. and remained there throughout the night, in spite of a temperature drop to 13°C. Chlorinities rose with the pH and temperature in the pools and dropped again as the pools were refilled by splash (insufficient water remained in the selected isolated pool for an actual determination). The pH of 9 maintained throughout the night is ample to provide a large precipitation of carbonates.

An even higher pH was observed in the same sort of splash pools under semitropical rainfall. Under conditions of almost continuous heavy rainfall Fairbridge traced a pH rise, over 3 days, to a maximum of 10.4.

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The problem of the erosional history of these intertidal splash pools is only partially solved, in spite of considerable study.

INORGANIC PRECIPITATION OF CALCITE

The existence of euhedral rhombs of calcite in an otherwise terrigenous deposit in Bass Strait (southeast Australia) was remarked by Chapman (1941, p. 149). In this case mixing of two water masses may be involved. Cold water upwelling from the Southern Ocean, rich in carbon-dioxide and plant nutrients, meets in Bass Strait the warm Eastern Australian current, saturated or supersaturated with calcium carbonate, moving down from the equatorial belt. Vigorous photosynthetic action in the mixing zone may remove carbon dioxide from the system. Under these relatively cold conditions, calcite, not aragonite, could be precipitated.

ORGANIC CARBONATE PRECIPITATION

In general, except for oölites and possibly other marine lime muds, such as "drewite", from specialized localities like Florida Bay and the Bahama Banks, fine-grained materials of most modern calcareous sediments have not been formed inorganically. The larger grains in calcareous deposits are usually recognizable skeletal fragments, and the fine materials appear to be products of the disintegration of these grains. If the finer particles had a different origin, one might expect that the ratio of $CaCO_3$ and $MgCO_3$ and of calcite to aragonite would vary markedly with particle size. This was not true in eight samples from Alaska, Maine, Florida, Bermuda, and Palau studied by Chave (1954b), except where differential fragmentation of the larger grains accounted for the variation. If inorganically deposited calcite were a dominant constituent of any modern marine sediment, the $MgCO_3$ content of the fine fractions should be less than 2 per cent, much lower than usually found (Chave, 1954b). Appreciable amounts of magnesium are never added to calcite in direct chemical precipitation (Kulp, Kent, and Kerr, 1951); the solid solution of magnesium carbonate results only when calcite is formed by plants or animals (Chave, 1952).

Thus, by far the greater part of the calcium carbonate being deposited at the present time must be laid down through the agency of organisms. Organic precipitation should be facilitated by favorable physico-chemical conditions in the environment, but the importance of these factors will be blunted in those animals and plants that have developed means of working against external thermodynamic gradients.

BACTERIA

From 1910 to 1935 a considerable controversy existed concerning the role of bacteria in precipitating calcium carbonate. Nadson (1903; 1928), Kalantarian and Petrossian (1932), and Williams and McCoy (1934) conducted experiments in which calcium carbonate was precipitated by bacteria isolated from the sediments of Russian and American lakes. Some of these bacteria produced ammonia from proteinaceous materials, while some reduced nitrate to free nitrogen or ammonia. Other things equal, both processes tend to increase the alkalinity and the pH of the water, and consequently the carbonate content. Other species studied by these authors apparently oxidized organic calcium salts, thereby increasing the calcium ion concentration.

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Nadson (1928) believed that bacterial reduction of sulfate also contributes to the precipitation of carbonates. Destruction of the strongly acid sulfate radicle and its replacement by sulfide ion tend to make conditions more alkaline. However, as pointed out by Rittenberg (1941) sulfate reduction is always accompanied by the oxidation of organic matter. If this oxidation proceeds to completion, so that CO_2 is produced in amounts corresponding to the production of sulfide, the medium may actually become more acid. Under other conditions the organic acids produced by partial oxidation may or may not offset the increase of alkalinity resulting from the substitution of sulfide for sulfate.

Emery and Rittenberg (1952) reported a pH of 9.5 in sulfide containing sediments several feet below the surface in cores off lower California. Drew (1911; 1913), Kellerman and Smith (1914), Kellerman (1915), Molisch (1925), and Smith (1926) isolated denitrifying and ammonifying bacteria from the bottom sediments of the Bahama Banks and conducted experiments with these organisms in which calcium carbonate was precipitated in media containing nitrates and calcium sulfate. Drew (1912) believed that a specific organism was involved, which he named *Bacterium calcis*. The name *Pseudomonas calcis* was used by Kellerman and Smith; an ammonifying species was called *Pseudomonas calciprecipitans*.

Lipman (1924; 1929) vigorously disputed the ability of marine bacteria to precipitate $CaCO_3$ in the sea, and Berkeley (1919) found no evidence of denitrification by bacteria in sea water. Bavendamm (1931; 1932) concluded that there are no specific calcium bacteria, although he believed that microbiological calcium precipitation in tropical seas may be an important process, particularly in mangrove swamps where the organic content and bacterial population are high. (*See* also Black, 1933a, 1933b.) Smith (1940) could not detect calcium-carbonate precipitation in the mangrove swamps of Andros Island; such swamps elsewhere are usually areas of calcium-carbonate solution. (*See* below.)

As ZoBell (1946) implied, if significant $CaCO_3$ precipitation by bacteria occurs in the interstitial waters of sediments it must be confined largely to environments in which there is an abundance of organic matter. The number of moles of calcium carbonate precipitated by bacteria should not appreciably exceed the moles of ammonia produced or nitrate or sulfide reduced, except in so far as the bacteria may catalyze the precipitation. In most limestone-forming areas the total amount of organic matter in the sediments is only 1–2 per cent, and nitrogen compounds make up less than one-seventh of this total. The amount of reducible sulfate depends on the content of interstitial water in the sediments. With 80 per cent interstitial water by weight (a high value) the total sulfate amounts to 0.6% of the weight of sediment. An extensive review of the possible roles of bacteria in calcium-carbonate precipitation and solution was given by Baier (1937).

Studies of modern calcareous deposits show that in fact a large amount of the calcium carbonate can be accounted for as the remains of plant or animal skeletons (Thorp, 1939; Emery, Tracey, and Ladd, 1954; Chave, 1954b), except for the aragonite needles and oölites from the Bahama type of environments which may result from inorganic processes. Bacterial precipitation of calcium carbonate in actual marine environments seems to be strictly limited in scope.

The largest area today where there is a possibility of bacterial control of carbonate precipitation is the deep floor of the Black Sea. (See Chapter 25 for detailed discussion.) More than 60 per cent of the deep bottom is covered by white calcitic mud, minutely interstratified with carbonaceous material. According to Shvetsov (1948, p. 87) the calcite is most probably precipitated by the liberation of ammonia from denitrifying bacteria. Earlier workers have attributed the precipitation to sulfate

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reduction rather than to denitrification (ZoBell, 1946). There is a possibility that the mud may be in part mechanically transported to its present position.

ALGAE

Calcium carbonate is laid down by members of five divisions of the algae: the green algae (Chlorophyta), the brown algae (Phaeophyta), the red algae (Rhodophyta), the blue-green algae (Cyanophyta), and the golden brown algae (Chrysophyta).

Marine genera of the green algae that are known to be calcareous (Pia, 1926) belong to two families of the order Siphonales (Iyengar, 1951)—the Dasycladaceae (*Neomeris*, *Cymopolia*, and *Acetabularia*) and Codiaceae (*Udotea*, *Halimeda*, *Rhipocephalus* and *Penicillus*). Odum and Odum (1955) suggested that unidentified filamentous green algae in coral skeletons underneath the living polyps may contribute to the deposition of calcium carbonate in the complex coral community. In the brown algae, marked calcification occurs only in the genus *Padina* of the family Dictyotaceae (Papenfuss, 1951). In the red algae, two orders of the subclass Florideae lay down calcium carbonate, the Nemalionales (*Galaxaura* and *Liagora*) and the Cryptonemiales (coralline algae, including the genera *Corallina*, *Lithothamnium*, *Melobesia*, *Lithophyllum*, *Porolithon*, and *Amphiroa*) (Drew, 1951).

The calcium carbonate-precipitating blue-green algae are mostly known from fresh-water rivers, lakes, and hot springs (Fritsch, 1945, p. 866–869). In the sea, the principal role of the blue-green algae in calcium-carbonate metabolism may be limestone destruction by filamentous boring forms, including members of the genera *Kyrtuthrix*, *Hyella*, *Dalamatella*, *Hormathonema*, and *Solentia*. According to Vinogradov (1953, p. 136) marine lime depositors among the blue-green algae include the genera *Rivularia*, *Calothrix*, and *Oscillatoria*.

Rothpletz (1892), Black (1933a, 1933b) and Nesteroff (1957) believe that some of the oölites and fine-grained ("drewite") lime deposits, such as those of the Bahamas or the Red Sea, may be produced by blue-green (Cyanophyta) algae. However, as observed in the section on "Inorganic precipitation of aragonite" it also seems possible that the oölites may be of inorganic origin, and the drewites, at least in part, may consist of disaggregated calcareous materials of red, brown, and green algae.

In the green and brown algae, and in the order Nemalionales of the red algae, the calcium carbonate is aragonite, while in the Cryptonemiales (coralline algae) and in the lime-depositing blue-green algae (at least in fresh water) only calcite is formed (Meigen, 1903; Prat and Glasnerova, 1937; Lowenstam, 1954).

Lime depositors among the golden-brown algae are all minute flagellated plankton forms belonging to the family Coccolithophoridaceae (Fritsch, 1951) and related groups (such as Discoasteridae). Tan Sin Hok (1928, quoted by Vinogradov) believed that the tiny complex plates called coccoliths, produced by coccolithophores, consist of aragonite. According to X-ray diffraction studies, however, they are calcite (M. N. Bramlette, personal communication).

In the coralline algae considerable amounts of magnesium carbonate, ranging from 7 to 30 per cent, depending on average water temperature, may be present in solid solution with the calcite (Lemoine, 1911; Clarke and Wheeler, 1922; Chave, 1954a; Emery, Tracey, and Ladd, 1954). Haas, Hill, and Karstens (1935) found a seasonal fluctuation in the amount of both calcium and magnesium in *Corallina squamata*. Chave (1954a) showed that the ratio of magnesium to calcium in the calcite laid down by *Lithothamnium* colonies during summer is higher by 2–4 per cent than in the winter-

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deposited calcite. His measurements throw doubt on Mägdefrau's (1933) observation that the magnesium in coralline algae is precipitated only in the older thallus and in dead parts.

On the other hand, Mägdefrau demonstrated that, in the dead algae, the $MgCO_3$ content increased progressively with depth (in the Bay of Naples); it has also been suggested that this increase of magnesium is due to inorganic enrichment around nuclei of existing cells of magnesium-rich calcite, as a function of depth and time (Fairbridge, 1956). According to Clarke and Wheeler (1922) the aragonite-precipitating algae contain less than 1 per cent magnesium carbonate.

The $SrCO_3$ content of the aragonitic green alga *Halimeda* is high, about 1.3 per cent, according to Emery, Tracey, and Ladd (1954), while the calcitic red algae have only about 0.35 per cent $SrCO_3$. (*See* also Thompson and Chow, 1955.) Recent analyses by Heinz Lowenstam (Personal communication), give $SrCO_3$ values up to 2.3 per cent for green algae, about the same as for oölites and the aragonitic muds from the Bahamas.

Lowenstam (1954) pointed out that the aragonite-precipitating green and red algae occur chiefly in tropical and subtropical waters or in warm environments of temperate latitudes, as in the case of *Liagora californica* on the east side of Catalina Island (Dawson, 1944). The aragonite-precipitating brown alga, *Padina*, is primarily tropical but is also present in the temperate zone. On the other hand, the calcite-precipitating coralline algae, although they attain their greatest development in the tropics, form extensive sublittoral banks in temperate and polar seas (Fritsch, 1945, p. 510). Fragments of *Lithothamnium* cast up by the waves form calcareous beach materials in Ireland and France. These are locally used for liming the soil.

Our knowledge of the physiology of algal calcification is meager (Blinks, 1951). The calcium-carbonate precipitation is often assumed to result from utilization of carbon dioxide in photosynthesis, with consequent rise of the carbonate ion to a concentration at which calcium carbonate can be precipitated. Diatoms and other marine algae are evidently able to utilize at least indirectly the bicarbonate ion in sea water. In laboratory experiments where contact with atmospheric carbon dioxide is prevented, these forms can raise the pH of their sea-water medium to above 9.0 (Harvey, 1955). Such a pH would certainly induce the precipitation of calcium carbonate. But many algae with apparently high rates of production of organic matter live immediately adjacent to lime depositors, yet show no calcification.

Craig (1953; 1954) measured the C^{13}/C^{12} ratios in the organic tissues and calcium-carbonate hard parts of three genera of aragonite-producing green algae (*Halimeda*, *Acetabularia* and *Penicillus*) and one calcitic red alga (*Corallina*). In all cases the organic matter was much enriched in C^{12} compared to oceanic bicarbonate. In the aragonite producers, the calcium-carbonate was enriched in C^{13} compared to the average of marine limestones, indicating that the bicarbonate in the sea water is partitioned into heavy and light components during photosynthesis, with the heavier component being precipitated as $CaCO_3$ and the lighter being taken up as organic compounds.

If the sea water were initially just saturated with calcium carbonate, then approximately 2 grams of $CaCO_3$ could be deposited for each gram of carbon dioxide reduced in photosynthesis and incorporated in the plant tissue. The ratio of $CaCO_3$ to organic carbon by weight should be about 8 to 1. *Halimeda* fragments analyzed by Emery, Tracey, and Ladd (1954, p. 62) had a $CaCO_3$/organic carbon ratio of nearly 30 to 1. This discrepancy may be due in part to the absence of $CaCO_3$ solution during respiration. More probably, in the heavily supersaturated tropical waters the aragonite precipitated during photosynthesis may furnish nuclei for further precipitation.

In the one calcitic red alga studied by Craig, both the $CaCO_3$ and the organic carbon were enriched in C^{12} compared to oceanic bicarbonate, suggesting that metabolic processes other than photosynthesis were involved in the precipitation. This is in agreement with the observation that in algal calcite large amounts of $MgCO_3$ are present in solid solution, something that never occurs in inorganically formed calcite.

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Algal $CaCO_3$ deposition normally occurs in or outside the cell walls. Baas-Becking and Galliher (1931) demonstrated the presence of calcite crystals in the cell wall of coralline algae. According to Fritsch (1945), incrustations of $CaCO_3$ first appear in the pectic layer of the wall and then penetrate the cellulose layer. The protoplast remains enveloped by an uncalcified lamella. The cells of coccolithophores possess a comparatively thick gelatinous envelope in which the discrete coccoliths are deposited (Fritsch, 1951). Electron microphotographs show that these are often beautifully complex structures. In at least one alga (*Acetabularia*), calcareous spicules are found in the cavity of gametangia (Blinks, 1951). This is surprising because the pH within the protoplast or vacuole of algae is usually somewhat acid; it ranges between 4.0 and 6.8. In cell extracts of one species (*Desmarestia*) Blinks found pH values as low as 1.0. Sometimes crystals of calcium oxalate are found both in and outside algal cells.

MARINE INVERTEBRATES

As with the plants, little is known about the mechanisms of calcium-carbonate deposition in marine invertebrates. We cannot say with certainty whether the calcium is taken up directly from sea water or from the food of the animals, or whether the carbonate is derived from the water or from metabolic processes. Does the deposition of calcium carbonate occur within or outside the living cells? Is the initial deposit calcium carbonate or some other substance? What is the rate of skeletal growth? Answers to these questions can be given for only a few forms, and consequently it is difficult to estimate the importance of physico-chemical factors of the environment in controlling limestone deposition.

More is known about the mineralogic composition of the hard parts (Lowenstam, 1954) and the contents of magnesium (Chave, 1954a) and strontium (Odum, 1950; 1951a; 1951b; Kulp, Turekian, and Boyd, 1952; Thompson and Chow, 1955). A valuable review of the modes of formation and the functions of calcareous skeletons in marine invertebrates was given by Robertson (1941). The following notes are partly based on his discussion.

Protozoa—The tests of Foraminifera consist of a calcified chitinoid membrane. According to Heron-Allen (1915), the degree of calcification depends upon the amount of calcium in the surrounding medium. This author cultivated calcareous Foraminifera in small aquaria. When distilled water was added to the original sea water to counteract evaporation, the individuals tended to become transparent and "chitinous" instead of calcareous. Addition of hard water resulted in the formation of marked varieties characterized by the development of shells with strae, ridges, and spines. Tests of pelagic Foraminifera from Atlantic bottom sediments analyzed by Craig (1954) have a C^{13}/C^{12} ratio higher than that in oceanic bicarbonate and much higher than the ratio in invertebrate tissue. As with other invertebrates the test carbonate appears isotopically to contain a mixture of carbon derived from sea-water bicarbonate and carbon derived from metabolic activity (Craig, personal communication).

Pelagic foraminiferal tests from deep-sea *Globigerina* ooze (Revelle, 1944) and benthonic forms from tropical reefs (Emery, Tracey, and Ladd, 1954) and from other cold- and warm-water environments (Chave, 1954a) nearly always consist of calcite. Of an estimated 1700 to 2000 species of Recent and fossil Foraminifera tested by Bandy (1954), only 9 contained aragonite. Two of the aragonitic species were Recent and live in cold water 30 to several hundred fathoms deep; 4 were Eocene,

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and 4 were Cretaceous. Evidently aragonite, when it occurs in Foraminifera, can be quite stable. One of the two Recent species containing aragonite was arenaceous (*Bigenerina irregularis* Phleger and Parker); the aragonite was present as the cement of the detrital fragments that made up most of the test.

A wide range of $MgCO_3$ content, from 0.33 to 15.9 per cent, has been found in Foraminifera tests (Clarke and Wheeler, 1922; Revelle, 1944; Chave, 1954a; Emery, Tracey, and Ladd, 1954). According to Chave, there is at least a rough direct correlation between magnesium content and water temperature over the range from 0° to 28° C. The amounts of strontium carbonate are low, less than 0.4 per cent (Thompson and Chow, 1955).

Specimens of *Homotrema rubrum* from Bermuda and of *Discorbis* sp. from Point Barrow deposited carbonate only during periods of highest temperature in their respective environments, according to Lowenstam (1954) and Chave (1954a). Bradshaw (1955) found higher rates of population growth in cultures of Gulf of Mexico Foraminifera when the temperature was near the upper limit of the range observed in the natural environment.

Porifera.—The calcareous sponges are strengthened by a network of calcareous spicules. Each spicule consists of calcite and an axial fiber and surrounding sheath of organic matter. Minchin (1909) stated that the spicules arise intercellularly, but they may become larger than the cells that secrete them, and the secretion of calcareous material then becomes extracellular. Maas (1904) showed that carbonate ions in the surrounding medium are necessary for the formation of the spicules; sponge larvae reared by him in carbonate-free sea water did not produce spicules, whereas the spicules of normally metamorphosed young sponges placed in such a solution regressed even when calcium was present.

Two calcareous sponges were analyzed by Clarke and Wheeler (1922), and three by Chave (1954a). The $MgCO_3$ content ranged from 5.5 to 14.1 per cent; the higher amounts were found in specimens from warm waters. Thompson and Chow (1955) found less than 0.4 per cent $SrCO_3$.

Coelenterata.—With the exception of the genus *Heliopora*, the skeletons of Alcyonaria are built up of spicules of calcite secreted in the interior of certain ectoderm cells that have migrated into the mesoglea layer (Bourne, 1899). *Heliopora*, the hydrocorallines, and the madreporarians all form skeletons of aragonite (Meigen, 1903; Prenant, 1927; Chave, 1954a).

Robertson (1941), in summarizing the work of Koch (1882), Bourne (1899), Duerden (1904), Matthai (1918), and Hayashi (1937), concluded that "the madreporian skeleton is formed by the syncytial ectoderm, which secretes an organic matrix containing calcium carbonate in solution, which crystallizes out soon afterwards." Goreau (1953) is of the opinion that the deposition of $CaCO_3$ in the corallum may be related to the alkaline enzymes, phosphomonoesterases, which he has identified here; he showed their optimum activity to be at the extraordinarily high pH of 10.5 to 11.1. The skeleton of one specimen of *Porites* analyzed by Craig (1953) had a C^{13}/C^{12} ratio slightly below isotopic equilibrium with ocean-water bicarbonate.

The rates of precipitation of calcium carbonate in reef-building corals of warm tropical waters were measured by Vaughan (1915b) and Mayor (1924b). They found an average rate for vigorously growing colonies of about 0.75 grams of new coral per gram of coral per year. Slightly lower growth rates were found in colder waters by Tamura and Hada (1932) and by Ma (1934).

The $MgCO_3$ contents of Madreporaria—the aragonitic reef corals—range from 0.12 to 0.76 per cent, generally increasing with higher environmental temperatures. From 0.5 to more than 1.5 per cent $SrCO_3$ was found by Odum (1951b) and Thompson and Chow (1955) in Madreporaria and *Heliopora*. In the calcitic Alcyonaria, Chave reported that $MgCO_3$ ranges from 6.05 to 14.9 per cent; the higher values are found at temperatures above 25° C., and the lower at temperatures below 5° C. The $SrCO_3$ content is low, 0.5 per cent or less.

Annelida.—The serpulid worms deposit tubes of calcite, aragonite, or a mixture of the two minerals. Robertson and Pantin (1938) found that the tubes of *Pomatoceros triqueter* consist of a mucoid base containing aragonite crystals arranged in successive rings. In their experiments the calcium laid down in the tubes was apparently absorbed from the surrounding sea water. The tubes formed even in artificial sea water with half the normal quantity of calcium, indicating a marked metabolic control of the precipitation process.

Lowenstam (1954) found that in the Serpulidae the proportion of aragonite ranges from 0 to 20

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per cent at 5° C. to 60–100 per cent at temperatures above 22° C. In *Spirorbis*, 100 per cent aragonite was obtained at temperatures above 18° C. and 0–5 per cent at about 5° C.

The $MgCO_3$ content of annelid tubes varies inversely with the proportion of aragonite. In the specimens analyzed by Chave (1954a), $MgCO_3$ ranged from 6.4 to 10.8 per cent in entirely calcitic (low-temperature) forms, and from 9.1 to less than 1 per cent in tubes containing from 30 to 100 per cent aragonite. Thus in general there is an inverse correlation between environmental temperature and $MgCO_3$ content. Whether the proportion of $MgCO_3$ in the calcitic portions of the tube varies directly with the temperature during growth is not known. A greater than twofold variation in the amounts of $SrCO_3$, from 0.45 to 1.1 per cent, was found by Thompson and Chow (1955). By analogy with other forms, the strontium content would be expected to be a function of the proportion of aragonite.

Echinodermata.—In so far as known, the calcium carbonate in the hard parts of members of this phylum is entirely calcite (Chave, 1954a). The mechanism of precipitation has been much studied in larval echinoderms, but little is known concerning the adults. The spicules, plates, and spines of echinoderms are produced by the dermis or inner layer of the skin and thus constitute a true endoskeleton, covered by the epidermis.

The spicular calcite skeletons of larval echinoderms are formed by the mesenchyme cells that arise just after gastrulation. Experiments by Pouchet and Chabry (1889) and by Herbst (1904) show that spicules develop only in a sea-water medium containing the normal amount of calcium as well as carbonate, magnesium, and sulfate ions. Vlès and Gex (1925) and Hirabayashi (1937) found that the pH of the surrounding sea water rises markedly when the spicules are being formed, indicating that metabolic carbon dioxide alone is insufficient to furnish the carbonate radicle; bicarbonate ions must also be absorbed from sea water, in addition to calcium ions. Craig (1953) measured the C^{13}/C^{12} ratio in calcium carbonate from a sea urchin and a sea star. It was found to be significantly lower than in sea water, indicating that metabolic carbon dioxide is utilized in formation of the skeleton.

Cole (1940) studied the composition of the body fluid in the sea star *Asterias*. His results, shown in Table 7, indicate that the calcium concentration and the carbonate alkalinity are close to that of sea water. The observed pH of 7.37 is much lower than in ordinary sea water; consequently the ionic product of calcium and carbonate is considerably below the saturation value, even for calcite.

TABLE 7.—*Ionic products of calcium carbonate and solubility products of aragonite in sea water and some animal sera*

From Potts (1954)

Medium* (1)	μ	Ca^{++} mM./l	pH	Total CO_2, mM./l	$K_2H_2CO_3$, $\times 10^3$	$CO_3^{=}$, mM./l	$Ca^{++} \times CO_3^{=}$ $\times 10^6$	K (aragonite) $\times 10^6$†	Authorities for Ca^{++}, pH and ΣCO_2
Sea water	0.73	10.5	8.10	2.50	0.63	0.181	1.90	2.1	Sverdrup *et al.* (1942)
Mytilus	0.73	12.6	7.70	5.0	0.78	0.183	2.31	1.95	Potts (1954)
Asterias	0.62	11.2	7.37	2.50	0.76	0.0419	0.47	0.72 (Calcite)	Cole (1940)
Limulus	0.60	16.0	7.47	6.2	0.75	0.13	2.08	1.74	Cole (1940)
Homarus	0.58	14.7	7.61	6.2	0.73	0.17	2.50	1.68	Robertson (1949)
Astacus	0.19	12.8	7.75	15.0	0.33	0.263	3.37	0.64	Duval and Portier (1927); Bogucki (1934)
Helix	0.16	4.25	(7.5)	24.2	0.20	0.142	0.603	0.55	Florkin and Duchateau (1950); Duval and Portier (1927)
Anodonta	0.035	5.96	7.52	14.61	0.151	0.0562	0.335	0.093	Potts (1954)

* With the exception of *Mytilus* (10°C.) and sea water (2°C.) all calculations were made for 12°C. μ is the ionic strength of the solution.

† Apparent solubility product, K_A, for aragonite from Smith (1941) corrected for temperature from relation given by Wattenberg and Timmermann (1936).

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In the echinoids, a range of $MgCO_3$ from 4.5 to 15.7 per cent, very roughly increasing with increasing temperature, was found by Chave (1954a). Ranges of 8.6 to 16.2 per cent $MgCO_3$ were obtained in asteroids; from 9.2 to 16.5 per cent in the ophiuroids; and from 7.3 to 12.8 per cent in the crinoids. A close direct correlation between water temperature and $MgCO_3$ content was obtained for asteroids and ophiuroids, and a fair correlation was found in the crinoids. The tests and spines of echinoids commonly show different magnesium values within the same specimens, indicating that the mechanism of precipitation may be different in the two kinds of calcareous structures. Chave also suggested that the chemical conditions for carbonate precipitation in asteroids may vary somewhat with the age of the individual. As might be expected from the calcitic character of the hard parts, uniformly low values of $SrCO_3$, less than 0.35 per cent, were found by Thompson and Chow (1955).

Bryozoa.—Little is known about the mechanism of deposition or the character of calcium-carbonate skeletons in the Bryozoa, except that the calcareous parts consist of calcite, aragonite, or a mixture of the two (Chave, 1954a; Lowenstam, 1954). Preliminary investigations by Chave indicate that in the calcite portion of the test the $MgCO_3$ content is above 4 per cent. The proportion of $SrCO_3$ found by Thompson and Chow ranges from 0.4 to more than 0.5 per cent.

Brachiopoda.—The structure and formation of brachiopod shells has been reviewed by Williams (1956). In terebratuloids a periostracum is secreted first by the columnar epithelial cells of the outer lobe of the mantle, which then secrete a calcareous shell. In the adult, the periostracum is a thin, chitinous structure that forms a discontinuous lattice or honeycomb pattern over the calcareous shell. The shell proper consists of two layers; the primary layer, of uniform thickness, secreted by the columnar epithelial cells of the outer boundary of the outer lobe of the mantle, and the secondary layer, variable in thickness, secreted by the cuboidal cells back from the edge. The primary layer consists of fine fibers of calcite whose axes are coincident with their crystallographic *c* axes and normal to the shell surface. The secondary layer is composed of long thin fibers of calcite disposed at small oblique angles to the primary layer and normal to the mantle edge. Each fiber is secreted by a single cell. The formation of the shell is probably similar in the rhynchonelloids, according to Williams. Meigen (1903) demonstrated by using staining techniques that the shells of *Terebratula* consist of calcite. X-ray studies by Chave (1954a) and Lowenstam (1954) of a number of species of articulate brachiopods from various parts of the ocean, including the subtropical waters off Bermuda, gave calcite throughout. Less than 4 per cent $MgCO_3$ was obtained by Chave. The proportion of $SrCO_3$ found by Thompson and Chow (1955) is extremely low, less than 0.25 per cent.

Mollusca.—The molluscan shell is characteristically composed of three layers. The outermost, the periostracum, is a horny layer of an organic chitinoid substance called conchin or conchiolin. The next layer is the prismatic layer, composed of calcareous prisms in a framework of conchiolin arranged at right angles to the surface of the shell; both layers are deposited by the outer edge (epithelium) of the mantle and may not thicken. The innermost, or nacreous layer, consists of calcareous plates or lamellae alternating with conchiolin, laid down by the entire mantle surface. It is this part of the shell that thickens with the growth of the animal. In the pelecypods the ligament is also produced by the mantle and is morphologically part of the shell (Owen, Trueman, and Yonge, 1953). In some species only aragonite is present, in others only calcite, but most contain a mixture of the two. The proportions of aragonite and calcite vary in a single species, depending on the temperature and other ecologic factors (Lowenstam, 1954; Chave, 1954a). Earlier work on the mechanism of shell secretion was summarized by Robertson (1941). The most recent studies are those of Bevelander and Benzer (1948), Freeman and Wilbur (1948), Bevelander (1952), Wilbur and Jodrey (1952; 1955), Jodrey (1953), and Potts (1954). Previous investigators included Rawitz (1888; 1890), Moynier de Villepois (1892), Brooks (1905), Biederman (1914), Schmidt (1923), Prenant (1927; 1928), Crofts (1929), Bøggild (1930), DeWaele (1932), Kessel (1933), Dotterweich and Elssner (1935), Haas (1935), Greenwald (1938), Manigault (1939), Trueman (1942), and Bourne (1943).

According to Bevelander and Benzer two distinct processes occur in shell formation: (1) elaboration of a fibrous organic matrix, and (2) concentration and deposition of calcium salts. The substance of the organic matrix gives a positive test for protein and contains one or more reducing sugars. The matrix is elaborated by epithelial cells located on the surface of the middle mantle fold. It is first deposited as a thin sheet and later becomes arranged in prisms and striae. During the process of shell formation the folds of the mantle undulate back and forth over the organic matrix. Mucous glands

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are abundant and widely distributed in the mantle epithelium. These glands contain granules which according to Bevelander and Benzer give a positive test for calcium phosphate. A deposit of numerous minute granules becomes imbedded in the surface of the organic matrix. The granules undergo a typical crystal growth and eventually consist entirely of calcium carbonate without appreciable traces of phosphate. An enzyme, alkaline phosphatase, appears to be present on the surface of the cells in contact with the organic matrix and is probably in part responsible for the removal of the phosphate from the growing granules.

There is one exception to the general rule that the calcium carbonate of marine mollusks is deposited by the mantle. In the cephalopod genus *Argonauta* (the paper *Nautilus*), the egg case is deposited by specialized arms. This case is composed of calcite with about 7 per cent magnesium carbonate (Chave, 1954a), in contrast to the calcium carbonate deposited by other cephalopods, which is always low in magnesium carbonate.

The physico-chemical conditions for precipitation of calcium carbonate are apparently satisfied in the body fluids of pelecypods. Potts (1954) has shown that, in both the fresh-water form, *Anodonta cygnea*, and in the marine *Mytilus edulis*, the body fluids are saturated with respect to aragonite (Table 7). The ionic strength and calcium content of *Mytilus* blood are close to that of sea water, but the total carbon-dioxide content is almost twice as great. In *Anondonta*, the ionic strength and calcium content of the blood are respectively $\frac{1}{20}$ and about half that of sea water, while the total carbon-dioxide content is nearly 6 times higher. The relatively high pH's for both organisms (7.70 and 7.52) indicate that nearly all the carbon dioxide is present as carbonate or bicarbonate ions, balanced against metallic cations; in other words, the carbonate alkalinity is much higher than in normal sea water. This significant observation must mean that by some mechanism the mollusks are able to separate calcium or other cations from the chloride and sulphate ions of sea water. This could be accomplished by accumulating calcium from the food, by differential absorption across the cell walls, or by solution of some of the calcium carbonate precipitated in the shell.

Collip (1920; 1921), Kokubo (1929), Kühnelt (1938), and Dugal (1939) demonstrated that solution of a portion of the shell may take place under conditions of anaerobic respiration. It is therefore possible that the high carbonate alkalinity of the blood represents in part the establishment of an equilibrium between the solid calcium carbonate of the shell and the body fluids. On the other hand, Orton (1925; 1928) and Galtsoff (1934) showed that shell growth in oysters can take place in the practical absence of food and without loss of body weight, indicating that the calcium in the shells may be absorbed directly from sea water. Jodrey (1953), using radioactively labeled calcium, demonstrated that dissolved calcium in sea water is taken up directly by the mantle of oysters and rapidly deposited in the shell. Similar experiments with other species were made by Bevelander (1952). Rao and Goldberg (1954) showed that the mucus of the gills in *Mytilus californianus* absorbs dissolved calcium. This calcium is then accumulated in the body tissues, in amounts equal to the total body calcium every 24 hours, and rapidly localized in the outer mantle surface.

Jodrey showed that the oyster mantle can deposit calcium carbonate at a relatively low rate even when isolated from the remainder of the animal, indicating that some of the carbon dioxide for the precipitate is taken up directly from the sea water. Wilbur and Jodrey (1955) found that the rate of deposition is much greater when oxaloacetate and the corresponding enzyme, oxaloacetic decarboxylase, are made available to the mantle, whereas the rate of deposition is reduced in the presence of carbonic anhydrase inhibitors. They conclude that metabolic carbon dioxide is probably a more important source of the shell carbonate than is sea-water carbonate. Craig (1954) found significant variations in C^{13}/C^{12} ratios of the shells of different molluscan species, also possibly indicating the importance of metabolic CO_2 in shell formation. On the average these ratios were fairly close to isotopic equilibrium with oceanic bicarbonate.

The rate of shell deposition in oysters has been studied by Galtsoff and in mussels by Coe and Fox (1942; 1944) and Fox and Coe (1943). Their results can be stated approximately in terms of grams of new shell deposited per year per gram of average weight of the shell. For oysters, the growth rate is 0.75 gram of calcium carbonate per gram per year; for mussels about 1 gram per gram. A similar rate can be computed for the periwinkle *Littorina sitkana*, from data given by Lowenstam (1954). These growth rates are close to the average rates of coral growth given on a previous page.

That the deposition of calcium carbonate in mollusks is largely controlled by the organisms them-

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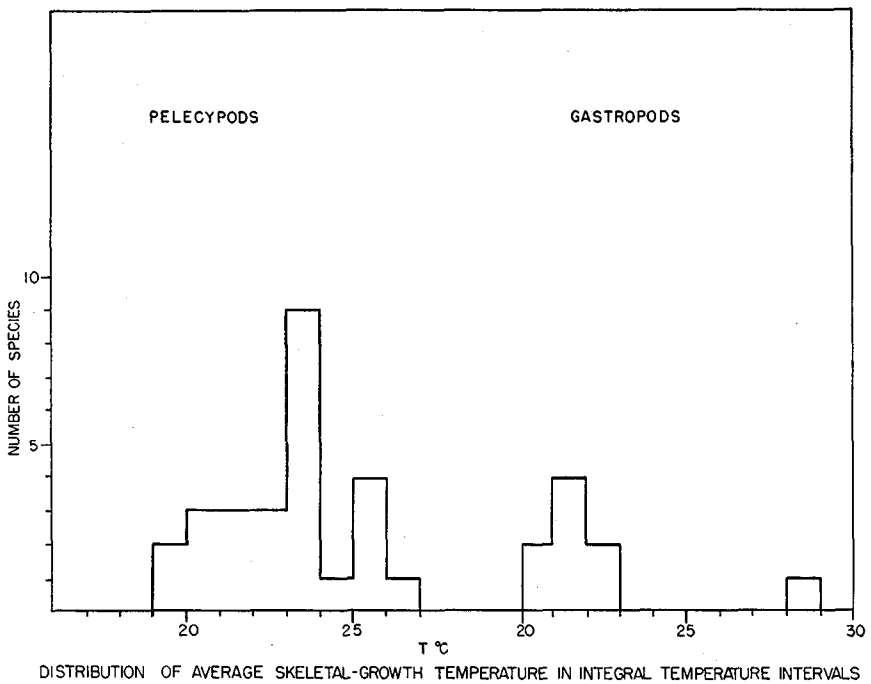

FIGURE 6.—*Numbers of molluscan species in shoal waters of Bermuda having the indicated average temperatures of skeletal growth*

After Epstein and Lowenstam (1953).

selves and not by the physico-chemical conditions of the environment is shown by the wide variation in the minimum temperature of shell growth in different species. According to Galtsoff, oysters in Long Island Sound have about the same rate of shell growth in winter, when temperatures are below 7°C., as in spring and summer when temperatures are above 20°C. Fox and Coe (1943) found that shell deposition in *Mytilus californianus* takes place the year round with temperatures ranging from 14° to 21°C. but increases with rising temperature. Different species living in the same area have different minimum temperatures for shell growth and exhibit different relationships between the rate of growth and temperature (Epstein and Lowenstam, 1953). This is well illustrated in Figure 6. Some mollusks, in adjusting shell growth to temperature changes, exhibit seasonal variations in the ratio of aragonite to calcite in the growing shell. In some species, the size of the shell varies markedly with environmental temperature. For example, the shell of the giant pelecypod, *Tridacna gigas*, may be less than 3 inches in length in temperate areas, but in the warm northern part of the Great Barrier Reef specimens longer than 4 feet are found. Rao (1953) showed that in *Mytilus californianus* the ratio of shell weight to body weight increases almost linearly with increasing latitude and decreasing temperature.

In both gastropod and pelecypod shells the amount of $MgCO_3$ is determined by the amount of calcite. Specimens consisting entirely of aragonite have 0.09 to 0.27 per cent $MgCO_3$ (Chave, 1954a). In pelecypods containing only calcite the content of $MgCO_3$ measured by Chave ranged from 1.30 to 2.80 per cent. Three gastropod shells analyzed by Chave ranged from 30 to 95 per cent calcite with corresponding $MgCO_3$ values from 0.71 to 2.40 per cent. Thus even in high-calcite shells the proportion of magnesium carbonate is much lower than in other calcite-containing organisms. Strontium-calcium ratios in 136 species of mollusks were determined by Thompson and Chow (1955). The lowest values, less than 0.2 per cent $SrCO_3$, are found in the pectens, oysters, and Anomiidae.

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Other pelecypods, shelled gastropods, and scaphopods contain between 0.15 and 0.4 per cent $SrCO_3$, while the shells of amphineurans (chitons) contain 1 per cent or more.

Arthropoda.—Many of the higher Crustacea possess a stiff outer covering of chitin, an epidermis-secreted organic material. This is hardened by deposits of calcium salts, chiefly the carbonate and phosphate (Richards, 1951). Because of the rigidity of the exoskeleton, increase in size is impossible except at the moult. The need for rapid recalcification of the new skeleton formed after moulting determines the mechanism of calcium-carbonate deposition. In fresh-water ostracods (Fassbinder, 1912), a special calcium-carbonate reserve is laid down by the epidermis before moulting. When the new shell is being formed, this reserve undergoes solution. In marine isopods such as *Ligia*, the calcium carbonate from the old skeleton is reabsorbed and held in the skin just before shedding and later redeposited in the new integument (Numanoi, 1934). In the suborder Brachyura of the decapod Crustacea (crabs) large amounts of calcium, (up to 10–12% of the dry weight) may be stored before moulting in the hepatopancreas, as spherules of calcium phosphate. These are redissolved and used in the formation of the new skeleton (Paul and Sharpe, 1916). In a crab of the genus *Carcinus*, analyzed by Robertson (1937), more than 40 per cent of the calcium in the hardening skeleton came from storage in soft tissues; the remainder was absorbed from the surrounding sea water. When the calcium reserve is being dissolved after moulting, before being reprecipitated in the new integument, the blood calcium is raised to 40 times its normal level (Numanoi, 1939).

In the lobster and crayfish, lenses of calcium carbonate known as gastroliths are found in the foregut, one on each side, immediately before the moult. The gastroliths represent material reabsorbed from the skeleton. A few hours after moulting they decrease in size and disappear (Damboviceanu, 1932) and apparently are used as a source of calcium for the new skeleton. Lobsters and crayfish, according to Robertson, also absorb calcium from sea water in considerable amount immediately after moulting. Elmhirst (1930) pointed out that the cast skeleton itself may sometimes be eaten, perhaps as a source of calcium.

Analyses of the blood of *Limulus* (Cole, 1940), *Homarus* (Robertson, 1949), and *Astacus* (Bogucki, 1934; DuVal and Portier, 1927) over a considerable range of ionic strengths gave calcium contents 25 to 50 per cent higher and total carbon dioxide severalfold greater than in normal sea water (Table 7). The pH of the blood of these animals ranged from 7.47 to 7.75, and the ionic product of calcium carbonate exceeded the solubility product. Evidently the carbonate alkalinity was considerably higher than in sea water.

In all the crustaceans analyzed by Chave (1954a), the calcium carbonate consisted of calcite, although the presence of vaterite has been claimed on the basis of X-ray diffraction (Dudich, 1931). All observers agree on the absence of aragonite (Prenant, 1927; Drach, 1939; Richards, 1951). Clarke and Wheeler's (1922) analyses show that in the barnacles, unlike other crustaceans, very little phosphate or organic material is present with the calcium carbonate. Decapod exoskeletons range in $MgCO_3$ content from 5.2 to 11.2 per cent; ostracods from about 2 to 10.2 per cent; and barnacles from 1.35 to 4.6 per cent. There is a good direct correlation between environmental temperature and magnesium content in the barnacles and ostracods, and a possible correlation in the decapods. Surprisingly, in view of their calcitic structure, the strontium content of barnacles and decapods is relatively high, from 0.5 to 0.8 per cent $SrCO_3$ (Thompson and Chow, 1955).

ECOLOGICAL ASPECTS OF ARAGONITE

Table 8 summarizes certain aspects of the mineralogic and chemical composition of carbonate skeletons laid down by marine organisms. This table and the present discussion emphasize the taxonomic base for the mineralogic composition of organic carbonates. In certain groups of algae and invertebrates, the skeleton consists entirely of calcite, in others of aragonite. In three invertebrate phyla—Annelida, Bryozoa, and Mollusca—both aragonite and calcite are deposited by the same individuals. Some species of gastropods and pelecypods contain nearly pure calcite, others nearly pure aragonite, while some have both, in a ratio depending on the species and the environmental conditions.

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TABLE 8.—*Crystal and chemical characteristics of organic carbonates*
Principally from analyses by Lowenstam (1954), Chave (1954), Thompson and Chow (1955), and Craig (1953; 1954).

Class of Organisms	(1) Aragonite Per cent	$MgCO_3$ Per cent		(2) Atoms Sr / Atoms Ca × 10^3		(3) δC^{13} (‰)	
		Min.	Max.	Min.	Max.	Min.	Max.
Marine Algae							
Chlorophyta (green algae)	100	<1.0		14	16(4)	+3.1	+4.3
Phaeophyta (brown algae)	100	n.d.		n.d.		n.d.	
Rhodophyta (red algae)							
Nemalionales	100	<1.0		n.d.		n.d.	
Crytonemiales (corallines)	0	7–30		2.93	3.45	−4.5	
Chrysophyta (golden brown algae)							
Coccolithophores	0	<1.0(5)		n.d.		n.d.	
Marine Invertebrates							
Protozoa							
Foraminifera	0(6)	0.33	15.9	2.78	3.28	+1.2	+1.9
Porifera							
Calcarea	0	5.5	14.1	2.30	3.34	n.d.	
Coelenterata							
Hydrozoa	100	(7)		6.83	11.2(8)	n.d.	
Alcyonaria							
Coenothecalia (Heliopora)	100	n.d.		7.57		n.d.	
All others	0	6.05	14.9	2.64	3.78	n.d.	
Zoantharia (Madreporaria)	100	0.12	0.76	8.85	10.7	−1.4	
Annelida							
Serpulidae	0–100	<1.0	10.8	3.86	8.24	n.d.	
Bryozoa	0–100	0	>4.0	3.00	3.94	n.d.	
Brachiopoda	0	<4.0		1.20	1.57	n.d.	
Echinodermata							
Crinoidea	0	7.3	12.8	2.56		n.d.	
Asteroidea	0	8.6	16.2	2.60	2.89	−5.9	

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Ophiuroidea	0	9.2		16.5	2.63		2.78	n.d.	
Echinoidea	0	4.5		15.7	2.46		2.89	−3.5	
Mollusca									
Amphineura	100		n.d.		7.32		9.35	n.d.	
Pelecypoda									
Pectinidae, Ostreidae, Anomiidae	0	1.30		2.80	1.01		1.33	−3.8	−0.4
All others	15–100	0.09		1.60	1.19		2.91	−0.4	+1.8
Gastropoda	5–100	0.08		2.40	1.25		2.48	−0.3	+0.4
Schaphopoda	100		n.d.			2.35		n.d.	
Cephalopoda	100 (9)	0.05		0.32		3.74		n.d.	
Arthropoda									
Cirripedia	0	1.35		4.6	3.77		5.28	n.d.	
Decapoda	0	5.2		11.2	6.00		6.69	n.d.	
Ostracoda	0	<2.0		10.2		n.d.		n.d.	

(1) Aragonite plus calcite taken as 100%. ‰ calcite = 100 − % aragonite

(2) $\frac{\text{Atoms Sr}}{\text{Atoms Ca}}$ for sea water ≈ Ca 8×10^{-3} (Thompson and Chow, 1955)

(3) δC^{13} (‰) = [(R sample/R standard) − 1] × 1000, where R is the ratio C^{13}/C^{12}. R standard, the ratio in the Chicago PDB Standard carbonate, is tabulated relative to the National Bureau of Standards and other isotopic reference standards by H. Craig (1957). Quantity δC^{13} for 5 samples of sea water bicarbonate from the Atlantic ranged from −1.3 to −2.9.

(4) Strontium values for green algae were kindly furnished us by Dr. Heinz Lowenstam. Published values by Emery, Tracey, and Ladd (1954) are somewhat lower, 9.0×10^{-3} atoms Sr/atom Ca.

(5) From Vinogradov (1953) based on composition of coccolith deposits; should be confirmed because of possibility of recrystallization

(6) A very few species of Foraminifera consist of aragonite

(7) % $MgCO_3$ in Hydrozoa grouped with Madreporaria

(8) Omitting 1 low value out of 10 analyses given by Thompson and Chow

(9) Except for egg case of *Argonauta*, which consists entirely of calcite

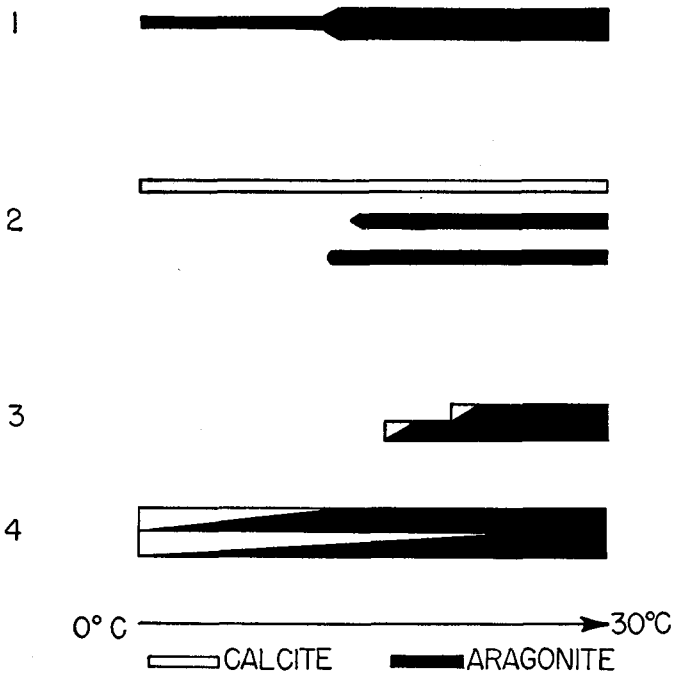

FIGURE 7.—*Four different taxonomic categories of aragonite-calcite temperature relationships* After Lowenstam (1954). For further explanation *see* text.

Ecological factors related to mineralogic composition were discussed by Lowenstam (1954). Aragonite is found principally in warm-water organisms. Lowenstam groups those carbonate-secreting animals and plants that show a temperature effect on mineralogic composition into four categories, depending on the character of the temperature response (Fig. 7). Category 1 includes such organisms as the madreporarian reefbuilding corals, which secrete only aragonite. The number of species is very much greater in tropical waters, with minimum temperatures above 18°–20° C, than in high latitudes. Category 2 is illustrated by the red algae and the alcyonarians. Aragonite-secreting orders such as the Nemalionales among the algae and Coenothecalia (*Heliopora*) in the alcyonarians are confined to warm or tropical waters, while calcite-secreting groups such as the coralline algae and the Alcyonaria, other than *Heliopora*, are very widespread in their distribution. The Chlorophyta (*Halimeda* and others), in which calcium-carbonate (aragonite) secreting genera are confined to warm waters, while noncalcareous forms are widespread, could also be placed in this category.

The third category, illustrated by certain species of the molluscan genera *Brachidontes* and *Littorina*, deposit only aragonite except in the extreme low temperature and of their range where minor amounts of calcite are also laid down. The fourth category includes many gastropods and pelecypods as well as certain bryozoans and serpulid worms. Here in widely distributed species the aragonite-calcite ratio varies directly with temperature over a considerable range. In these species the proportions

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of aragonite may change during the course of growth with seasonal changes in temperature. For example, specimens of *Mytilus californianus* examined by Lowenstam showed more than 50 per cent aragonite in the summer-deposited portion of the shell and slightly more than 30 per cent during the winter growth. Some species in temperate latitudes lay down carbonate primarily during the warm season, and these tend to have a higher aragonite content than those that grow over a wider temperature range. Even within the same genus or species, however, different organisms in the same environment may show a different—probably genetically determined—mineralogic temperature response.

Some indication was found that a mineralogic response to salinity may also exist. *Mytilus* populations from the Baltic, where the salinities are as low as 3–10 ‰, have higher aragonite contents than animals grown in the same temperature but at salinities of 18–34 ‰.

The rate of deposition of shallow-water calcium carbonate is very much greater in warm tropical waters than in colder seas. One of the best-studied sites of shallow-water organic deposition is Bikini Atoll, where Emery, Tracey, and Ladd (1954, p. 58–62) found that the dominant part of the calcium carbonate has been laid down by aragonite-secreting organisms. Thus, as Lowenstam suggests, the total quantity of aragonite being laid down in shallow-water deposits throughout the ocean probably exceeds the amount of calcite. This is in contrast to the other great site of modern $CaCO_3$ deposition, the deep-sea floor, where, because of the preponderance of pelagic Foraminifera tests and coccoliths, the deposits are mostly calcite.

Strontium carbonate is associated with both organic and inorganic aragonite in modern warm-water environments. Because of the rapid rates of deposition in coral reefs, some depletion of sea-water strontium might be expected. It is therefore interesting that Lowenstam (1954), from spectrochemical determinations by Oiva Joensuu, noted a reduction from about 8 atoms Sr per 1000 atoms Ca in sea water of cold latitudes down to 7 in reef waters.

MAGNESIUM CARBONATE IN PLANT AND ANIMAL SKELETONS

$MgCO_3$ as magnesite or as the double carbonate, dolomite, is not known in the hard parts of marine organisms. Moderate amounts of $MgCO_3$ are found, however, in solid solution in the calcium-carbonate crystal structures produced by many marine plants and animals.

A comprehensive review of early analytical determinations of magnesium in marine shells and skeletal parts by Forchhammer (1852), Damour (1852), Högbom (1894), Nichols (1906), and Bütschli (1908) was given by Chave (1954a). A relationship between the mineralogy of shells and the magnesium content was suggested by Clarke and Wheeler (1922) and later elaborated by Bøggild (1930), who believed that the $MgCO_3$ in carbonate shells occurs in (1) low-magnesium aragonite, (2) low-magnesium calcite, (3) high-magnesium calcite. Chave (1954a) showed that three major factors control the amounts of magnesium in the skeletons of calcareous organisms: skeletal mineralogy, water temperatures, and phylogenetic level of organisms.

Additional minor factors are salinity, depth of water, age of individual, and so on, but they do not appear important. Numerous analyses by Chave and others, summarized in Table 8, show that: (1) Aragonite is always low in magnesium and rarely contains more than 1 per cent $MgCO_3$ (assuming 100 per cent to represent total carbonate); a possible explanation is that aragonite crystallizes in the orthorhombic system, but there is no equivalent form of $MgCO_3$. Zeller and Wray (1956), not-

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ing that calcium has an ionic radius of 1.06Å and magnesium only 0.78Å, suggests that the smaller radius of magnesium tends to favor a more compact ionic arrangement, thus fitting into the calcite lattice rather than the more open aragonite lattice. (2) Organically deposited calcite generally contains more than 1 per cent $MgCO_3$ and sometimes as much as 25–30 per cent. Chave studied Bøggild's suggestion that the analyses fall into two distinct groupings, low-magnesium calcite (of the order of 1–2 per cent) and high-magnesium calcite (about 10–15 per cent). He found, in fact, that within any phylogenetic group there is a range of $MgCO_3$ content, varying according to the mean temperature at which the organisms lived. The Foraminifera range from less than 1 per cent $MgCO_3$ at 0°C. up to 16 per cent at 30°C.; in contrast, the barnacles have a smaller range, from more than 1 per cent $MgCO_3$ at 0°C. up to nearly 5 per cent at about 30°C.; the Mollusca have an even smaller variation in $MgCO_3$. Broadly speaking, the steepest Mg/temperature curves are found in the most primitive phylogenetic groups—for example, the calcareous red algae—while the flattest curves correspond to the higher marine invertebrates—*e.g.*, the barnacles and mollusks.

Vinogradov (1953) cites evidence for variations of magnesium content in different parts of the same skeleton; this might result from changes in temperature and growth, as shown by Chave (1954a) for the calcitic algae.

By "dolomitization" is meant a metasomatic replacement of up to half of the calcium by magnesium in carbonate compounds. The physico-chemical factors required for wide-spread dolomitization are not known, but apparently they do not exist at sea level today. These conditions may possibly exist at some depth of burial in certain types of porous atoll. (For a detailed review of the question *see* Fairbridge, 1957.)

Although dolomite has not been positively identified in living organisms, Schlanger (1957) suggests that nuclei of the double carbonate (of the order of only a few unit cells) may exist among some of the highly magnesian calcites such as those laid down by some warm-water algae. Weak traces of dolomite were found by Spotts (1952) in X-ray analyses of modern beach-rock deposits rich in algal detritus, but it is not clear whether these result from extremely rapid (penecontemporaneous) diagenetic dolomitization of the rather unstable calcites of the algae or were in fact primary, as Schlanger suggests.

CARBON-OXYGEN ISOTOPIC RELATIONSHIPS

The relationships between carbon and oxygen isotopes in the precipitation of natural carbonates have been subjected to extensive investigation by Dr. Harmon Craig. From a paper in preparation he has kindly supplied the following summary:

"If isotopic equilibrium is attained in the precipitation of calcium carbonate, then the C^{13} content of the carbonate is a function of the temperature and of the C^{13} content of the dissolved HCO_3^-, while the O^{18} content is a function of temperature and of the O^{18} concentration in the water. Figure 8, based on some 200 isotopic analyses, shows the range of isotopic composition of molluscan shells and limestones in relation to the C^{13}-O^{18} temperature-dependent equilibrium relationship for precipitation from ocean water. The δ values plotted are the per mil enrichments of the ratios C^{13}/C^{12} and O^{18}/O^{16} relative to the Chicago PDB isotopic standard, normalized for the isotopic composition of the precipitation medium by the factors A and B.

"The straight line across the figure, marked C^{13}-O^{18} carbonate equilibrium, shows the isotopic composition that would be attained by carbonates, precipitated under equilibrium conditions from average ocean water, at temperatures from 0–200°C. (The temperature scale across the top of the diagram, when projected vertically down to the diagonal line, shows the temperature relationship.) The isotopic equilibrium relationship was determined by analyzing inorganic precipitates from thermal springs whose temperatures covered the range shown, and normalizing for marine conditions. Thus B is the difference between the C^{13} content of the HCO_3^- of the spring and of average ocean

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water, the latter having the δ value -1.5 ‰; likewise A is the difference between the O^{18} content of the spring water and of average ocean water, the latter having the δ value 0 ‰. In plotting the shells and limestones, B was taken as 0, and A as $+1$ because of the O^{18} enrichment of surface ocean waters, relative to average ocean water, by evaporation (Epstein and Mayeda, 1953).

"If one plots the normalized O^{18} values for the thermal spring carbonates and the marine molluscan shells against absolute temperature, a straight line results. Thus the oxygen paleotemperature scale, previously established for marine shells by Epstein *et al.* (1953) holds over the entire temperature range shown, and the isotopic distribution represents thermodynamic equilibrium, independent of the mechanism of precipitation. However, a similar plot for the carbon isotopes shows that only the thermal spring carbonates give a straight line, and the shells deviate widely, their composition being independent of the temperature of precipitation. Foraminifera in deep-sea cores exhibit more or less constant C^{13} composition over wide ranges of temperature variation. We thus conclude that the carbon in marine shells is not in isotopic equilibrium with the ocean bicarbonate, and that the range of marine shells shown in the diagram deviates from the equilibrium relationship solely because of some factor affecting the carbon isotopic composition of the shells.

"The most likely cause of the carbon deviation is admixture of metabolic CO_2 with the carbon being laid down in the shells. The organic carbon in marine organisms has a δ value of about -14 ‰, and if the metabolic carbon has this composition, then a ratio in the shell of about 70% of carbon precipitated in equilibrium with dissolved bicarbonate, and about 30% of carbon derived from metabolic activity, is indicated.

"Table 8 shows the carbon isotopic composition, obtained by Craig (1953), of calcium carbonate from marine green algae, which precipitate aragonite, and of calcite from one coralline alga. The carbon δ values for the aragonitic algae are intermediate between the values expected for isotopic equilibrium at 20–25° and the values characteristic of marine molluscan shells. Two plausible hypotheses for this isotopic composition are:

"1. The C^{13} content of the algal carbonate is determined purely by the kinetics of precipitation; i.e., the precipitation is so rapid that isotopic equilibrium is not achieved, and, as a result of the kinetic partitioning of carbon, the resultant carbonate has a lower C^{13} content than that corresponding to the equilibrium concentration.

"2. The C^{13} content of the aragonitic algal carbonate reflects partial derivation of the carbon from respiratory CO_2 with a δ C^{13} of about -14 ‰, or partial isotopic exchange with such carbon.

"The very light δ value of the calcitic coralline alga indicates that organically derived carbon was probably incorporated in its skeleton.

"The limestone range outlined in Figure 8 reflects the effect of oxygen isotopic exchange between limestone, originally lying in the modern shell range, and fresh water, over long periods of time. The fresh waters of the temperate regions range in composition from δ O^{18} of about 0 to -20‰ (Epstein and Mayeda, 1953; H. Craig, in press) and higher temperatures during exchange would enhance the effect. Since limestones appear quite generally to have undergone extensive isotopic exchange, no significance can be attached to variations in their C^{13} content, unless it can be shown from O^{18} and petrographic data that no such exchange has occurred in particular instances."

DISINTEGRATION AND RECRYSTALLIZATION OF CALCAREOUS SKELETONS

Disintegration and recrystallization of organically deposited $CaCO_3$ occur after deposition. In the first there is no actual mineral change, but in the second there is normally an inversion of aragonite to calcite, as well as rearrangement within calcite itself. These changes may be carried out in a matter of months or may occur over tens of thousands of years.

In disintegration the original calcareous crystals in shells and skeletons turn into microgranular and crypto-crystalline material without change in the identifiable minerals or in chemical composition. The process is well shown in the subsurface limestones at Bikini. According to Emery, Tracey, and Ladd (1954, p. 88):

"Coral and mollusk fragments have disintegrated to a chalky powder. In thin sections the original

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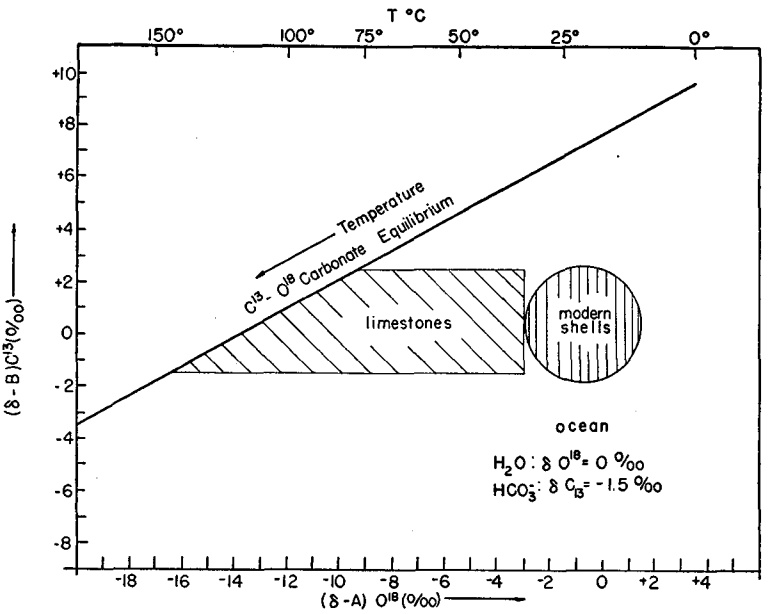

FIGURE 8.—*Variations of the C^{13} and O^{18} content in naturally occurring calcium carbonate* $\delta = [(R_{sample}/R_{std}) - 1] \times 10^3$, where R is the ratio C^{13}/C^{12} or O^{18} O^{16}. Hence δ is the per mille isotopic enrichment relative to the Chicago PDB standard. From a paper by H. Craig (in preparation).

fibrous crystalline structure of aragonitic organisms is seen to be altered to finely granular or microgranular material. *Halimeda* segments in particular are altered from brown microgranular to brown cryptocrystalline material. Unaltered *Halimeda* in thin section shows a mat of minute needles about one micron in size, but altered segments of the alga have scattered needles of high birefringence in a brown isotropic matrix. The calcite tests of small foraminifers are likewise changed from fibrous calcite, oriented normal to the cell walls, to brown isotropic materials.

. . . mollusk shells . . . [may] have an original nacreous luster and traces of color patterns, but in thin section the laminated aragonite layers are seen to be less well crystallized than in Recent shells. The septa and dissepiments of corals are likewise perfectly preserved, but the original fibrous aragonite is broken down to microgranular material . . . .

X-ray analyses indicate that there is no change in the mineral content of the altered corals and shells, and spectrographic studies revealed no apparent change in the amount of strontium contained in the carbonate."

In the process of recrystallization both aragonitic (Jamieson, 1953) and calcitic organisms and grains are altered to new crystals of calcite. Crickmay (1945, p. 239) reported that skeletons of different organisms show different susceptibilities to recrystallization; the order of decreasing susceptibility is corals (aragonitic), mollusks, *Halimeda*, thin-walled (pelagic) Foraminifera, thick-walled (beach) Foraminifera, larger Foraminifera, echinoids, and *Lithothamnion*. At Bikini, Emery, Tracey, and Ladd (1954, p. 88, 89) found that corals recrystallize readily to a mosaic of calcite. In *Halimeda* skeletons the central pores and boundaries are attacked first. Only rarely is the whole segment crystallized to a calcite mosaic. Thick-walled Foraminifera such as *Calcarina* and *Amphistegina* recrystallize from fibrous compact calcite to coarsely

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crystalline calcite which has a more or less radial orientation. Echinoids and *Lithothamnium* are rarely recrystallized.

The strontium/calcium ratio diminishes markedly when recrystallization occurs, for example, from about 1.4 per cent strontium carbonate in unaltered coral to about 0.7 per cent in corals recrystallized to microgranular calcite and less than 0.2 per cent in completely recrystallized coral. More than 50 per cent of the organic aragonite laid down by some of the marine invertebrates studied by Lowenstam (1954, p. 288) inverted to calcite within a year. Ancient aragonites are known in sedimentary rocks, but their occurrence is rare as we go back in time.

SOLUTION OF CALCIUM CARBONATE

In the second half of the last century there was a protracted controversy over the origin of the lagoons in coral atolls. Charles Darwin's theory of subsidence coupled with upgrowth of corals was opposed by Sir John Murray's hypothesis that inorganic solution of calcium carbonate in the interior of the reef caused the lagoons.

Murray's theory has been rejected, in part because modern measurements show that at equilibrium surface sea water under tropical or subtropical conditions is supersaturated with calcium carbonate. Unfortunately the field observations that carbonate solution can be observed on any limestone coast, which were the base of Murray's theory, were also largely forgotten.

EROSION OF LIMESTONE IN THE INTERTIDAL ZONE

Erosion of limestone in the intertidal zone has been reported from the warm and temperate belts in many parts of the world. Macfayden (1930), Kuenen (1933), Fairbridge (1952), and Guilcher (1953) have summarized the work. The morphologic expression of intertidal erosion is a broad reef flat or platform at or slightly below low-tide level, which may run up to nearly a mile in width. It is usually bounded at the inner margin by a low cliff, which may be undercut by a notch or nip of variable size, ranging from a few feet up to 30–50 feet in depth.

This erosional pattern is characteristic of all porous limestone coasts. It is best developed in the Quaternary reefs of tropical waters, but it is also found in the dense Mesozoic and Paleozoic limestones of cooler seas. The erosion is as effective in sheltered bays as on exposed shores.

Coral-reef platforms customarily consist of a core of dead truncated reef rock, the foundations of reefs that once rose above present sea level. By the evidence of residual (not jetsam-type) negro heads as well as small islands of emerged coral, the former levels of such reefs can easily be identified. The principal new growth of coral forms a relatively narrow fringe around the periphery of this older structure. Revelle and Emery (1957) have described some of the erosional features of the reef flat at Bikini:

"Above the low tide line the beach rock and reef rock form a highly irregular surface with numerous small basin-shaped depressions, many of which are separated only by knife-edge ridges. The walls of other basins are overhanging so that their maximum diameters are below their rims. Some very irregular basins are obviously the results of lateral coalescence of two or more smaller ones. Where two basin floors are at different levels, their junction may form a step-like structure and cause complete drainage of the higher basin. The floors of the basins are fairly flat, but the floors and especially the walls exhibit small sharp irregularities suggestive of corrosion rather than abrasion.

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Similar irregularities are present on the surfaces of melting ice, dissolving salt pans, and some meteorites. The basins seldom contain cobbles that might have served as tools to abrade potholes; moreover, some are floored by a thin mat of fragile foraminiferal sand held together by filamentous algae."

Solution basins of this type in the upper parts of reef flats, nips (deep notches or undercuts) and caves at the base of sea cliffs, and nips around negro heads atop reef flats are common and widespread in tropical waters. This erosion, limited principally to the intertidal zone, has been described by Kuenen (1933) as a "horizontal sawing" into the limestone. Calculations (Fairbridge, 1948; 1950; Fairbridge and Teichert, 1953) of the approximate rate of the process, based on measurements in southwest Australia, assuming a continuous attack over a reef front 1 cm wide and 65–100 cm high, give 270 to 670 cm^3 per year.

INORGANIC CARBONATE SOLUTION

Emery (1946) concluded that basins in the sandstone along the shore of La Jolla, California, form chiefly through solution by biochemically modified sea water. The calcium-carbonate cement of the sandstone is dissolved during the night, when the temperature is lowered and the carbon-dioxide content of the water in the pools is raised, not only because of the greater solubility of CO_2 at low temperature but also by animal and plant respiration. In the daytime carbon dioxide is removed both by photosynthesis and by transport from the water to the atmosphere because of the lower solubility of the gas at high temperature. The rise in temperature also lowers the solubility of calcium carbonate. Calcium carbonate is precipitated, in part as small loose crystals that are washed out of the pool at the next high tide. Computations based on Smith's (1941) apparent solubility product for aragonite show up to 425 per cent saturation in the daytime and only 45 per cent saturation at night. Thus, by alternate solution of calcareous cement and flushing of the precipitate, the calcium carbonate is removed. Growth of the pools is aided by sand-ingesting organisms, particularly snails of the genus *Littorina* (North, 1954). At La Jolla the characteristics of intertidal rock surfaces indicate that some chemical and organic erosion also occurs outside of pools.

In the tropics, however, the geological evidence for solution is in conflict with the results of laboratory studies of the solubility of calcium carbonate in sea water. The problem has been well stated by Kuenen (1950):

"Geological observations . . . appear to establish beyond doubt the solvent action of tropical surface waters on reef limestone. . . . Investigation of sea water from the surface in tropical seas has led chemists to the conclusion that it is always saturated or even supersaturated with lime. Hence they have concluded that solution of limestone is not possible. But it is exceedingly difficult to establish whether solution under natural conditions is really excluded."

Solution in the upper part of the intertidal zone of low latitudes has been attributed to rain water or to fresh ground water by some workers (Wentworth, 1938), but this is not likely to be important where rainfall is slight and where ground water cannot reach basins or nips, as on negro heads. The same objections apply to the theory of Hills (1949), who believed ground water produced an indurated layer at or about low tide level and the reef platform was then the result of differential wave erosion. Series of pH, salinity, and temperature measurements were carried out on reef pools by

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Fairbridge, assisted by M. A. Carrigy and J. H. Spotts, on the Western Australian coast. While the pH of the adjacent sea remained about 8.2, pools filled during early darkness hours and then cooled (5° or 6° C.) by the night air showed drops to a minimum of 7.5, followed by daytime heating and evaporation with figures reaching 9.4.

Revelle and Emery (1957) also studied the chemical conditions in intertidal basins. at Bikini and Guam marked diurnal changes were observed in the alkalinity-chlorinity ratio of the waters in the depressions. These strongly indicate that intertidal solution of calcium carbonate does in fact occur, probably at a comparatively rapid rate. But computations based on the measured pH, temperature, salinity, and alkalinity and on the experimentally determined solubility product of aragonite in sea water show an apparent supersaturation in the basin and reef waters at all times ranging from 175 per cent at night to 800 per cent in the daytime. Possible rationalizations of the opposing lines of evidence are: (1) solution may occur in the micro-environment produced by burrowing organisms in the limestone of the basin floors, or in the interstitial waters of the algal mats that cover some of the floors; (2) solution may occur in the films of water left on the basin walls by the receding tide; (3) much of the calcium may be complexed or hydrated, and the time constant for the complexing or the hydration reaction may be much longer than the times required for solution or precipitation. If this is the case, solution can occur when the carbonate concentration and/or temperature is rapidly decreased even though the product of the concentrations of total calcium and carbonate remains above the equilibrium saturation value.

Erosion of calcium carbonate in warm ocean waters, although very widespread, is largely confined to the intertidal zone, where marked diurnal changes in conditions occur. These facts coupled with the slow attainment of calcium-carbonate saturation equilibrium in the laboratory support the hypothesis of slow complexing or slow hydration and dehydration.

Mayor (1924) and Odum and Odum (1955) estimated the average rate of deposition of calcareous materials in coral reefs below the low-tide line at about 1 cm yr-1. This is 30 times the rate of chemical erosion in the intertidal zone estimated by Revelle and Emery. Observations of notch and cliff retreat suggest that the overall rate of intertidal erosion is not very different from that of reef build-up.

ORGANIC MECHANISMS OF CARBONATE SOLUTION

There is a large variety of restricted environments or micro-environments in shallow waters, developed by organisms in the rock or bottom sediment, or within tissues or organs of the organisms themselves, in which a remarkable amount of carbonate solution occurs.

Intertidal algal borers.—In the intertidal belt, wherever there are limestones in the tropics or subtropics, microscopic algae (mainly blue green) bore into the rock in a thin zone 1 to 5 mm below the surface (Duerden, 1902; Nadson, 1927; Gardiner, 1931b; Ginsburg, 1953c; Odum and Odum, 1955). A considerable variety of algae is known to be involved (Duerden, 1902; Nadson, 1927; Weber van Bosse, 1932; Ginsburg, 1953c), including: (1) Chlorophyceae (*Ostreobium, Gomontia, Siphonocladus*); (2) Myxophyceae (*Plectonema, Hyella, Mastigocoleus, Entophysalis*); and (3) Rhodophyceae (not well known).

In thin section the algae form an active zone of intense burrowing about 2–3 mm thick, bright

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green and connected to the outside by fine filaments. Small plates of the superficial rock are flaked off by the activity of these algae. This superficial layer is often denser than and somewhat different in composition from the underlying substrate. The calcareous framework is the same, but the pore spaces are largely occupied by a secondary calcareous cement of "pelagosite" character. Ginsburg (1953b) observed that aragonitic material was more readily attacked than calcite by the algae.

The mechanism by which the algae bore is not known. They may liberate an organic acid that dissolves the limestone. Or, they may be involved in a diurnally reversible reaction. Through respiration at night they liberate CO_2 into the watery micro-environment of their filamentous network, leading to progressive solution; in daylight CO_2 is absorbed during photosynthesis and an alkaline condition is set up, amplified by the heat of the sun and evaporation, leading to precipitation of $CaCO_3$ and the other components of "pelagosite". Thus there may be an alternation of corrosion and precipitation. Evidently corrosion gains progressively, assisted by various mechanical processes: wave action, abrasion; nibbling by fish; scraping and suction by gastropods, chitons, etc.; tearing by crabs.

Micro-environments under algal mats.—In many reef areas mats or blankets of algae cover portions of the rock surface. When a mat is disturbed, the odor of hydrogen sulfide is sometimes observed. This clearly shows that the water under the mats is relatively isolated from the overlying sea water; as a result, the metabolic activity of the algae and the decay of organic matter can cause wide variations in the carbon-dioxide content and other properties of the water. On the CAPRICORN Expedition of the Scripps Institution of Oceanography in January 1953 the authors, together with Henry Rotschi, found pH's of 6.5 and 8.7 in water samples collected at low tide from beneath thick algal mats on the outer reef at Pa'ea in Tahiti. Such extreme ranges of conditions may cause both solution and precipitation in limited areas.

Invertebrate boring organisms.—Limestone rocks, both in the intertidal belt and down to depths of 15 to 20 fathoms are burrowed, bored, or riddled with holes and tubes of marine invertebrates in many places (Gardiner, 1903; Otter, 1943; Bertram, 1937; Ginsburg, 1953c). Specimens of limestone dredged from greater depths (sometimes 50 to 250 fathoms) are similarly affected, but probably not by living organisms (Agassiz, 1888; Bøggild, 1916); they may indicate Pleistocene glacial lowering of sea level, tectonic subsidence, or submarine landslides on steep slopes.

Boring animals make their holes by mechanical or chemical means. Among the mechanical borers are such bivalves as *Petricola*, *Arca*, and *Tridacna*, some polychaete and sipunculid worms, echinoids (*Echinometra* and *Echinostrephus* on coral reefs, *Strongylocentrotus* on temperate coasts), and pedunculate barnacles. (*See* annotated bibliography of marine borers.) On coral reefs certain fishes contribute to the breaking down of the reef substance by nibbling at the coral. Large surfaces of intertidal rocks are constantly "grazed" and scraped by crabs, gastropods, and chitons. Many organisms, while not strictly borers, erode depressions in the rock—for example, limpets (*Patella* and related forms), *Haliotis*, and *Marinauris*.

Chemical borers make their holes by production of CO_2, liberated at the surface of contact, with the consequent solution of $CaCO_3$. They include sponges of the families Clionidae and Spirastrellidae, and a number of pelecypods (especially *Lithophaga* on coral reefs. While in general the borers contribute to the breakdown of limestones and calcarenites (carbonate-cemented sandstones), such borers as *Lithophaga* (*Lithodomus*), which redeposit the carbonate as a hard lining of their burrow, may actually strengthen the structure in which they live (Otter, 1937).

Gardiner (1931b) estimated that not more than 40 per cent of the destruction of emerged coral reefs is carried out by invertebrate borers; he believed that the bulk is caused by algal borers or by inorganic solution.

Acid digestion in the gut of invertebrates.—The Holothuria or "sea cucumbers" inhabit lagoons and reef-flat pools in great numbers. They possess a gut in which a remarkably low pH (*ca.* 4.5) is claimed to have been observed. These animals are scavengers, processing through their gut large quantities of unconsolidated sediments, and it has been said that they play an important role in reducing larger calcareous fragments to the fine-grained silt-sized particles that make up part of the lagoon sediments (Gardiner, 1903, p. 338; Mayor, 1924a; Otter, 1937; Moret, 1940). The digestive operation involves not only mechanical breakdown in the muscular crop but must also include some chemical solution. Finck (1904), Crozier (1918), Bertram (1937), and Nesteroff (1955) studied the amount of sediment

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"processed" in this way; calculations have been made based on the observed quantity of feces passed by selected specimens. There is in fact little change in the grain size or texture of the sediments. The feces often contain complete and unbroken specimens of large disc-shaped Foraminifera (*Peneroplis pertusus*), which suggests that the mechanical role of the crop may have been overstated, and the solvent action requires further study (Bertram, 1937).

Molluscan production of acid to buffer anaerobic glycolysis.—Many marine pelecypods and gastropods survive for long periods (several weeks or even months) out of water. In 1787, Spallanzani determined that snails kept out of water in a hydrogen atmosphere continue to produce CO_2. Collip (1921) found an increase of calcium in the body fluids suggesting solution of $CaCO_3$ from the shell of the organism. Dugal (1939) observed that after a few weeks of isolation under anaerobic conditions the interior of a *Venus mercenaria* shell became visibly eroded. The CO_2 and lactic acid in the body fluid gradually increased, while the pH dropped slowly from about 7.5 to 6.8. After a critical period (about 2 weeks, varying with the temperature), the pH began to drop sharply. Up to this point the pH had remained fairly high, owing to the buffering of the rising acid concentration with $CaCO_3$ from the shell; after the critical point was passed decay set in, and death followed. However, if the animal was replaced in water before the final collapse, normal metabolism was re-established, showing that the early CO_2 and lactic-acid production was not due to decay.

It may be important for the paleontologist to distinguish between the molluscan shell etched on the interior, by internally produced catabolic acids (for example, resulting from exposure above tide level or oxygen-poor conditions in the water), and other shells etched from the exterior (generally *after* death) by a regional acidification of the environment—*e.g.*, in a mangrove swamp or in sediments. However, the interior of the shell may also be etched by the action of decay bacteria following burial and death of the animal in its shell.

Solution in mangrove swamps.—Calcareous materials are dissolved in mangrove swamps, as well as in most other intertidal mud flats of high organic content and rapid decay processes (Abel, 1926). Progressive stages in the etching of calcareous shells are shown by *Pyrazus*, the mangrove snail commonly found on the east coast of Australia; first the larger whorls develop holes, then the smaller ones, until only the columella is left, and this in turn eventually breaks down.

In some fossil mangrove swamps, little of organic origin remains except the chitinous carapaces of crustaceans, mangrove roots, and occasional worm tracks. Rapid corrosion of $CaCO_3$ occurs in mangrove swamps on coral reefs. This was first noted by Wharton (1887) at Aldabra in the Indian Ocean; later descriptions of Aldabra and similar reefs were given by Gardiner (1906) and by Fryer (1911). At Low Isles in the Great Barrier Reef lagoon, Marshall and Orr (1931) observed that in the mangrove swamp at low tide the pH drops to 7.75 and returns to normal at high tide; in a similar swamp on the adjacent mainland coast (Daintree R.), it drops to 6.6 at low tide. Fairbridge and Teichert (1947) concluded that irregularly shaped pools, several feet deeper than the reef flat at Low Isles and elsewhere, are due to solution of the $CaCO_3$ reef platform by swamp acids.

The mechanisms of solution in mangrove swamps are not well understood. The principal agent is probably carbonic acid, produced by decomposition of organic matter. Other acids possibly active in this environment are tannic acid from the mangrove bark and perhaps some of the "humic acids."

Solution in freshly buried sediments.—Bacterial oxidation of organic matter in sediments produces carbon dioxide and thus tends to lower the carbonate concentration and the pH. Under aerobic or moderately anaerobic conditions carbonate shells may be etched or even dissolved. In muds of low calcium-carbonate content, the interstitial water may become acid. Debyser (1952) found that estuarine muds in the west of France had a pH as low as 6.5 within 5 cm of the surface. He later (1955) recorded extremely low pH values (down to 5) in the muds of west African coastal lagoons and noted that here carbonate shells disappear with great rapidity. Shells falling into such low pH muds are likely to be destroyed. Destruction of this kind may have occurred in some geological formations of relatively shallow origin that are disappointingly barren of fossils even though they might be expected to carry an abundant fossil fauna (Richter, 1931).

The concentration of organic matter and the porosity of the sediment play important roles in the amount and rate of calcium-carbonate solution. If the sediment is an impervious mud, low in organic matter, clean shells may be buried and dug up after several months, with no trace of etching (Hecht, 1933). With limited circulation the surface area/weight ratio of the carbonate shell is im-

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portant. Hecht found that thin large shells lost greater amounts of lime than did thick stocky ones.

When a burrowing animal dies in the mud, decay bacteria become concentrated in the resulting micro-environment. Hecht (1933) demonstrated that shells with rotting contents lost 10–24 per cent of their $CaCO_3$ in 1–2 months, in one case 25 per cent in 2 weeks. Relics of such shells are represented merely by casts or molds and a trace of insoluble chitinous material.

Extreme anaerobic conditions may prevail at some depths below the mud surface. If sulfate-reducing bacteria are active at these levels the pH of the interstitial water may be raised to 8.3–8.5 because of the replacement of the strongly acid sulfate radicle by sulfide, a weak Brönsted base. Calcium-carbonate solution will not occur, and any calcareous skeletons falling into the anaerobic layers may be perfectly preserved. If free iron is not available to react with the sulfide, however, dissolved hydrogen sulfide will diffuse upward to the oxygenated levels near the sediment surface, where it will become reoxidized to the acid sulfate. The pH will thus tend to be low in the upper zone, and solution of calcium carbonate can occur.

When the reducing environment is a restricted one, because of the rotting of an organism, for example, sulfide oxidation may occur on the outer surface (Quenstedt, 1928). The resulting sulfate radicle may react with shell or bone carbonate material to precipitate a crust of gypsum (illustrated by Hecht, 1933).

In ancient seas (*e.g.* Paleozoic), the appearance of etched and corroded horizons within limestone sequences indicates periodic action on the bottom by a powerful acid (Weiss, 1954). The presence of pyrite (Fe_2S) along the etched corrosion surfaces suggests that sulfuric acid produced by the oxidation of hydrogen sulfide may have caused the corrosion.

RECENT CARBONATE SEDIMENTATION

The major concentrations of Recent carbonate sediments occur in two quite separate regions, each marked by distinctive mineralogy: (1) in the moderately deep seas far from shore but not the extreme abyssal depths below 4500 meters, and (2) on continental or insular shelves and slopes where there is little detrital sedimentation. The deep-sea deposits are dominantly calcitic, the shallow-water deposits are largely aragonitic. Both are restricted to the warmer latitudes, and the great bulk of them is of organic origin.

DEEP-SEA SEDIMENTATION

The principal realm of calcium-carbonate deposition at present is that of the deep sea in low and middle latitudes. In the warm subsurface waters, particularly where productivity is high, calcium carbonate is precipitated by pelagic marine plants and animals, especially Coccolithophoridae, Foraminifera, and pteropods. After death the calcareous remains of these organisms sink to the bottom through the deeper, colder waters (usually less than 5° C.) rich in carbon dioxide. Sediments with more than 30 per cent calcium carbonate cover nearly half the area of the deep-sea floor (Chapter 22, Fig. 3). Nearly all the calcium carbonate is of pelagic origin; bottom organisms on the average contribute less than 4 per cent of the total $CaCO_3$. The average rate of deposition of pelagic calcareous deposits is probably greater than 1 cm per 1000 years over the area of occurrence (Kuenen, 1950; Arrhenius, Kjellberg and Libby, 1951; Emiliani, 1955).

Calcareous deep-sea sediments are more restricted in high latitudes, because of the difficulty of organic precipitation of $CaCO_3$ in the cold subsurface waters, in spite of the high photosynthetic activity which tends to remove carbon dioxide and thereby to increase the carbonate concentration.

Several additional sedimentation processes influence the distribution of pelagic

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calcareous deposits. Dilution or masking of calcareous skeletons with other types of sedimentary material—volcanic, terrigenous, or glacial—causes continental slopes and shelves off well-drained land areas to be low in carbonates. Exceptions are certain narrow shelves subject to severe on-shore winds, and thus "invasion" by pelagic organisms, and shelf margins of excessively arid land masses where there is little contribution of terrigenous material—for example, near the edge of the Sahul Shelf, northwest Australia (Fairbridge, 1953).

A second process is solution at great depths, owing to the increase in solubility of calcium carbonate with increasing pressure. At depths of more than about 4000 meters, the water is undersaturated for calcite and the pelagic skeletons are dissolved. Further solution may occur beneath the surface of sediments, particularly where these are relatively high in decomposable organic matter and can support a population of mud-eating, carbon-dioxide-producing animals or bacteria (Revelle, 1944). The amount of solution increases with increased depth, so that, at average depths of more than 4200 meters in the Pacific and 4700 meters in the Atlantic, the bottom deposits consist chiefly of the less-soluble components of pelagic sedimentation, ferruginous clay, manganite, zeolites, and, in regions of high organic productivity siliceous and phosphatic organic remains. The amount of solution for any given depth is related to the free CO_2 content of the bottom water, and this in turn to the water's source region; in the Atlantic, for example, there is a northward movement of cold CO_2-rich bottom water from the shores of Antarctica into the tropical latitudes and the depth of carbonate dissolution appears to increase from south to north.

Pelagic calcareous deposits occasionally occur in anomalously deep waters. Many of these, on microscopic examination, prove to be of Tertiary age (Bramlette and Riedel, 1954), laid down when the deep waters had temperatures of 10°C. or more (Emiliani, 1954). The occasional occurrence of Recent pelagic calcareous deposits at abnormally great depths may be due to gravitational displacement of sediments of originally more shallow deposits by mass sliding, slumping, or turbidity flow into greater depths, where they become rapidly buried and thus protected from normal dissolution (Kuenen, 1950). The relative rate of accumulation and thus the concentration of pelagic calcareous material in the deep-sea sediment also depends on the organic productivity of the subsurface waters. In regions of high productivity, relatively more calcium carbonate is laid down by pelagic organisms, and the amounts of calcareous skeletons in the bottom deposits, relative to inorganic components, are higher.

Valuable insight into the complex interplay of factors determining the calcium-carbonate content of deep-sea sediments has been gained by studying the variations of $CaCO_3$ with depth below the sea floor. For example, in the eupelagic area of the eastern tropical Pacific (Arrhenius, 1952), the topmost layer of sediments is usually considerably lower in calcium carbonate and also in number of siliceous diatom frustules, but contains relatively more shells of certain warm-water species of Foraminifera than the material 10–25 cm below the surface. At greater depths in the sediment there is a series of alternating layers of high and low $CaCO_3$. The fluctuations in calcium-carbonate content become smaller in amplitude with increasing depth below the sea floor.

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Similar alterations between layers of high and low calcium carbonate occur in the tropical Atlantic (Schott, 1939) but with the remarkable difference that in many areas the surface layer is higher in calcium carbonate than the layer 25 cm below the surface.

Both of these sequences are believed to reflect changes in oceanic circulation and in the character of the surface waters during the glacial and interglacial stages of the Pleistocene. The top layers in both cases have probably been deposited since the last retreat of the glacial ice.

Arrhenius correlated the layers of high calcium carbonate and high diatoms and low warm-water Foraminifera in the tropical Pacific with the Pleistocene glacial stages. He supposed that during epochs of maximum glaciation the trade winds were narrowed and intensified. The resulting stronger divergence in the wind system near the equator brought about a corresponding divergence of the surface waters accompanied by marked upward motion of nutrient-rich deeper water. Consequently, photosynthesis and organic producitivy greatly increased, the rate of precipitation of calcium carbonate and silica in the shells of planktonic plants and animals was accelerated, and the quantity of shell material settling through the water increased. At the same time the circulation of the deep-cold waters of the ocean was speeded up; correspondingly the rate at which calcium carbonate could be dissolved in these deep waters increased. Arrhenius believed that in the Pacific the increased productivity overbalanced the increased rate of solution. Hence the glacial stages were periods of high calcium-carbonate deposition. This has been confirmed by paleotemperature determinations (Emiliani, 1955). In the Atlantic the intensification of the trade winds and of the vertical water circulation in the equatorial zones was much less pronounced while the acceleration of the deep-water circulation was greater, and thus the supply of free carbon dioxide in the deep water was increased. Hence the glacial stages were times of relatively low calcium-carbonate deposition.

This hypothesis differs radically from the explanation proposed by Schott (1939). He believed that the surface waters of the tropics were cooled by as much as 10° during the glacial stages, with the result that organic precipitation of calcium carbonate was greatly reduced. At the same time, because of the relative elevation of the continents, their contribution of non-calcareous detrital materials to the sea floor increased. Hence the deposits laid down during glacial periods are low in calcium carbonate, while those of interglacial or postglacial periods such as the present have high calcium-carbonate content.

Actually the hypotheses of Schott and Arrhenius are not necessarily contradictory. In some regions cooling of the surface waters may have had the predominant effect on biological precipitation of calcium carbonate during the glacial period; in others the increased organic productivity brought about by the intensified atmospheric and oceanic circulation may have been more important; elsewhere, the increased circulation of bottom water may have resulted in solution of calcium carbonate before it could be buried, thereby determining the character of the sediments.

NERITIC SEDIMENTS

In contrast to those of deep-sea environments, neritic sediments occur in an immense variety of types, with grain sizes ranging from clay-size particles to boulders.

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The majority of neritic carbonate sediments are biogenic, but inorganic factors are important in extremely shallow tropical waters and in the intertidal belt.

Some of the neritic carbonate sediment types, roughly in order of grain size, are:

(1) *Drewite.* White, fine-grained impalpable aragonitic lime muds (as described by Drew, 1911; named by Field, 1919; 1931).

(2) *Bahamite.* (Name recently proposed by Beales, 1956; *see* earlier descriptions by Thorp, 1936; Illing, 1954.) Silt- to sand-sized grains, of shallow marine origin and chiefly organogenic, consisting of broken molluscan shells, echinoid fragments, Bryozoa, Foraminifera, corals, calcareous algae, and fecal pellets—initially a mixture of aragonite and calcite, many of the latter magnesium-rich—sometimes with aragonitic oölites, or pisolites.

(3) *Beach rock.* A lime clastic or calcarenite, mixed aragonite and calcite, dominantly of wave-worked shell debris, but also in places foraminiferal or oölitic; characteristically inorganically cemented under conditions of intertidal exposure with an aragonitic cement (Ginsburg, 1953a; 1953b). A minor intertidal formation is pelagosite, a lime crust formed by alternate solution and precipitation (Fairbridge, 1957).

(4) *Eolianite.* Beach clastics in sand-sized particles, transported short distances (up to 2–3 miles) by wind and cemented inorganically below ground-water level (Sayles, 1931; Fairbridge, 1950a; Spotts, 1952). Although of marine origin, the sediment is nonmarine at its final point of rest and cementation.

(5) *Coquina and calcareous breccias.* Large fragments of molluscan, bryozoan, crinoidal, algal, or coral debris, with some fine-grained cementing material, which may be primary (of contemporary drewite and bahamite character) or secondary (diagenetic). Widespread beds or lenticles of layered sediment of this sort are described as "biostromal" (Cumings, 1932).

(6) *Bioherm structures.* Massive accumulations of organic origin, the result of progressive building by organisms upon the structural remains of their predecessors (Cumings, 1932). If such structures reach near enough to the surface to cause breaking of waves, an oceanic or fringing reef develops. There are many types, each characterized by a wide range of particular habitats (Ladd, Tracey, Wells, and Emery, 1950; Fairbridge, 1950b; Cloud, 1952). Biohermal environments are peculiar in that the organisms responsible for the structure build and control their own habitats.

(7) *Biohermal suites.* Derivative sediments resulting from exposure of a bioherm to wave action (Fairbridge, 1955). Petrologically they may contain all the sediment types under (2) to (5) and include secondary growths of (6). Geographically, however, they are localized and ultimately controlled by the reef itself. In these assemblages the special environments of almost the entire range of neritic carbonate sediments may be concentrated within a very restricted area.

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Chapter 11

Nutrient Elements

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INTRODUCTION

In addition to the well-known conservative elements which constitute most of the ions in sea water (Chapter 8) there are other ions, present by comparison in small quantities, yet of fundamental importance in the economy of the sea. In contrast to the conservative elements, their concentrations, which vary considerably in both space and time, are not a function of salinity. These substances, the nutrient elements, are required in the nutrition of the primary producers, the phytoplankton, and their study has therefore often been closely bound up with these organisms. The substances concerned are compounds of phosphorus, nitrogen, and silica (required for the skeletons of diatoms and radiolarians); the other elements required in phytoplankton nutrition are present either in relatively large quantities and are maintained as conservative elements (the inorganic cations, for example) or as trace elements (Chapter 12). It will be necessary to consider both the spatial and seasonal distribution of each of the above substances in the various forms in which they occur, as well as their relation to one another. In their simpler form as components of the inorganic ions, phosphate, nitrate, and silicate, they are used up in phytoplankton nutrition. Considerable attention will therefore be given to the cycle by which they are regenerated.

The detailed study of these nutrient elements in the sea was begun much later than that of the conservative elements; at first their importance was not appreciated, and later, when it became recognized, the analytical methods for their quantitative estimation, where such existed, were difficult and tedious. The introduction of colorimetric methods, largely as the result of the work of Atkins, Harvey, and Cooper, ended many of these analytical difficulties (*see* Barnes, 1949, for a review), but even now the amount of information available on the nutrient elements is in many cases a reflection of the relative ease of the techniques required in their estimation; phosphorus data, for example, are far more abundant than nitrate data.

Two types of investigation will be considered: (1) "Field" work, in which estimates of the concentration of these nutrients are made over a given region at a series of depths and at a number of stations; in many cases the sequence is repeated at intervals. Field work can be divided, somewhat artificially, into surveys in shallow coastal waters, bays, and fjords, and oceanic surveys. Ease of access to marine biological stations has led to a disproportionate amount of work in the inshore waters. (2) Laboratory investigations are carried out, under more or less controlled experimental conditions, particularly on the regeneration cycle undergone by these ele-

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ments; in some cases this type of information is supplemented by larger-scale experiments in tanks or small ponds.

Various methods of expressing the results have been used: in the following account all the values have been converted to mg. atoms per cubic meter—in accord with modern convention. Where necessary, and where the information was available, all values for phosphate have been corrected for salt errors. (*See* Cooper, 1938.)

PHYSICAL PROCESSES IN THE NUTRIENT CYCLE

The utilization of inorganic nutrients takes place in the upper layers of the sea where the quantity of light is sufficient for photosynthetic activity. During this process the simpler inorganic ions are built up by anabolic processes into more complex organic derivatives and then, via herbivores and carnivores, pass through a complex food chain. At various stages of this food chain, soluble, colloidal, and particulate organic matter is returned by excretion, by death, and by decay to the sea and is then available for the action of regenerative processes leading back to the inorganic forms of the nutrient elements. In some of the simpler products of the catabolic processes, some regeneration may take place *in situ*; this seems particularly true with excretory products containing phosphorus and simpler nitrogen derivatives. Thus there is evidence that planktonic organisms may excrete considerable amounts of readily hydrolyzable, low molecular weight, organic derivatives of phosphorus, or even perhaps inorganic phosphate. (*See* Chapter 14 for a discussion of particulate organic matter in sea water.)

Gardiner (1937), for instance, found a great increase in inorganic phosphorus content when living zooplankton was kept for several hours in normal sea water. Similarly, in the case of urea, which is an important excretory product of animals, rapid chemical hydrolysis may be effective and important at the site of excretion.

In general, however, it is considered that much of the regeneration takes place from the organic debris, which sinks and in shallow waters reaches the bottom in greater part probably before the final decomposition is complete; in these circumstances much of the regeneration must take place in the bottom muds. Zooplankton, which rise at night to feed in the photic zone and migrate downward at day, also carry down stocks of nutrients. Whether the organic material reaches the bottom or not, mechanisms are required to return regenerated nutrients to the surface waters, so that they may become available for a further cycle. These mechanisms are considered below.

UPWELLING

Under certain circumstances, particularly on the western seaboards of the continents, subsurface currents may at certain times rise to the surface and replace the impoverished coastal water by nutrient-rich deep water; this process is associated with a prevailing component of wind parallel to the coast, carrying surface water away from it, and is important, for example, along the Californian coast, the Peruvian coast, and the West African coast (Moberg, 1928; Sverdrup, 1938; Sverdrup and Allen, 1939; Gunther, 1936; Hentschel, 1928; Currie 1953; Hart, 1953).

The stages in this process of upwelling can be illustrated by a more detailed consideration of that taking place on the California coast. The prevailing winds during certain seasons carry the lighter

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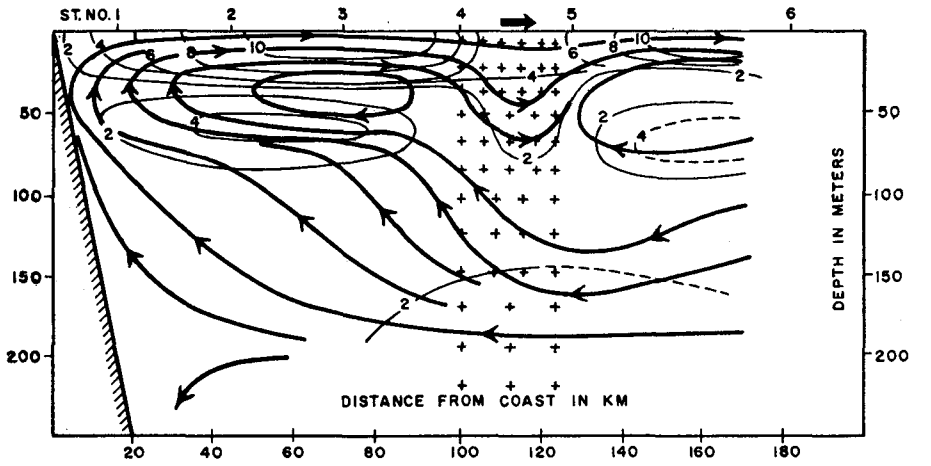

FIGURE 1.—*Circulation off the California coast showing movement of surface water away from the coast and upwelling of deep water*

From Sverdrup (1938)

surface water away from the land, and as a result, over a period of 41 days, this light water has been found to be banked up about 100 km offshore. Between the coast and the banked-up light surface water, deep water flows up from below to take the place of that displaced, and in this region a cellular circulation then develops; its offshore boundary gradually moves away from the coast, and its inner boundary is fed by the nutrient-rich water from below (Fig. 1). In a later stage the hydrographic conditions become more complicated; instability may lead to the formation of eddies, which are detached from the coastal side of the boundary.

Where water flows away from a coast in this way the region is said to be a region of divergence; this term is also applied to any region, even in mid-ocean, where surface waters flow away from one another. As in the coastal conditions discussed above, any such displacement of surface water must result in upwelling, with a consequent renewal of nutrients in the surface. Figure 2 is a section across the Pacific Equatorial currents. Here there are two parallel regions of divergence where nutrients are brought up with the deeper water; between these lies a region of convergence associated with the southern boundary of Equatorial countercurrent, where surface water sinks, so that by contrast the upper layers are very poor in nutrient content.

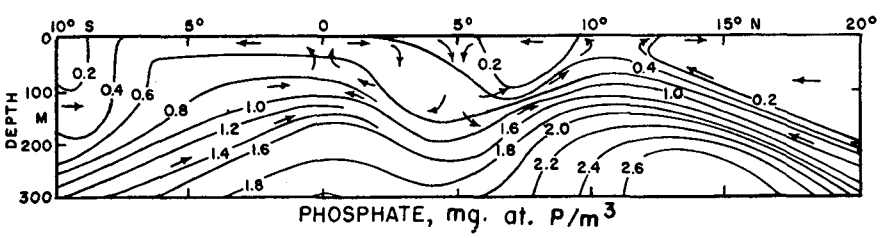

FIGURE 2.—*Section across the Pacific Equatorial Countercurrent, showing two regions of divergence with high surface phosphate values*

Between the regions of divergence is a region of convergence with low phosphate values. From Sverdrup, Johnson, and Fleming (1942)

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TURBULENCE AND EDDY DIFFUSION

A second mixing mechanism is due to turbulence caused by the passing of currents, commonly tidal in character, over an uneven bottom or through narrow straits. This is illustrated by the work of Gran and Braarud (1935) in the Gulf of Maine and and the Bay of Fundy.

In the open waters of the Gulf the cycle is that typical of temperate coastal regions: winter cooling and convection follow a high degree of stratification in the summer. On the shallow banks, such as Georges Bank and along the coast, including the islands, mixing due to turbulence caused by the tidal currents flowing over the shallows (Georges Bank) gives in some cases almost homogeneous water even in summer. In the Bay of Fundy, at the head of which the mean tidal range reaches 17 meters, the rush of the tidal current results in sufficient turbulence to give effective mixing at all seasons. Renewal of nutrients to the photic zone in this way need not necessarily result in their efficient utilization, since when such processes are sufficiently vigorous, the mud stirred up at the same time, by reducing the penetration of light, decreases the depth of the photic layer to such an extent that only moderate phytoplankton production can take place. In addition, such vigorous turbulence may result in the diatoms themselves being carried below the photic layer, so that less time is available for their photosynthetic processes and ultimate reproduction. Thus on Georges Bank the increase in nutrient concentrations leads to a moderate plankton production throughout the summer, but in the Bay of Fundy, although at the same season the water may contain 0.3 mg. at. PO_4-P/m^3 and up to 4 mg. at. N/m^3, diatom production is poor.

This equalization of nutrient concentration throughout the water column by fast tidal currents is only an extreme form of the general transport of nutrients into the upper layers as a result of turbulent motion: its effect is great in this case because of the high velocity of the currents.

If in any physically homogeneous fluid a concentration gradient of a dissolved substance exists, then because of molecular motion there will be a transfer from places of high concentration to those of lower concentration, and this will continue until the gradient is eliminated. This process is termed molecular diffusion and is very slow. In a moving body of water turbulent motion will bring about a similar but much more rapid exchange of properties between different levels. If such a fluid contains dissolved substances with regard to which there exists a concentration gradient, then turbulent motion will tend to reduce this gradient. This process, which can be considered analogous on a macroscale to the diffusion processes brought about by molecular motion, is termed eddy diffusion. Because of the sinking of the plankton and consequent regeneration and accumulation of nutrients in the lower layers, and because of the utilization of nutrients in the upper layers, there is a gradient in the nutrient concentration; eddy diffusion will tend to equalize the concentration, and a net transport of nutrient material to the upper layers will result from this process. The magnitude of this transfer depends upon the coefficient of vertical eddy diffusion, which in turn is determined by the over-all stability of the water column. In general, great turbulence follows low vertical stability and high velocity. Values of the vertical eddy coefficient range from 4–10 C.G.S. units in the deeper parts of ocean (Seiwell, 1935a) to 30–40 C.G.S. units in the upper layers (Helland-Hansen, 1930; McEwen, 1919). Seiwell (1953b) tabulated the eddy coefficient and resultant upward transport of phosphate in the North Atlantic and found it to range between 0.01 and 0.02 mg. at. P/cm^2/year.

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VERTICAL CONVECTION, CASCADING, AND CAPSIZING

In the temperate zones, where these is a marked seasonal change in the climatic conditions, vertical convection is of extreme importance in maintaining a supply of nutrients to the upper layers. Convection arises as a result of the winter cooling of the surface waters, so that the density of the surface waters increases sufficiently to cause them to sink and to be replaced by upward movement of lighter nutrient-rich waters from below.

The concept of cascading was first put forward by Nansen (1913) to describe the effects of winter cooling over the Rockall Bank; recently its importance, particularly in the area of the Celtic Sea, has been stressed by Cooper and Vaux (1949). The process is also important in understanding the water movements over the banks around Bermuda (Boden and Kampa, 1953) and Bear Island (Lee, 1952).

As a result of vertical mixing during the winter, equalization of nutrient conditions throughout the water column overlying a continental shelf takes place. Consider, however, a section across the Continental Shelf and Slope. If two positions with the same initial temperature, salinity, and density are considered, and if at both purely vertical mixing is sufficient to equalize the temperature, then the fall in temperature at the deeper station will be less than that at the shallower station. The shallower water, therefore, becomes not only colder but heavier and will tend to flow downhill in what has been termed a cascading current. If other factors are equal, cascading should develop most strongly in winters when low air temperatures produce cold dense water over the shallow parts of the shelf. The dynamics of such water movements have not been worked out, but Cooper and Vaux suggest that the water flows below the level of vertical mixing as a relatively cold blanket of water until it reaches a depth or slope where its density is equal to that of the ocean water. They suggest that at this point lateral mixing along surfaces of equal σ_t may take place, or if canalized within a submarine canyon, such as those that cut into the Continental Shelf, it might become a core of water which might penetrate many miles into the ocean at its appropriate σ_t level. As Cooper points out, such a core would retain its identity when the surrounding envelope is moving in the same general direction.

Nutrients carried over the slope in cascading water are, of course, lost from the shelf, and the nutrient content of the upper layers will depend upon the relations between the nutrient content of the cascading water and that of the compensation water, which must of course take its place. In the Celtic Sea the major quantity of compensating water seems to be the nutrient-poor surface waters of the Atlantic Ocean and the Bay of Biscay, so that in this region cascading tends to reduce the stock of nutrients in the shelf water. In addition, since the cascading of the lower layers of water may continue beyond the time when the vernal plankton outburst takes place, the sinking of feces and detrital matter into this layer also tends to carry toward the ocean abyss not only dissolved nutrients but also heavy metals and potentially valuable organic materials associated with light suspended matter near the bottom. This process may severely reduce stocks over the shelf.

Upwelling is one method by which deeper nutrient water is brought up into the photic zone, and recently Cooper (1952a) suggested a further process which may be of considerable importance in certain regions. Although its contribution is not proved and the dynamics not worked out, the stimulating ideas put forward are of interest and importance.

When a strong wind blows on to a continental slope the light surface water will be forced against the slope, forming, while the wind lasts, a cushion of water of considerable depth (Sandström, 1918; Cooper, 1952a). When the wind drops the cushion will rise, and the momentum of the rising water mass will bring up nutrients from the deeper water. Since a continental slope, however, is usually bordered by a continental shelf, these conditions may result in spillage of the deeper water over the

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edge of the slope on to the shelf. Some mixing and enrichment with nutrients of the shelf water can then occur. If the energy derived from the wind in this way becomes canalized within a submarine valley cutting into the shelf, such canalized spillage water may then be projected many miles onto the shelf; areas lying shoreward of such submarine valleys could be especially rich in nutrients as a result of such submarine eagres. If the wind forces are sufficiently high, then the sloping isoteres (surfaces of equal density) slope up, with resultant spillage, and may become vertical; should the external forces exceed the force required to produce vertical isoteres, the surface water will capsize. Light water is then brought down beneath the heavier, the stability is upset, strong vertical convection ensues, and enrichment with nutrients from the bottom water takes place. Conditions to initiate capsizing are likely to occur over continental slopes backed by extensive shallow seas, for there the surface ocean waters are relatively free to press inward, whereas the root of the water mass will be stopped by the continental slope.

SITE OF THE DECOMPOSITION

All these processes tend to bring nutrients from subsurface levels, where they tend to accumulate, back to the surface. In regions where the depth of water is considerable, decomposition and regeneration may take place in the water masses; in shallow waters, where much organic matter reaches the bottom and the nutrients are regenerated in the mud, the mud-water interface must initially be of primary importance. The most extensive studies of the part played by this mud-water interface are Mortimer's (1941; 1942) studies of fresh-water lakes. He has shown that in those shallow oligotrophic lakes where there develops a greatly reduced oxygen concentration in the hypolimnion (the layer cut off by thermocline from the upper epilimnion), the liberation of nutrients such as phosphate from the bottom muds is controlled by oxidative processes at the mud surface. With high hypolimnion oxygen concentration, an oxidized layer is formed on the mud surface and acts as a barrier to the removal of ions. (*See* Chapter 9.) With a fall in the oxygen content consequent upon the development of the thermocline later in the season, reducing conditions are set up, the oxidizing conditions disappear, and the oxidized barrier is removed. Return of nutrients to the hypolimnion can then take place, probably by horizontal water movements (Mortimer, 1952). Even in a deeper lake (65 meters), where the oxygen content of the hypolimnion fell to only 71 per cent saturation, the effect was thought to play a part. In general, the rate of removal of ions from the mud surface depends upon seasonal changes in the amount of vertical mixing, in the first place at or near the mud surface; these changes in turn depend on stratification and/or factors related to the air and climatic conditions. However, the physical and chemical changes at an interface in the mud surface, such as those caused by oxidation barriers, determine the concentration gradient of the ions in the water in immediate contact with the mud. The thickness of any such oxidized mud layer is the result of a balance between the rate of diffusion of oxygen into the mud (a function of oxygen-concentration gradient at the mud surface) and the reducing power of the mud. The bacterial activity within such muds could also be related to its redox potential.

Recently the use of radioactive tracers has been introduced in attempting to elucidiate the process of utilization and regeneration of phosphorus in small lakes. (*See* Coffin *et al.*, 1949; Hayes *et al.*, 1951; 1952; Hutchinson and Bowen, 1947.) A rapid loss of added P^{32} has been found, and the results show that there is an active exchange between dissolved phosphorus and phosphorus present in the lake solids; the two form a single dynamic system in the lake.

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There is little information, comparable with Mortimer's work on lakes, on the nutrient content of marine muds and its release. Stephenson (1949) has shown that on stirring muds with sea water the results suggest that the agitation destroys organisms, probably bacteria, with the release of phosphate phosphorus, and that in experimental tanks this may be absorbed by bacteria growing on the walls of the vessel. Moore (1930) analyzed a number of Clyde muds. These muds are in general soft, even at the surface, but lower down they become more clayey and sticky. The phosphate content of the muds was considerable and in general decreased with depth in the mud, suggesting that some is leached out.

In experiments designed to fertilize a small basin (averaging only 6 meters in depth), which was partially isolated from a sea loch, enormous quantities of added phosphate were found by Orr (1947) and Marshall and Orr (1948) to disappear rapidly—far more rapidly than could be accounted for by the increase in phytoplankton production. Although some may have been used by the fixed algae, considerable quantities were probably absorbed at the surface of the mud. A similar finding was reported by Pratt (1949; 1950), who stressed the dynamic aspects of the phytoplankton-phosphorus cycle, as a result of his large-scale experimental work in concrete tanks. Thus the rate of assimilation of phosphorus depends upon the rate of population increase rather than upon the standing crop; a large population which is not increasing may be satisfied by a relatively low rate of phosphorus assimilation. Pratt found that the rate of regeneration was lower than the rate of assimilation and solution; in this case the rate of regeneration limits the velocity of the entire cycle. The rate of release of particulate organic phosphorus was related to the size of the standing crop, as was the regeneration of inorganic from dissolved phosphorus.

It is clear from the foregoing that in shallow waters the bottom plays an important part in phosphate regeneration and release, but as the depth increases the regeneration may take place in the water column (Harvey, 1948; Armstrong and Harvey, 1950). Redfield, Smith, and Ketchum (1937) studied the inorganic, dissolved organic, and particulate phosphorus cycle in the Gulf of Maine where the station depths were about 250 meters. There was no seasonal change in the total phosphorus present in the water column, as would be the case if material containing phosphorus was lost from a part of the cycle on the bottom and withdrawn therefore from circulation; the results are explicable on the basis of a closed system within the water column; bottom absorption followed by release plays no part in the process. However, Cooper (1948) indicated that enrichment of bottom water takes place over bottoms which are overlain with mud or ooze.

CHEMICAL AND BIOLOGICAL PROCESSES OF THE NUTRIENT CYCLE

These processes, (in contrast to the physical processes discussed above), which are applicable to all nutrients, may be widely different according to the nutrient element under consideration, and it is therefore necessary to consider each element separately.

PHOSPHORUS CYCLE

The original inorganic phosphorus is built up into a variety of organic phosphorus compounds, such as the phospho-proteins, nucleo-proteins, phospholipids (all of

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high molecular weight), and the important but relatively simpler compounds involved in various intermediate oxidative metabolic processes. In almost all these substances, as far as is known, the phosphorus is present as a phosphoric acid residue: in the phospho-protein as an ester of the hydroxy-amino acid, in the nucleo-proteins as a sugar-phosphoric ester component of the nucleic-acid portion, in the phospholipids as an ester of glycerol or hydroxy-amino acid, and in the simpler intermediates as sugar esters. The fact that the phosphorus is present as phosphoric acid residues in the organic products of anabolism indicates that on *a priori* grounds it might be expected to be more easily regenerated in the form of inorganic phosphate than, for example, nitrogen, which is more closely built into the organic molecules and is ultimately largely returned as nitrate.

Although a rapid return of inorganic phosphorus to the upper waters of the sea may take place as a result of the decomposition of the simpler excretory products, in general, autolytic or bacterial decomposition of organic debris is usually considered to be necessary for the return of most of the inorganic phosphorus.

Cooper (1935) has shown that in sea water containing decaying phytoplankton and zooplankton material there is a rapid liberation of inorganic phosphate: about 0.3 mg. at. P/m³ from 1.5 mg.

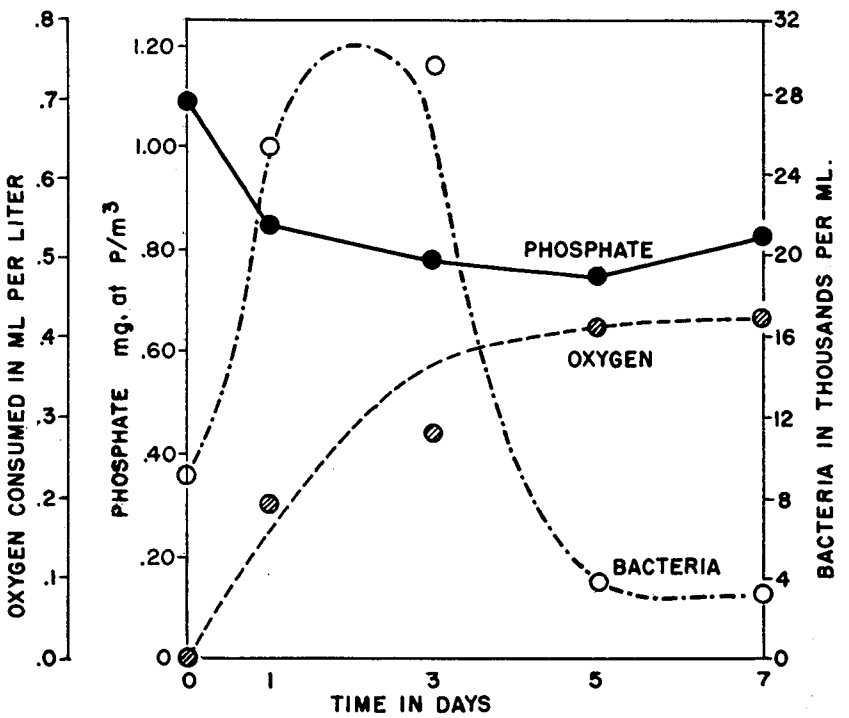

FIGURE 3.—*Assimilation and regeneration of phosphate by bacteria; oxygen consumption*
From Renn (1937)

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at. P/m³ of added zooplankton was found to be set free in the first 12 hours. He found that, at the same time, inorganic phosphate was set free from the dissolved organic phosphorus originally present in the water. He found a delay in the release of inorganic phosphate from plant material; perhaps in the case of zooplankton some chemical release took place in the early stages, whereas with diatoms the development of an appropriate bacterial flora was essential. No information exists, however, on the bacterial population in these experiments. It is known that when sea water is stored there is a rapid rise in the bacterial population, and that this is accompanied initially by a large decrease in the phosphate concentration, but Renn (1937) found that this is followed by a rise in the phosphate content caused by subsequent autolysis of bacterial cells (Fig. 3). As he points out, bacterial numbers are usually low, but there may be a rapid turnover; rate of growth and rapidity of autolysis are the critical factors in determining the importance of bacteria as regenerating agents.

NITROGEN CYCLE

The end product of oxidative processes in the case of organic compounds in nitrogen is the nitrate ion, and in this form it can be returned to the cycle. However, in contrast to phosphorus, which is present almost entirely as phosphoric acid residues, nitrogen is much more closely "built" into the organic molecules during anabolic processes. Further, not only are the reactions concerned in the breakdown of the nitrogenous organic material more complex, but intermediate inorganic compounds—in particular ammonia and nitrite—may be formed; these compounds, in addition to being intermediate stages in the oxidative processes leading to nitrate, may under certain circumstances by utilized directly by the phytoplankton organisms. That all three forms of inorganic nitrogen and simpler organic substances containing nitrogen, such as glycine, can be used by diatoms has been established by culture experiments (Schreiber, 1927; Braarud and Föyn, 1931; Harvey, 1939); that all three can be simultaneously used up in the sea is strongly indicated by Cooper's results (1933a) of the 1931 season, when at one stage all three substances were almost absent from the water column. It is usually considered, however, that in higher latitudes the nitrate ion is the most important form of nutrient inorganic nitrogen.

In addition to particulate organic material containing nitrogen, soluble and simpler organic nitrogen compounds—*e.g.*, amines and urea—resulting from breakdown of organic material and from excretory products, exist in sea water. A partial fractionation of these compounds in lake water (where the absence of salts allows the water to be evaporated and gives a more concentrated solution for the analyses) has been made by the Wisconsin workers, Domogalla, Juday, and Peterson (1925), and Robinson and Kemmerer (1930); the albuminoid and organic nitrogen in Pacific waters have been determined by Robinson and Wirth (1934a; *see* 1934b, for earlier references).

In the case of some of the simpler substances, urea for example, chemical hydrolysis with the production of ammonia may be effective and important (Cooper, 1937), although ZoBell and Feltham (1935) demonstrated the presence in the photic layer of urea-decomposing bacteria which could liberate ammonia. However, again, autolysis and bacterial action are considered necessary for the major part of the oxidative processes leading to inorganic nitrogen regeneration from particulate matter. Strong evidence exists that ammonia is the first product of bacterial action and that this is then oxidized to nitrite and subsequently to nitrate. In the surface

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layers some photochemical oxidation of ammonia may take place, but except possibly in the surface waters of tropical regions, it is of little importance (Rakestraw and Hollaender, 1936).

The most extensive investigations of nitrogen regeneration under experimental conditions have been carried out by von Brand and his colleagues, who followed the decomposition of organic matter under laboratory conditions (1937; 1939; 1940; 1941; 1942; 1947). The experimental procedure was similar throughout this work and, in general, consisted in allowing various kinds of planktonic and other material to decompose in carboys of sea water kept in the dark; samples were withdrawn at intervals and analyzed, so that the changes in the ammoniacal, nitrite, and nitrate nitrogen fractions could be followed throughout the decomposition process. A similar decomposition sequence was observed in all these experiments (Fig. 4); particulate matter first gave rise to ammonia, as had been demonstrated by Keys *et al.* (1935), Waksman and Carey (1935), and ZoBell and Anderson (1936), and this was then oxidized to nitrite; the latter was in turn oxidized to nitrate. Although the length of any stage varied from one series of experiments to another (the total duration of the nitrite stage was particularly irregular), the sequence of events was always similar. The rate of this decomposition was greatest in the first few days with the production of ammonia; ultimately the rate of formation of ammonia slowed down and ceased. During this period neither nitrite nor nitrate was formed, and although not conclusively demonstrated, the chemical evidence suggested that soluble organic nitrogenous compounds do not play an important part as precursors of ammonia. However, when a second cycle was carried out in the same culture, by further addition of decomposable material, there was a lag in the appearance of ammonia in comparison with the disappearance of particulate nitrogen; under these circumstances the formation of intermediate soluble nitrogenous compounds of high molecular weight may take place. Concurrent with the production of ammonia was a rapid development of the bacterial flora, and it was therefore suggested that autolytic decomposition plays a comparatively small part. However, the absolute numbers of bacteria were never high, in fact not much higher than the numbers present in stored unfiltered sea water without added material. The rate of change of the bacterial population may have been high, however, and thus gave rise to a large turnover of organic material. Nitrate appeared only when nitrite disappeared, which never happened as long as a sufficient quantity of ammonia remained. Under anerobic conditions a small amount of ammonia may be formed, but a strong odor of hydrogen sulphide was observed, and no nitrite ap-

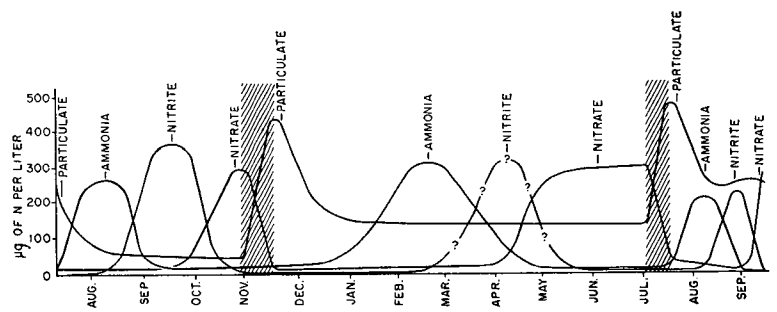

FIGURE 4.—*Decomposition of diatoms in sea water*

Shaded areas represent regeneration periods with culture exposed to light. From von Brand, Rakestraw, and Renn (1939)

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peared. The behavior of ammonia, nitrite, and nitrate in these experiments is similar to that obtained by other workers using pure bacterial cultures and the appropriate substrate.

The slowest of the three stages is the oxidation of nitrite to nitrate, and it is suggested that the reason for this is that an efficient population of the requisite specialized *Nitrobacter* flora develops at a slower rate. When decomposition had stopped there was still 20–35 per cent residual nitrogen (calculated on plankton basis), and this was presumably present either as nondecomposable residues, bacterial cells, or other forms. The concentration of particulate matter had little effect on the rate of the processes, but the source of material had some effect. The rate of decomposition was most rapid with mixed plankton, slower with pure diatoms (from cultures), and slowest with added yeast cells. A ciliate behaved like diatoms in harbor water, but decomposition did not proceed to nitrate in deep-sea water.

The course that the decomposition took when new organic matter was added to a decomposing sample depended on the bacterial flora that then predominated. There was no evidence of the inhibition of the formation of nitrite or nitrate by ammonia; in general a shortening of the cycle takes place, so that, for example, ammonia and nitrite appear only in small quantities if new organic matter is added after the development of a vigorous nitrate flora. Low temperature may prevent part of the processes; nitrite formation may be prevented or only retarded, depending upon the particular organisms present, but the effect of temperature is less on the nitrite to nitrate conversion. The cycle can be repeated; exposure to light at the nitrate stage and inoculation of the sample with living diatoms resulted in a rapid growth of the latter and a consequent depletion of the nitrate. Three successive cycles were in this way carried through, and since each addition of new organic matter resulted in an undecomposable residue, the total level of refractory residual nitrogen gradually rose with each successive cycle. Further, inoculation and exposure to light either at the ammonia maximum or before the nitrate stage lead to a depletion of the inorganic nitrogen present and to a vigorous growth of diatoms as well, indicating that at these stages no toxic compounds had been formed which would inhibit the development of phytoplankton.

The source of the water had an important influence on the decomposition. Decomposition in samples of water from the oxygen-minimum layer at 800 meters and from the surface of a deep-sea station was similar to that in samples of inshore water, with which the experiments described above were made; in samples of very deep water (1200 meters), decomposition did not proceed further than the formation of ammonia. None of the samples showed any difference between sterilized (by filtration) and untreated subsamples, and this suggested that the necessary bacterial inoculum was carried by the diatoms. It therefore follows either that the deep water contains a factor inhibiting the production of an oxidizing bacterial flora, or that it lacks an essential factor necessary for its development. That it was the lack of an essential constituent, rather than the presence of an inhibiting factor, is suggested by the fact that evaporation and ignition of harbor water, before the addition of particulate matter, resulted in a retardation in the formation of ammonia, whereas production of nitrite was even more retarded, and no nitrate formed. However, boiled diatoms showed little difference from living material when introduced into either untreated or sterilized sea water, and von Brand and his colleagues question the maintenance of aseptic conditions. The evidence suggests that it is easier to eliminate the organisms responsible for oxidation than those for ammonia formation. However, in one experiment the decomposition of diatoms proceeded normally, and nitrate was ultimately produced in deep-water cultures.

In their most recent paper (Part VI), the authors studied the effect of a number of enzyme poisons on various stages of the cycle. The production of ammonia by micro-organisms may take place by hydrolytic, reductive, and oxidative deamination, depending both on the conditions and on the micro-organisms present. That potassium cyanide was found to retard the production of ammonia in the decomposition cultures but did not completely suppress it suggests that oxidative deamination

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(known to be prevented by KCN in all examples studied) is the most important route to the liberation of ammonia; that some ammonia production took place, even in the presence of cyanide, may be due either to a weakly developed alternative mechanism by the same bacteria or to a slow production of a different bacterial flora liberating ammonia by an alternative method. Nitrifiers are more sensitive and were destroyed by the usual well-known poisons. Cyanides, carbamates, iodates, and fluorides interfered with nitrite and nitrate formation, suggesting that dehydrogenases are involved in their formation.

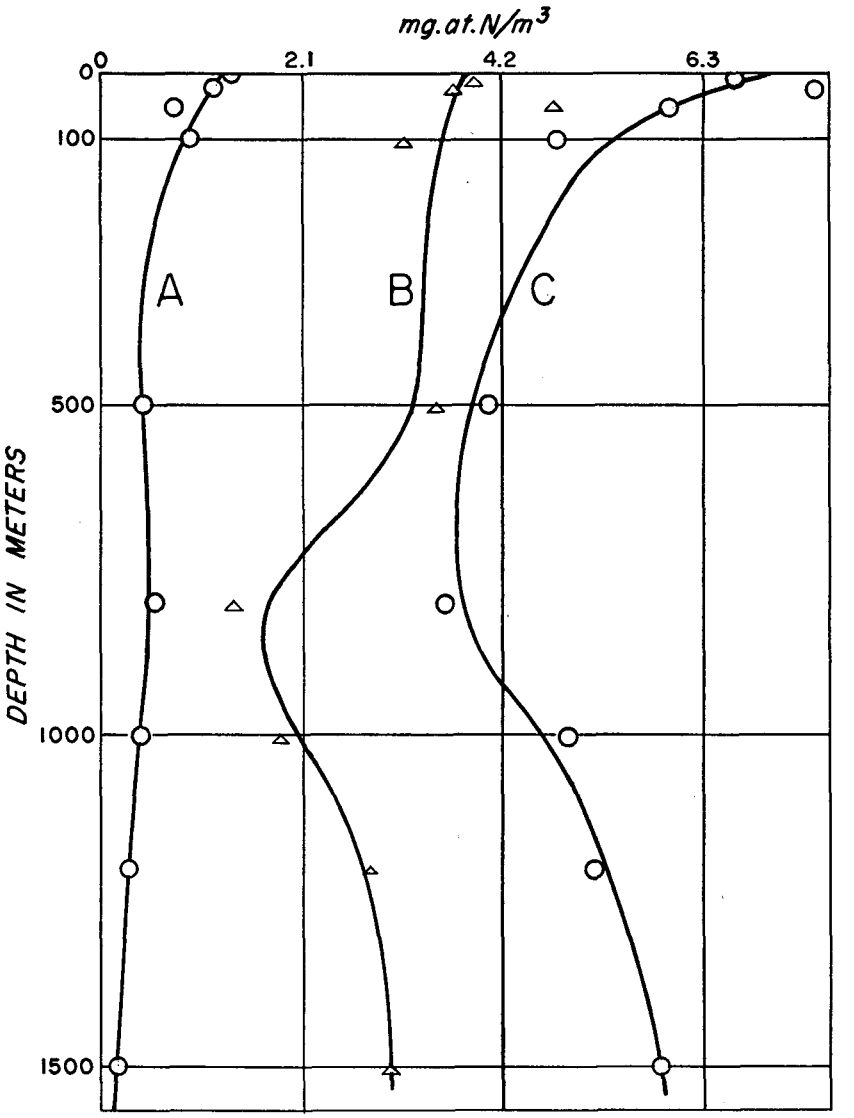

FIGURE 5.—*Average free ammonia (A), albuminoid nitrogen (B), and organic nitrogen (C), in the waters of the Pacific*

From Robinson and Wirth (1934)

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Attempts to isolate the bacteria responsible for these oxidative processes have not always been successful. Nitrifying bacteria have been found in muds and in the sea, but both Waksman *et al.* (1933a; 1933b) and Carey (*see* 1938 for a review of literature) found them only in the mud and in the surface waters near land. Von Brand *et al.* failed to isolate the nitrate-forming bacteria from their plankton experiments, and both Waksman and Carey emphasize the difficulties of demonstrating their presence. From the field work it seems clear, however, that although in shallow waters much of the decomposition may take place in or at the mud surface, it also takes place in the upper layers; perhaps the difficulty of isolation is related to the constant occurrence of the bacteria in connection with solid surfaces. Thus Waksman *et al.* (1937) found that bacteria occurred only to a very limited extent except in association with plankton organisms; although the actual populations are small in numbers (ZoBell, 1943), however, the dynamic character of the process involved should be stressed.

The results of determinations of the distribution of ammonia and nitrite in coastal regions indicate that their production is confined largely to the topmost 200 meters of the water (Rakestraw, 1936; Redfield and Keys, 1938; Cooper, 1933 b). Further, a correlation was found between nitrite and ammonia. In the work of Robinson and Wirth (1934 b) ammonia was not found except in very small amounts in the upper layers. Their results show a minimum (Fig. 5) in both the albuminoid and total nitrogen, but this is not paralleled by an increase in the ammonia. The minimum values are correlated with the minimum oxygen layer, where oxygen had been consumed in the oxidation of plankton products. The lack of a maximum in the ammonia values suggests that ammonia has been rapidly converted to a further stage of oxidation and that this has taken place in mid water. The same results show a nitrate maximum and no indication of nitrite, suggesting that complete oxidation had taken place.

SILICON CYCLE

Silicon in some ways is different from the two elements discussed above, since it is not required for nutrition in the strict sense but only for the formation of skeletal material by diatoms and radiolarians. Little experimental work has been done on the conversion of soluble silicate ion into what must be presumed to be a polysilicic complex in the skeletal material, and little evidence exist on the processes involved in the regeneration of the silicate ion. It is generally presumed that after the death and decay of the organisms, dissolution of the silica takes place in the alkaline sea water by direct chemical solution. King and Davidson (1933), however, found that unboiled diatomaceous material gave off silica into solution more rapidly than a boiled sample. Possibly there is something of an enzymatic nature in the unboiled portion, but the general autolysis of the organic material may leave the skeleton more susceptible to solution; alternatively, boiling may coagulate the protoplasm in the skeleton sufficiently to decrease the solution rate simply by reducing the area available to chemical attack or preventing access of the dissolving liquid. The results of Cooper (1933 a; 1933 b), which showed irregular changes in silicate concentrations, suggest that in the region to which his results apply, and at the depths

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investigated, solution of silica may take place anywhere. Cooper's work also suggests that the time taken to complete the silicon cycle is shorter than that of the other nutrients, and his results indicate that the skeletal material from an early diatom increase can be returned in a matter of months. Cooper (1933a; 1933b), by calculations of the differences between winter maxima and summer minima of nutrient concentrations, obtained estimates of plankton production, and the values so calculated from the silicate data were only one-fifteenth of those from nitrogen and phosphorus data. He therefore suggested that the silicate is used up several times in one season. He also points out that the thickness of the siliceous skeleton varies according to the amount of available silicate.

This problem of the re-solution of silica is, however, little understood, and a critical summary of the conflicting evidence has been presented by Cooper (1952).

The two lines of available evidence, both of which are equally well documented with the reliable data of careful workers, lead to different conclusions. As pointed out above, a comparison of annual production based on depletion of nitrogen, phosphorus, and silicon suggests that in the absence of a major utilization by autotrophic flagellates, silica is redissolved and utilized rapidly. By contrast, experimental evidence indicates that the siliceous tests are resistant to solutions even at pH 10.6 (Atkins, 1945; *see* Conger 1941; Rogall 1939). Furthermore, the fine markings of the test are evident in the frustules present in diatomaceous ooze. As Cooper (1952b) pointed out, in spite of much work on the subject, the chemistry of dissolved silica is still in an unsatisfactory state. The metasilicate ion probably does not exist, since the simplest ion is the orthosilicate, SiO_4 , or more commonly a hydrated silicate ion, $HnSiO_4^{(4-n)}$. In all cases the central units are SiO_4 tetrahedra linked through oxygen bonds; in vitreous silica, such as exists in colloidal silicates and in diatom skeletons, the tetrahedra are linked to produce a random three-dimensional network. Aggregated hydrated silica is in the main electrochemically neutral, and the acidity usually ascribed to it is the result of anions held in the interstitial fluid or to surface charges or a double layer; only at pH values greater than 12.0 is it to be considered the true anion of a silicic acid. There is no barrier to the solution of hydrated silica in alkaline solution—saturation is not approached in sea water. Cooper therefore suggested that the apparent insolubility of diatom tests may be due to a surface layer of organic molecules, which by saturating the residual valencies of the SiO_4 tetrahedra form a protective barrier. No direct experimental evidence exists for such a barrier, which need be only a few molecules thick. The passage of diatoms through the stomachs of herbivore crustaceans may not only remove such an organic layer but also break up the tests exposing newly fractured surfaces; freshly fractured silica surfaces have been shown to possess a very high rate of solution compared to the old surfaces. In support of this hypothesis is Hart's finding that the recognizable diatom species in Krill—*Euphausia superba*—are those most strongly silicified.

REGIONAL DISTRIBUTION OF NUTRIENTS

Knowledge of the distribution of nutrients is most detailed for the relatively shallow coastal waters—particularly for those of the northern hemisphere. Little information exists concerning nutrient concentrations in the great oceanic regions, and most of it is derived from the results of limited surveys undertaken as only a part of the programs of major expeditions. In the Antarctic region, however, as a result of the work of the Discovery Committee, data are available in some detail over a great area. Because of the difficulties of technique, there is a great lack of proportion between the amount of data available on the different elements: inorganic phosphate is most easily determined, and phosphate data are by far the most abundant; the following account must therefore appear biased toward a discussion of this nutrient.

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COASTAL AND INSHORE WATERS

The study of nutrients in the sea was initiated largely by the German worker Brandt and his colleagues, in the waters neighboring upon their marine stations. The modern work originated with W. R. G. Atkins' realization of the necessity for sensitive colorimetric methods (which to a large extent he therefore developed) for nutrient-salt estimation, and the most detailed studies of coastal waters originated from the Plymouth school of Atkins (1926; 1928; 1930a; 1930b) and his colleagues Harvey (1926; 1928; 1939) and Cooper (1933a; 1933b; 1935; 1937; 1938). These writers paid particular attention to the changes taking place in regard to the chemistry of the nutrients. Marshall and Orr (1927; 1930) stressed the relation to plankton over the short period of the spring increase, and their chemical results are less detailed. Similar studies followed in most marine laboratories; the waters of the Gulf of Maine have been thoroughly explored by American workers. A large body of data has therefore been accumulated, particularly in the Norht Temperate Zone, on the sequence of events in such regions, and some attempt will be made to summarize it; limitations of space will not allow justice to some of the pioneer studies. Even in these coastal surveys there has been a marked tendency to concentrate on the most easily determined nutrient—phosphate.

In temperate regions an annual cycle results from the alternation of the seasons, and this affects the physical and biological state of the sea. Air temperatures drop during the winter and cause cooling of the upper water layers and eventual establishment of isothermal conditions throughout the water column. The winter gales assist vertical mixing, which distributes the nutrients more or less uniformly throughout the water column. In spring increasing sunshine and length of days initiates the vernal outburst of diatoms, so that as a result of their rapid multiplication nutrients are removed from the water. This starts in the surface layers and extends to such depths as the penetration of light allows photosynthesis to proceed. At this stage the nutrients, even in the deeper layers of coastal waters, may be reduced almost to zero, and their absence may then limit any further plankton production. As the season progresses, increased air temperatures lead to a warming of the surface waters, absorption of thermal radiation eventually becomes so great that the heat cannot be effectively transmitted to the lower layers; a thermocline is set up, or layering is said to take place, in which the lower parts of the water column are to a large extent cut off from exchange of nutrients with the upper layers. In consequence, diatom production in the upper layer, or photic zone, is limited. This situation may persist throughout the summer months, although intermittent strong winds or unusual temperature conditions may destroy the thermocline and allow some mixing and return of nutrients to the upper layers and consequent renewed diatom growth. In some places a secondary autumnal diatom outburst is more or less a normal occurrence. During the summer period the plankton population initiated by the spring diatom outburst sinks, and regeneration begins to take place either on the bottom in shallow waters or in the lower parts of the water column in deeper waters. With the onset of winter conditions the water column gradually returns to the homogeneous state generally characteristic of the season, and mixing of the regenerated nutrients can take place. The general picture given above is sub-

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ject to modifications resulting from variations in climatic conditions from year to year. Thus Cooper (1933a; 1933b) found in the English Channel a main diatom outburst early in March, caused by a large amount of sunshine, and the unstable condition of the water allowed complete utilization of the nutrients; the average value of the phosphate was reduced to 0.04 mg. at. P/m³ from a winter maximum of about 0.42 mg. at. P/m³.

In general, nitrate and phosphate agree in this seasonal cycle, but since the chain of reactions required for the regeneration of nitrate is more complex and probably takes longer than in the case of phosphate, regeneration of nitrate after depletion may be more nearly complete than that of phosphate. Silicate values are commonly variable and in many cases difficult to interpret, but great increases during the summer indicate that a rapid resolution of the spring diatoms takes place; this resolution occurs at all levels. Calculations based on the consumption of the three nutrients strengthen the suggestion that silica is the most rapidly regenerated, and it may therefore be utilized more than once in a given season. Nitrate was even found to increase during a diatom outburst, and this again was explained by the long cycle of its renewal; although as a result of the length of its cycle nitrate is more likely

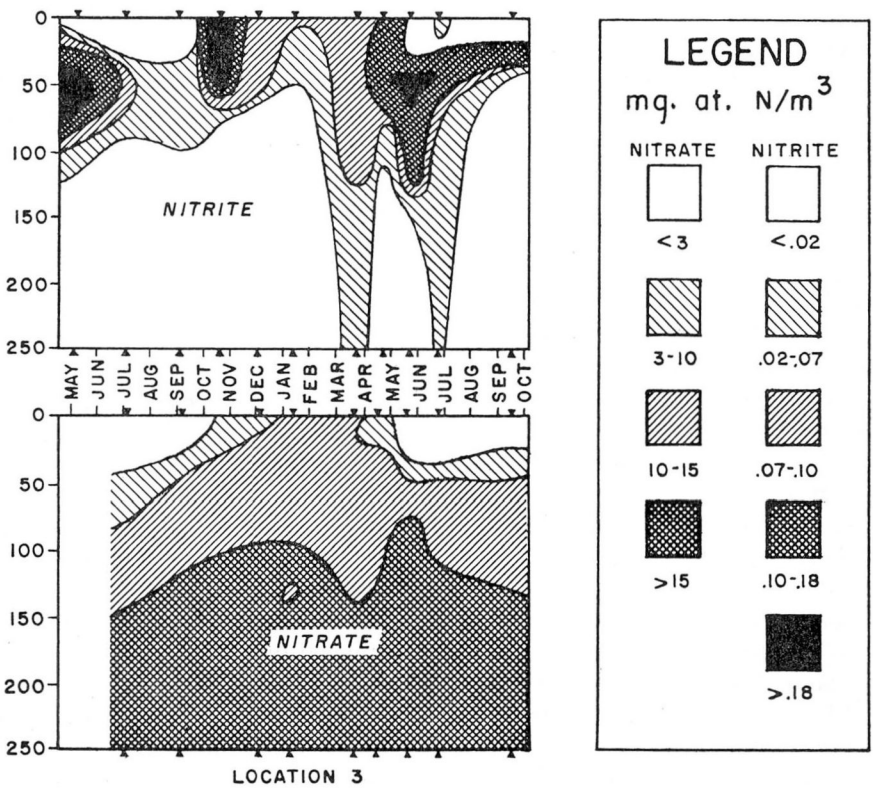

FIGURE 6.—*Seasonal variation in nitrite and nitrate, Gulf of Maine*
Note surface concentration of nitrite. From Rakestraw (1936)

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to be a limiting factor in growth than phosphate, bacterial action is considered necessary for both nitrogen and phosphorus regeneration, and the intermediate products in the nitrogen cycle, ammonia and nitrite, can be used directly by diatoms. Ammonia is generally found in the upper layers in winter (Cooper, 1933a), and this has been confirmed by Redfield and Keys (1938) in the Gulf of Maine. In shallower water, however, Seiwell (1931a) found increasing concentration in the layers near the mud. In general, high nitrite values are associated with high phosphate and nitrate values in the upper levels, but this is not true at lower depths; all three tend to disappear with the diatom outburst. Nitrite formation, like that of ammonia, appears to take place commonly in the upper layers (Fig. 6). This fact is confirmed for several regions, *e.g.*, Gulf of Maine (Rakestraw 1936), the Barents Sea (Verjbinskaya, 1932), and the Norwegian Fjords (Soot-Ryen, 1932); as pointed out by Redfield and Keys, utilization in the summer at the surface layers leads to a maximum value at intermediate depths (Fig. 7). As the inflection in the density curve moves down (with the establishment of the thermocline), the nitrite moves down as well; this supports the above suggestion, although there is vertical mixing in a less stable water column with the production of more uniform conditions. However, Atkins (1930a) and Cooper (1933b) found regeneration of nitrite in bottom water during the autumn, and the actual depths of the bottom and its character here again play an important part. Redfield and Keys (1938) point out that ammonia and nitrite are to some extent analogous to soluble organic phosphorus compounds in that they are intermediates in the oxidative cycle. In general, all three are correlated with one

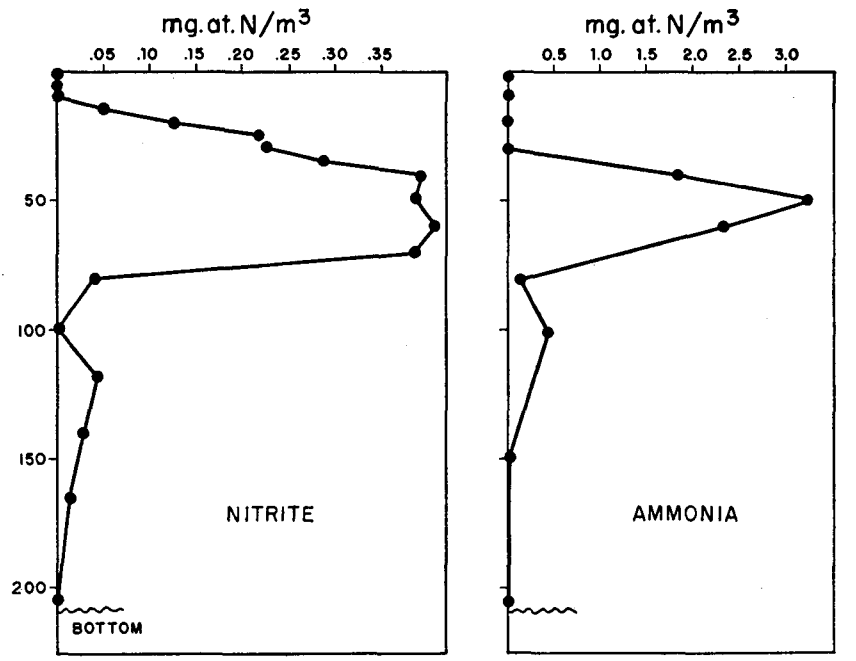

FIGURE 7.—*Vertical distribution of nitrite and ammonia in the Gulf of Maine in May*
Development of a maximum concentration at mid-depths. From Redfield and Keys (1938)

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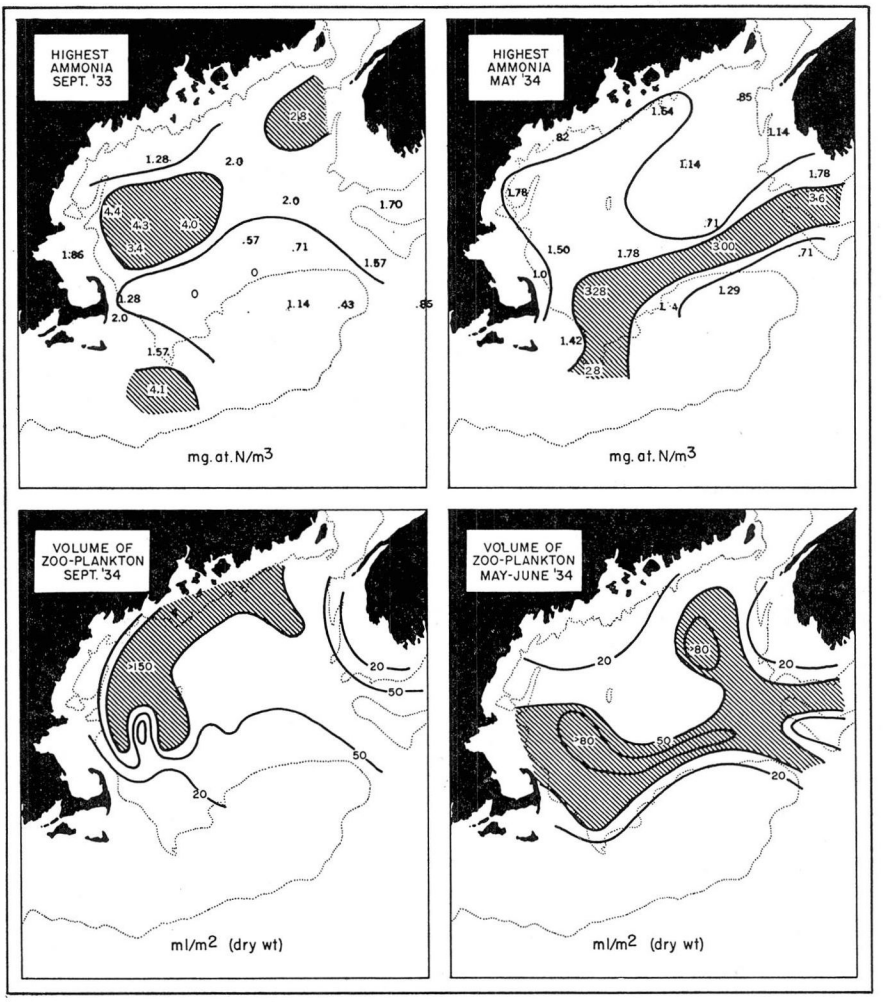

FIGURE 8.—*Highest concentration of ammonia* (NH_3-N) *in upper 80 meters, Gulf of Maine, compared with catches of zooplankton*

From Redfield and Keys (1938)

another, and their distribution and quantity mark the place and intensity of organic decomposition (Fig. 8).

In the Gulf of Maine at depths of 200–250 meters, the suggestion is that for all nutrients the cycle can be considered as a closed system within the water column, with little or no part played by absorption and release from bottom deposits. Armstrong and Harvey's work (1950) on the inorganic and total phosphorus content also suggests no marked deposition of detritus containing phosphorus in the English Channel, although in some areas of the Celtic Sea Cooper's (1951) results suggest that enrichment of the bottom water with phosphorus takes place over mud and ooze.

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Long-continued observations in the English Channel enabled Cooper (1951) to attempt to correlate some long-term nutrient changes with fisheries statistics. (*See* Harvey, 1950, for further estimates.) The phosphate available is measured by the winter maximum. From 1921 to 1928, this fluctuated around 0.65 mg. at. P/m^3, but from then onward it declined and is now of the order of 0.45 mg. at. P/m^3. Cooper (1948) correlated these changes, which are concomitant with a change from water containing *Sagitta elegans* to water containing *S. setosa*, with changes in the landings of fish in the area; the phosphate changes were closely paralleled by the landings of the spurdog (*Squalus acanthias*). Cooper suggests that, unless the dogfish markedly and directly favor phosphate-rich water, the correlation is a chain via the plankton to the prey of the dogfish. A similar correlation is noted between the bottom-feeding fish, such as rays and skates, and the phosphate values; there is a marked lag presumably, since the food chain from plankton production to bottom fauna takes longer to become effective. Meyer and Kalle (1950) made similar estimates with regard to the changes in the state of the Baltic fisheries and phosphate and suggest that the changed nutrient status over a period of years has had a differential influence in the different fisheries.

This pattern in northern temperate waters can be affected, not only by changes in the seasonal pattern from year to year, as indicated above, but also by any mass water movements into or out of the region or by local changes in current systems or bottom topography.

Thus Thompson and Robinson (1934) showed that the entire Puget Sound region is particularly rich in nutrient salts because of upwelling at the entrance to Juan de Fuca Strait and because of turbulence caused by fast currents in the many channels and islands in the upper reaches of the sound.

Nevertheless, the surface layers may become depleted. Thus, whereas in the photic zone off the shelf they found no nitrates 3.6 mg. at. Si/m^3 and 0.2 mg. at. P/m^3, at a depth of 2500 meters there were 37.36 mg. at. N/m^3, 250 mg. at Si/m^3, and 3.00 mg. at. P/m^3. Over the shelf as a result of upwelling the corresponding values were 16.0 mg. at. N/m^3, 39.0 mg. at Si/m^3, and 1.6 mg. at P/m^3 in the surface layers.

The dependence of silicate on water movements has also been stressed by Phelps (1937) in a 3-year study of silicate in Monterey Bay. The station sampled lay where the water was 900 meters deep, over a submarine canyon bisecting the bay. Only in the upper 200 meters was any marked annual rhythm found with a decrease from the average amounts in January and February, then a rise giving a maximum amount during late spring, followed by a decline in the winter. This increase is considered to be due to a strong period of upwelling (Skogsberg, 1936) and is marked by cold water in the upper layers. Phelps considers that the silicate decrease in the autumn is due to the gradual depletion of the rich upwelled water, and this depletion continues until the next occurrence of upwelling in the later winter and spring. In the winter the Davidson Current is banked up against the coast, and since it is largely surface water it results in low silicate gradients. Below 200 meters there was no regular sequence in the 3 years: in 1932 and 1934 there was no general trend, but in 1933 there was a marked increase in January and February and a subsequent decline. In general silicate increased with depth; further, there was a deep-water maximum gradient, a layer which was usually at 500–600 meters and in 2 months at 600–700 meters. Phelps points out that this gradient is similar in both amount and position with that recorded by "Carnegie" for other Pacific stations. No regular annual rhythm of plankton occurs in the region, but the large weekly fluctuations in the upper layers are considered to be due to biological changes either *in situ* or in the water brought into the area by currents.

The effects of water movement and topography can further be illustrated by reference to the results obtained by various workers in the North Sea, the Eastern Baltic, and the Barents Sea.

Phosphate distribution in the southern part of the North Sea has been investigated by Graham (1938) in connection with studies of the plankton and hydrology. The water in May is well mixed and in certain regions, *e.g.*, the "Inner Trawling Grounds," the surface phosphate is zero, but in the lower layers a reserve is present, and over shallow regions by upwelling and vertical circulation the surface water has some phosphate (Fig. 9). In June two large masses of phosphate-rich water reach to the surface, one in the southwest Dogger Swirl and one to the northwest over the Inner Trawling

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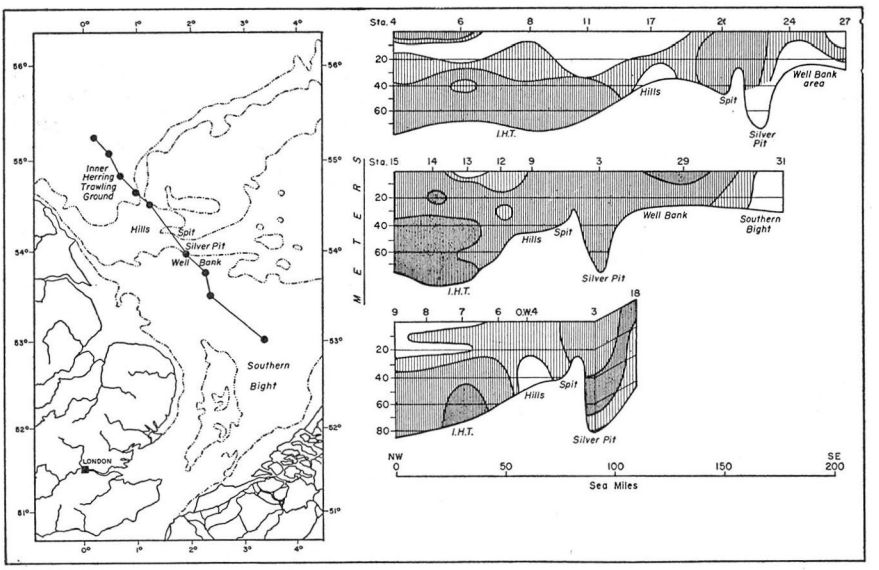

FIGURE 9.—*Distribution of phosphate in the North Sea at indicated stations*

Arbitrary units of concentration; density of cross hatching greater with increased phosphorus concentration; June, August, and September. From Graham (1938)

Grounds. Over the deeper water a permanent thermocline is being developed, and another thermocline, not permanent, occurs at the edge of the Dogger Bank. As the season advances the reservoir of phosphate on the Inner Trawling Grounds is maintained, with considerable vertical stability, and it is considered that the supply in the swirl is obtained from the lower layers of the Inner Trawling Grounds. Local concentration, formed during conditions of temporary stability and later scoured out, was also found in other areas (*e.g.*, the "Pit"). The origin of these phosphate patches in relation to the outflow of fresh water from the river Humber, and their effect on the influx of Atlantic water from the north are evidently related to the growth of the diatom *Rhizosolenia*, which in turn has a marked effect on the herring fishery. The greater the influx of nutrient-rich Atlantic water, the greater is the success of the diatom patches and the greater the effect on the herring fishing.

Seiwell (1931b), Thomsen (1933), and Kalle (1933) reported on the phosphate and nitrate contents of the North Sea and adjacent more northerly waters. In the southern North Sea Seiwell found homothermal conditions and mixing, even in summer, when the phosphate content was reduced almost to zero. North of the Dogger Bank, however, surface values increased from about 0.10 mg. at. P/m^3 near the Shetlands to 0.62 mg. at. P/m^3 in the Faroe Shetland Channel, dropping sharply over the Faroe Bank. These high values are considered to be due to mixing of several water masses: the East Icelandic Arctic Current, bottom water of the Norwegian Sea, and surface Atlantic water. Over the Wyville Thomson ridge there was a decrease in phosphate, and this is ascribed to vertical circulation. The phosphate content of waters south of Iceland was found to be correlated with the vertical stability; in general it is high in the deeps away from the shore. During the early months of the year Thomsen found the highest nitrate values (4.3 mg. at. N/m^3 and 0.66 to 1.14 mg. at. P/m^3) in western and northwestern parts, as a result of mixing in the vicinity of Orkney and Shetland (Figs. 10, 11).

In the Barents Sea nitrate and phosphate estimations, and later some total phosphorus estimations, were made by Kreps and his co-workers (1930; 1932; 1933). A drift current of Atlantic water flows around the North Cape into the Barents Sea and divides into several branches; the current moving along the Murman coast is designated the Murman current, and that which crosses the Kola meridian between lat. 75° and 76°N is known as the Franz Joseph branch. Cruises were made particularly along the meridians 33°30′E. and 38°E. In March there is no vertical layering in this region.

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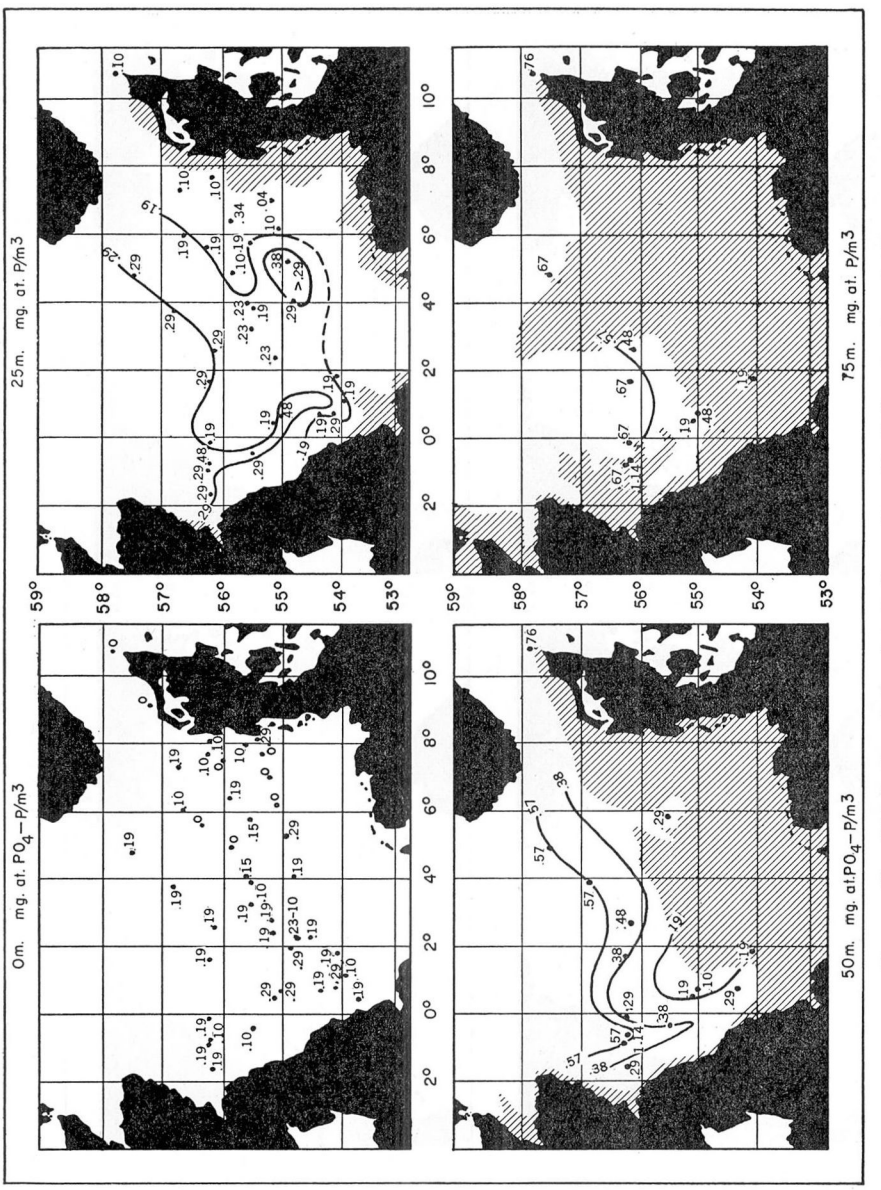

FIGURE 10.—*Distribution of phosphate in the northern North Sea at various depths*
Shaded portions indicate shallow water. From Thomsen (1933)

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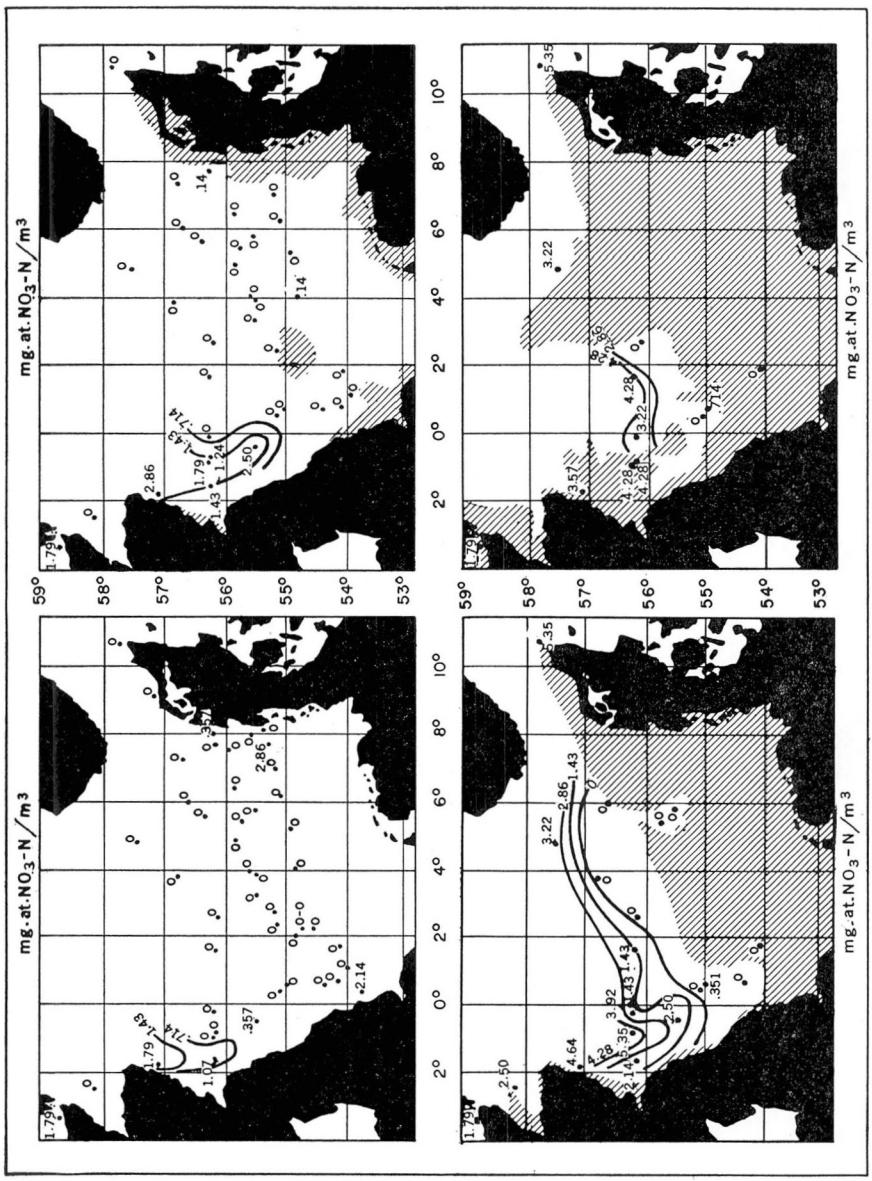

FIGURE 11.—*Distribution of nitrate in northern North Sea at various depths*
Shaded portions indicate shallow water. From Thomsen (1933)

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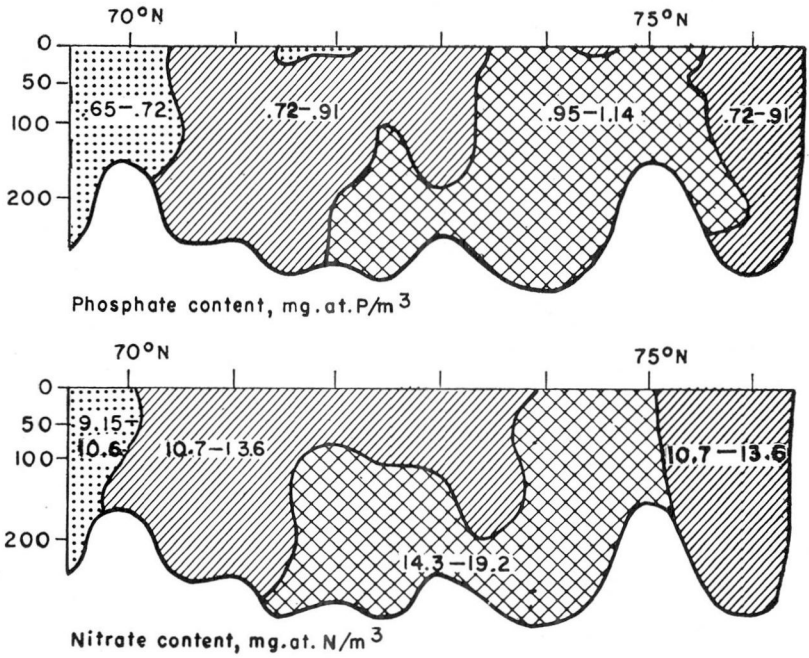

FIGURE 12.—*Phosphate and nitrate content along Kola meridian, 33° 30′ E., in March*

Showing uniform vertical conditions but intrusion of various water masses. From Kreps and Verjbinskaya (1930)

A complete mixing takes place during the winter, and both nitrate and phosphate are uniform throughout the water column. Relative concentrations change over the region, however, and the changes are similar for both nutrients (Fig. 12). The region could be divided into three parts: (1) an inshore region about 50 miles wide with phosphate below 0.76 mg. at. P/m³ and nitrate below 10.7 mg. at. N/m³; (2) a central region between 70°30′N. and 73°N. with a phosphorus content of up to 0.89 mg. at. P/m³ and nitrate up to 14.4 mg. at. N/m³; (3) a northern region, 73°30′ to 75°N., with more than 0.95 mg. at. P/m³ and nitrate greater than 14.4 mg. at. N/m³. The first region corresponds to the low-temperature—coastal-water belt and the central region to that of Atlantic water with a considerably higher temperature. The latter is penetrated and divided by a wedge of Arctic northern water with higher nutrient contents. In May, conditions in the regions of Atlantic water still resemble those of winter, with uniform nutrients, but the inshore and Arctic waters then show diatom production. The reason for this earlier diatom outburst in the cold Arctic water is not clear, but it may be due to the different diatom spores or possibly to a lower intensity of vertical mixing as a result of low surface salinities near the ice and consequent greater stability of the water. By September, diatom activity has reduced the nutrients in surface waters, and layering has taken place. At the same time, nutrients in the bottom water tend to increase as a result of the decomposing and sinking of plankton organisms: phosphate reaches 1.14 mg at. P/m³ and nitrate almost 22 mg. at. N/m³ over wide areas. By this time the plankton outburst has also occurred in the Atlantic water and has depleted the surface layers of nutrients. Over any plateau there is a tendency for nutrient-rich water to upwell. The strength of the influx of Atlantic water varies from year to year: in years of low influx a decrease in the over-all store of nutrients takes place, and this in turn affects the time and amount of the diatom outburst.

The same authors presented preliminary data (Kreps and Osadchih, 1933) on soluble organic phosphorus (which probably includes arsenic) in samples taken from the same region; their results indicate that its concentration varies both regionally and with depth. However, its distribution runs

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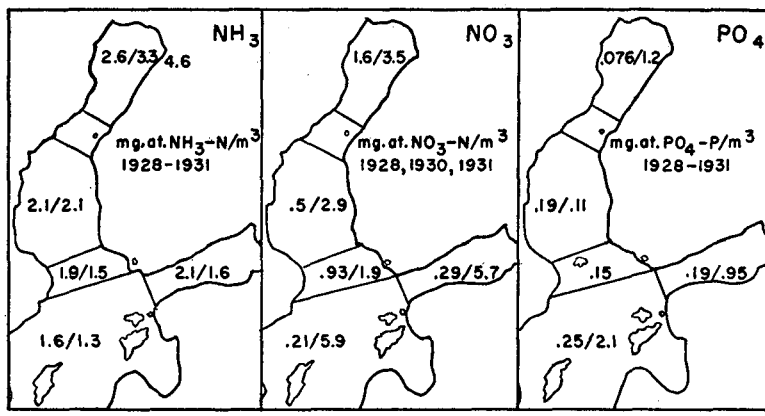

FIGURE 13.—*Ammonia, nitrate, and phosphate in the Baltic, Gulf of Finland, and Gulf of Bothnia*

Superscript indicates surface value; subscript indicates bottom value. From Buch (1932)

closely parallel to that of the inorganic phosphorus and is similar in quantity. It is at a minimum in summer and a maximum in winter; the authors assume that organic phosphorus accumulates in the lowest unsampled layers and is then uniformly distributed in winter. Complete conversion was slower than expected, since considerable amounts were also found in January.

Buch (1932) determined nutrient salts in the Gulf of Finland, the Gulf of Bothnia, and the north part of the Baltic; most of the samples he analyzed were surface and bottom samples (Fig. 13). High ammonia values were found, about 3.0 mg. at. N/m^3, in the north at both surface and bottom, decreasing to half this amount in the northern Baltic. Buch suggested that this ammonia is derived from affluents, particularly in the Gulf of Bothnia, where the organic matter from peat-containing waters sank and decomposed. Lower surface values of nitrate and phosphate, <1.0 mg. at. N/m^3 and <0.27 mg. at. P/m^3, were found, but high values up to 6.0 mg. at. N/m^3 and 0.95–2.16 mg. at. P/m^3 were obtained at the lower depths. In the Gulf of Bothnia, however, bottom concentrations were low, and it is considered that nutrient salts are brought in by bottom currents, whereas organic matter is carried out in surface currents; access of bottom currents to the Gulf of Bothnia is limited by the barrier of the Islands. (For further details on hydrography and topography of the Baltic *see* Chapter 24.)

Dakin and Colefax (1935) showed in a preliminary survey that in southern temperate inshore regions the sequence of events is similar to that in the northern hemisphere, but they indicated that after the diatom outburst had reduced the surface layers to zero, phosphate regeneration was much more rapid. After 3 weeks the surface values which had been reduced to zero during the diatom outburst were 0.8 mg. at. P/m^3, perhaps as a result of upwelling or the breakdown of the thermocline, or perhaps because of prevailing high temperatures.

WESTERN BASIN OF THE NORTH ATLANTIC

An account of the distribution of inorganic phosphate in this extensive oceanic area, based largely on data from "Atlantis" cruises but including some from "Meteor" (Wattenburg, 1927; 1933) and "Dana" (Thomsen, 1937) cruises, has been published by Seiwell (1935a; 1935b; 1935c). The differences observed in the vertical distribution of phosphate depend largely on variations in the thickness of the upper phosphate-poor layer and variations in both the position and value of the maximum phosphate concentration. For the porpuses of discussion it is convenient to adopt the subdivisions by which Seiwell divides the area.

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In the northeastern Sargasso Sea, between Bermuda and the 35th meridian (Fig. 14*a*), the surface content is 0.04–0.14 mg. at. P/m³, and this layer extends to depths of 350–550 meters, below which the phosphorus increases to a maximum of 1.35 mg. at. P/m³ at 800–1000 meters. A slight decrease in concentration takes place at lower levels, but over this region the phosphate maximum characteristic of the oceans is not so well marked. The thermocline begins at about 500 meters, and in winter the surface layer down to this depth is probably well mixed. During the summer, because of surface heating, a thinner temporary thermocline develops and increases the resistance to mixing. This thick layer is probably an accumulation of surface water and hence would be expected to be poor in nutrients.

In the mid-Atlantic along the 40th meridian, between 35°N. and the Equator (Fig. 14*b*), the phosphate distribution changes from north to south. The phosphate-poor layer extends to about 400 meters north of 26°N., but at 8°N. it is only 25 meters thick and increases to about 100 meters at the equator. The maximum is 1.35 mg. at. P/m³ at about 900–1000 meters north of 27°N. but twice this amount south of 27°N. At 2000 meters it is again about 1.35 mg. at. P/m³. A low value below the phosphate-poor layer is found in the northern part, which is possibly a different water mass. The depth of the thermocline varies along the section: in the north with the deep layer of phosphate-poor water it begins at not less than 200 meters from the surface and is not well marked off from the underlying water; in the south, where only a shallow phosphate-poor layer exists, it is better marked off and begins nearer the surface.

A section (Fig. 14, *e*, *f*) between Bermuda and Chesapeake Bay crosses the principal American coastal thermal convergence. East of the convergence surface values are low, but to the west toward the continental shelf seasonal variations are well defined, and the conditions described under coastal waters begin to pertain. However, as the conditions in the spring are also associated with a westerly displacement of the convergence by a consequence westerly inflow of phosphorus-poor water, the spring diatom increase may not be entirely responsible for the reduction of phosphate concentration in the surface layers which takes place at this sesaon. The phosphate-poor layer (<0.22 mg. at. P/m³) extends to 400–500 meters east of the convergence but only to 100 meters west of it. The maximum (1.35–1.62 mg. at. P/m³) is not well defined, and it lies much deeper to the east of the convergence.

A section between Nova Scotia and Bermuda (Fig. 14*g*) also crosses the principal convergence, as well as two convergences which possibly represent a large cyclonic vortex; the phosphate-poor layer in all cases rises at the convergences. Thus, the phosphate-poor layer extends to a depth of 200–400 meters between Bermuda and the first convergence, to 30–40 meters between the first and second, to about 340 meters between the second and the thrd, and decreases to 100 meters after passing through the third.

The maximum is not usually well defined from the underlying water (1.03–1.26 mg. at. P/m³), but the position where the vertical gradient ends above the deeper water is lower between the convergences.

The regional variation at various depths is shown in Figure 15. The surface values are usually between 0 and 0.14 mg. at. P/m³, and any variations are probably due

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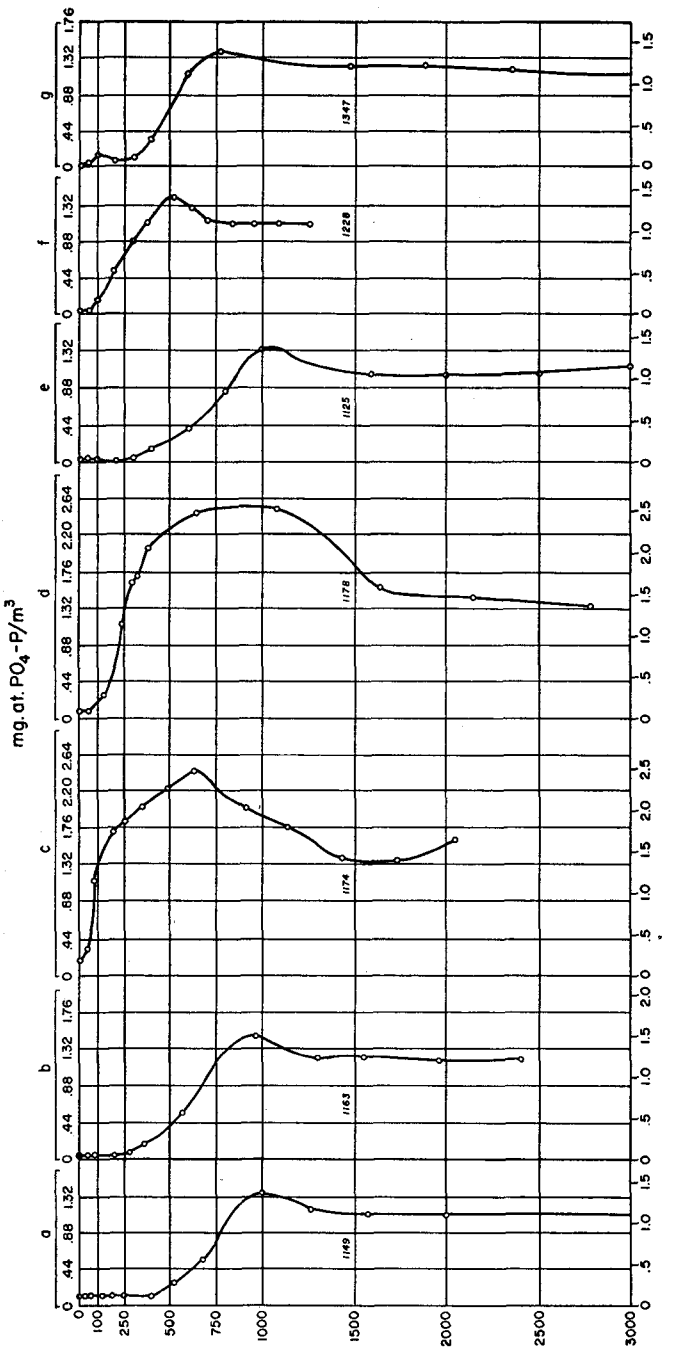

FIGURE 14.—*Vertical distribution of phosphate in the northwestern Atlantic*
(a) Northern Sargasso Sea; (b) along 40th meridian, north of 27°N.; (c) the same, at about 8°N.; (d) the same, at the Equator; (e) along a line from Bermuda to Chesapeake Bay, east of convergence; (f) the same, west of convergence; (g) between Nova Scotia and Bermuda at a position between second and third convergence. From Seiwell (1935)

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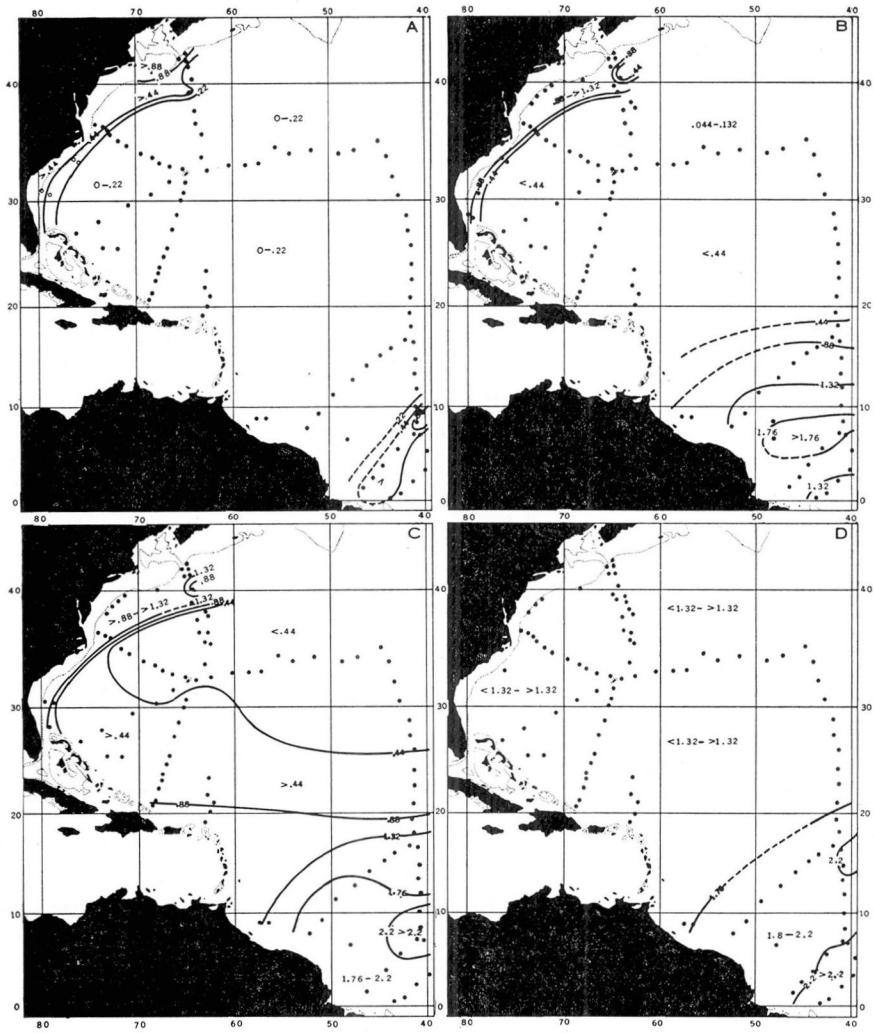

FIGURE 15.—*Horizontal distribution of phosphate in the northwestern Atlantic* (A) at 100 meters; (B) at 250 meters; (C) at 500 meters; (D) at 1000 meters. From Seiwell (1935a)

more to local and seasonal changes (discussed below) than to regional differences. At 100 meters the phosphate concentration is less than 0.22 mg. at. P/m³ throughout the greater part of the area, and there is no doubt that this is the result of the mixing of this somewhat unstable upper layer of water, although in the extreme western and southeastern regions it rises to 0.86 mg. at. P/m³, possibly as a result of restraints to vertical mixing. At 250 meters the concentration is less than 0.43 mg. at. P/m³ in the entire central region. The coastwise convergences are clearly marked at this depth, and here an increase to more than about 1.35 mg. at. P/m³ takes place. The phosphate values at the 500-meter level are higher, but the general

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distribution is very similar to that observed at the 250-meter level. At 1000 meters the phosphate concentration is approaching the uniformity characteristic of the deeper layers: it is 1.35 mg. at. P/m^3 north of 25°N. and 2.70 mg. at. P/m^3 south of this line; in deeper waters it is even more uniform, ranging only from 1.35 to 1.76 mg. at. P/m^3.

The presence of a maximum layer of phosphate in the deep water (this is also true of nitrate) has been indicated for all the regions discussed; it is present in all the oceans. Seiwell and Seiwell (1938) suggested that this oxygen depletion arises as a result of the consumption of oxygen in the oxidation of organic matter derived primarily from the surface layers; the nutrient accumulation takes place at the level where the decomposing organic matter has the same density as the water. Active regeneration and consequent oxygen consumption take place therefore in this layer, and the renewal of oxygen is assumed to depend on horizontal circulation. However, Redfield (1942) pointed out that this hypothesis does not explain why the depth of the oxygen minimum varies so greatly from place to place, nor does it explain its relation to the particular nutritive conditions at the sea surface where the particulate matter available for regeneration arises. In many places, the tropics for example, the surface layers are very poor in plankton. Redfield therefore considers the first few hundred meters to be the source of the plankton and also considers that the layers of maximum phosphate concentration occupying the temperate and tropical South Atlantic are derived in part from isentropic movement of the water from the subsurface of the Antarctic convergence. This water carries a residuum of inorganic surface phosphate and is supplemented by regenerated phosphate obtained by oxidation and decomposition of organic matter during its passage northward; its oxygen content is consequently low. In the northern Atlantic Ocean the maximum phosphate and minimum oxygen layer is derived chiefly from water which is at the surface in 50°N. Lat. These mass changes are due to mixing processes —along surfaces of constant potential density—which may easily occur even in the absence of directional flow. In the tropical regions, however, between 20°S. and 25°N. Lat., it is difficult to explain the observed results without assuming a contribution as a result of active sinking and decomposition, as suggested by Seiwell and Seiwell, down to 600–800 meters depth. The great difficulty—the barren character of the surface layers in the middle latitudes where little material is available for direct addition—is therefore obviated in this hypothesis. Major decomposition takes place either in the subsurface waters of the polar convergences or under the Equatorial Current in the tropical latitudes.

There is a comparatively small amount of data for nitrate, and even less for silicate, for this region. Existing data show that the nitrate concentration closely parallels that of phosphate. Available results show that silicate distribution in depth does not follow that of the other nutrient elements. There is no marked intermediate maximum, and the concentration increases with increasing depth.

ANTARCTIC OCEAN

As a result of the work of the Discovery Committee there is a considerable amount of data on the plankton, the hydrographic features, and some of the nutrients in

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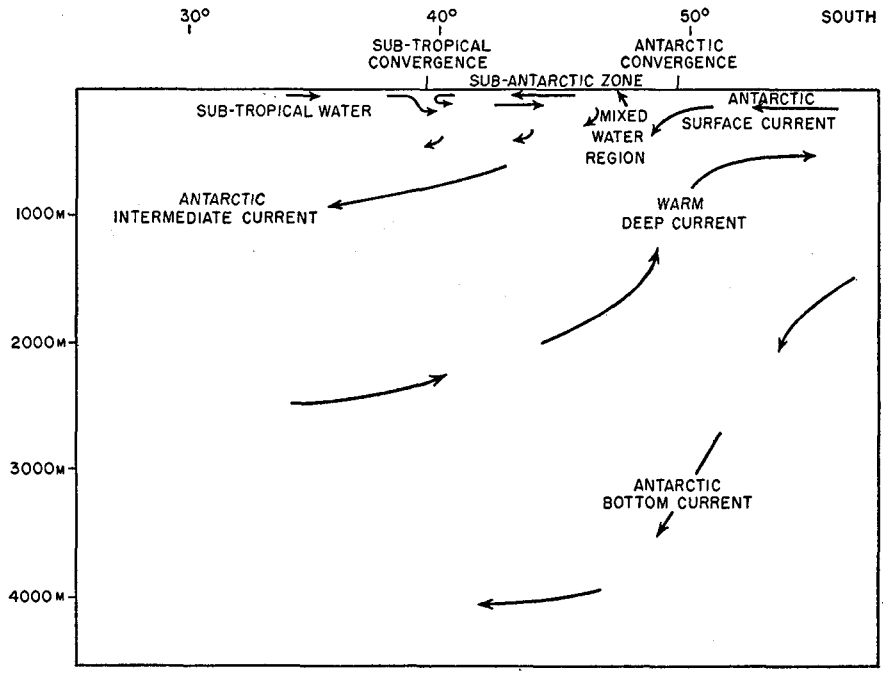

FIGURE 16.—*Vertical circulation in the South Atlantic*
From Deacon (1937a)

the Antarctic seas and the southern oceans. An account of the phosphate and silicate concentrations has been given by Clowes (1938).

It is first necessary to consider briefly the chief water layers of the Antarctic and their movement around the continent. (For a detailed account, *see* Deacon, 1933; 1937a; 1937b). All around the Continent surface water spreads northward in a shallow layer (Fig. 16) until it reaches the region known as the Antarctic convergence, where it sinks below the surface layer of the sub-Antarctic water. In a region of mixing, 100–200 miles north of the convergence, the Antarctic surface water becomes mixed with the warmer surface and subsurface waters of the sub-Antarctic zone and eventually forms part of the Antarctic intermediate current which also has a northerly component. Underneath the Antarctic surface water is warm deep water, with a southerly component (that is, flowing toward the pole); this water lies at a great depth north of the Antarctic convergence and flows almost horizontally until it approaches the Antarctic zone, where it rises quite steeply. Below this warm deep water is Antarctic bottom water with a northerly component, over which the former climbs steeply. North of the Antarctic convergence and south of the subtropical convergence, the upper part of the water column consists of sub-Antarctic water, a much thicker layer than the Antarctic surface water; it also includes a subsurface current and the Antarctic intermediate current.

The winter values of phosphate (2.70 mg. at. P/m^3) and silicate (50–60 mg. at. Si/m^3) are extremely high in the surface zone at the ice edge. These nutrients, either free as inorganic ions or, par-

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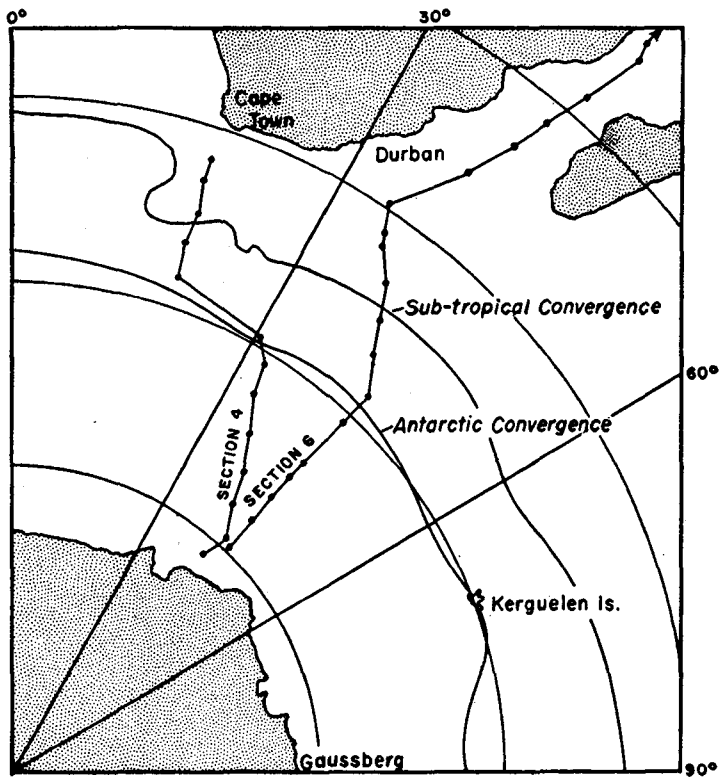

FIGURE 17.—*Location of the sections shown in Figures 18–21*
From Clowes (1938)

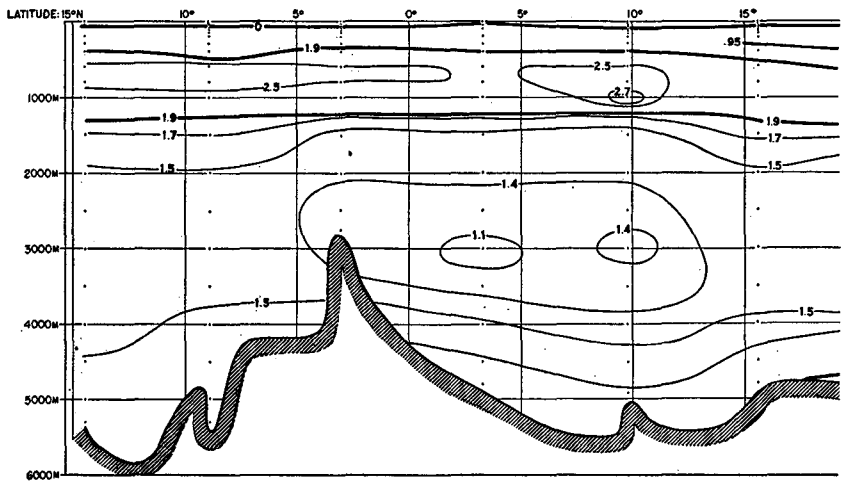

FIGURE 18.—*Distribution of phosphate in western part of the South Atlantic along 30°W. from 57°36′S. to 14°27′N.*
(*See* fig. 17.) From Clowes (1938)

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ticularly after the diatom outburst in spring and summer, as living and dead organisms are being continually drained away from the southern region by the Antarctic surface water and the Antarctic bottom current, both of which have northerly components. (*See* Fig. 16.) If the Antarctic zone is not to be denuded of nutrients some return process must exist, and it is evident from Figure 16 that this must result largely from the southward-flowing warm deep current. The details of this return vary from region to region, and they may be illustrated by reference to some typical sections.

In the western part of the South Atlantic Ocean (Fig. 17), north of the Rio Grande Ridge (about 35°S.), maximum phosphate is always found in the Antarctic intermediate water; the warm deep water contains less phosphate; thus, the latter, *per se*, cannot be the source of the high phosphate concentrations in the Antarctic zone. Phosphate is added to the warm deep water south of the Rio Grande Ridge, and the source of this phosphate must lie in the rich plankton, carried from the Antarctic surface waters, which decomposes as it sinks into the bottom of the sub-Antarctic layer. The decomposition of plankton appears to be greatest between 38°S. and 43°S. and between the northward-flowing sub-Antarctic and Antarctic intermediate waters and the southward-flowing deep warm waters; in this region much vertical mixing takes place, so that phosphate passes into the mixed water present in the upper layers of the southward-going warm deep current.

Section 4 of Figures 18 and 19, laid between the ice edge and Cape Town, shows clearly the phosphate cycle in this region; phosphate leaves the region in the surface water, which sinks at the Antarctic convergence, and in the bottom water. However, here the intermediate current, even at 38°S. with 2.70 mg. at. P/m³, is depressed much deeper by the bulk of subtropical water brought in by the Agulhas Current. Upwelling toward the coast of South Africa leads to some loss from the Antarctic intermediate water, but the large amounts of phosphate in 48°S. in the upper parts of the southward-going warm deep current indicate transfer and return; the major portion again returns in the upper layers of the warm deep water.

Between the Antarctic and the western part of the South Indian Ocean, the rise in bottom topography, with the interposition of the Prince Edward-Crozet Ridge, on which stand the Crozet Islands, prevents to some extent the loss of phosphate from the Antarctic zone in the bottom water. In the far south this bottom water has a phosphorus content of about 2.84 mg. at. P/m³, whereas north of the cross ridge at 45°S. it is only 2.57 mg. at. P/m³ (Fig. 20). East of the Crozet Islands and west of Kerguelen, however, a large gap between the Cross Ridge and the Kerguelen-Gaussberg ridge must allow the passage of bottom water northward.

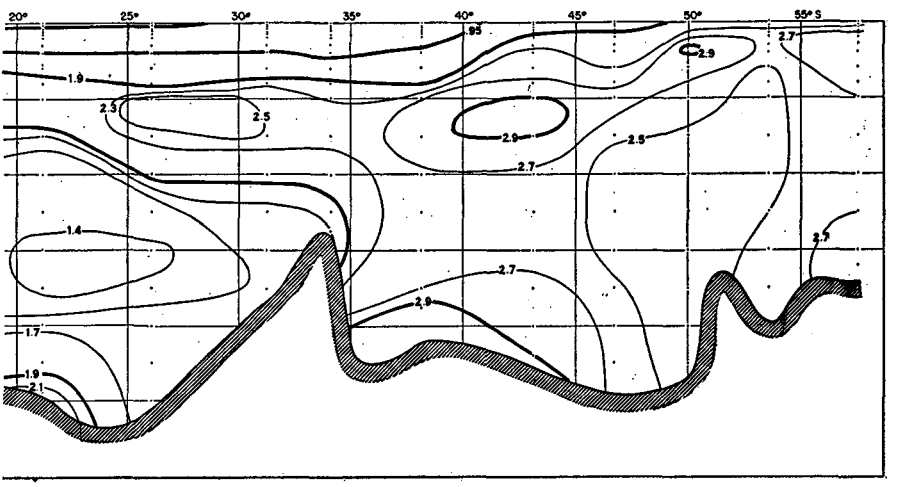

FIGURE 18.—(*continued*)

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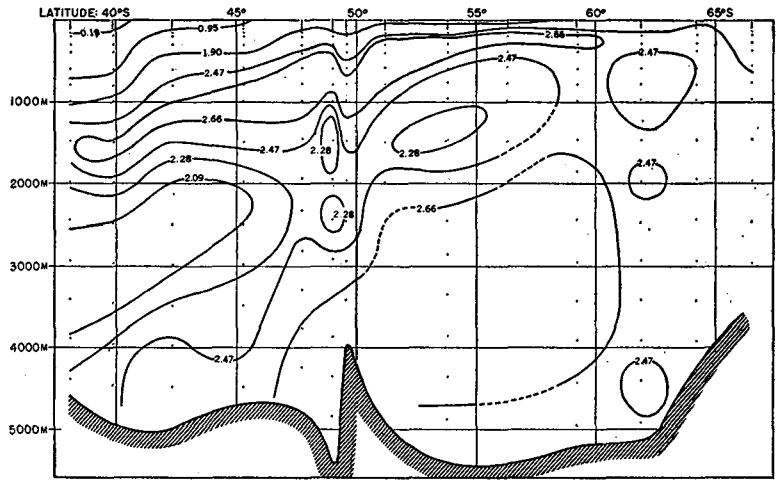

FIGURE 19.—*Distribution of phosphate along a section from Cape Town tothe ice edge in 66°30′S., 42°30′E., north of Enderby Land*

Discovery section 4. (*See* Fig. 17) From Clowes (1938)

A further complicating factor in this region is the fact that in contrast to the North Atlantic deep water (Fig. 17), the North Indian deep water has a very high phosphate content; thus, between 40½°S. and about 29°S. the Antarctic intermediate water has a greater phosphate content than the warm deep water, but north of 29°S. the warm bottom water has the greater phosphate content. It is not certain how far south the last traces of North Indian deep water extend in the upper layers of the warm deep water, which is mainly of North Atlantic origin south of 20°S. However, the southward-going deep water rises steeply toward the surface on the northern side of the Atlantic-Indian cross ridge and also continues to rise to the Antarctic convergence. On the southern side of the ridge phosphate is transferred to its upper layers and carried back to the ice edge.

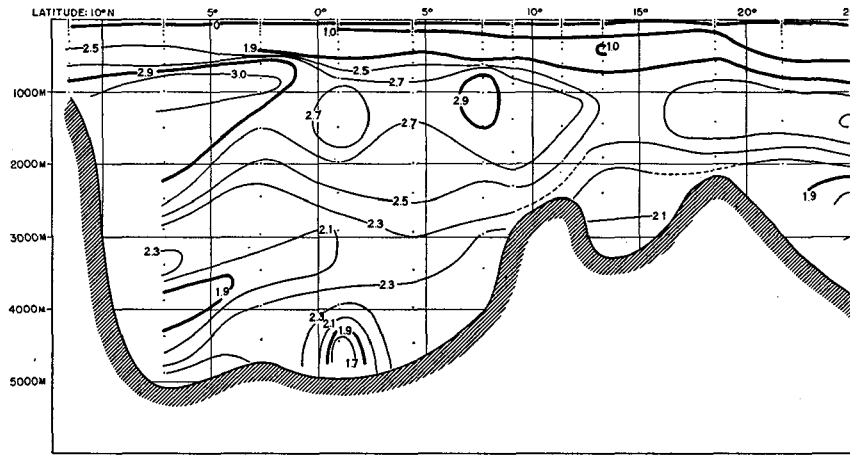

FIGURE 20.—*Distribution of phosphate, Antarctic to western Indian Ocean, in 34°–52°E. from the ice edge in 64°38′S. to 11°32′N.*

Discovery section 6 (*See* fig. 17.) From Clowes (1938)

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The silicate cycle is different from the phosphate cycle in that regeneration probably takes place more rapidly, so that in general the silica taken up into the organisms is not carried so far from the region of uptake before being returned in the form of silicate. Unlike phosphate, silicate is invariably at a maximum in the Antarctic zone; it is lost to the zone partially in the surface currents, as with phosphate, but chiefly in the Antarctic bottom water, and its return is again effected by the warm deep water by mixing at its upper and lower boundaries; however, since the greatest amount is carried north by the bottom water, the greatest amount is returned to the south in the lower levels of the warm deep water.

Thus, in the South Atlantic Ocean the surface water sinking at the Antarctic convergence carries a silicate content of about 42 mg. at. Si/m^3 as free silicate and some bound silica. Silicate is steadily lost to the upper layers of the deep warm water, but even at 4°N. the silicate content of the intermediate water is still 16.7 mg. at. Si/m^3. The bottom water has a content of 84 mg. at. Si/m^3 in the south, and this is gradually transferred by mixing to the lower layers of the warm deep current. As with the phosphate cycle, interposition of ridges and the intrusion of other currents complicates the picture. The cross ridge hinders northward transport of silicate as it does phosphate, and in the South African section upwelling from the intermediate current, which in this region at 38°S. contains as much as 100 mg. at. Si/m^3, must be lost to the continental shelf of South Africa. Again the North Indian deep water has a high silicate content compared with the North Atlantic deep water, so that up the East African coast the warm deep water has a greater silica content than the Antarctic intermediate water.

In the Pacific section the position is more complicated by the complex nature of the deep currents, and here the currents—intermediate, warm, and bottom—are not so well separated by distinct boundaries. Extensive mixing no doubt takes place. According to Deacon a large part of the current which flows southward between 1500 and 2000 meters, north of 50°S. in the more central part of the ocean, sinks between 50° and 55°S. to mix with the bottom water—so that silicate will be carried northward with the bottom current. The volume of intermediate water carried back to the south by the warm deep current in this region is considered to be large.

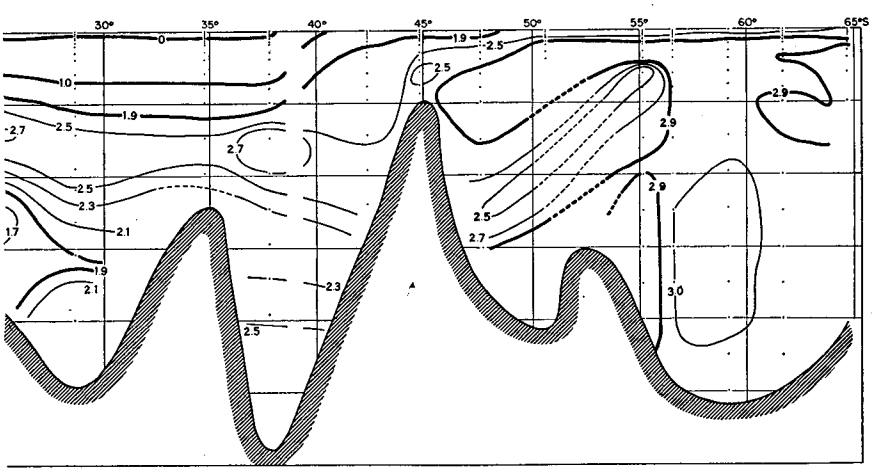

FIGURE 20.—(*continued*)

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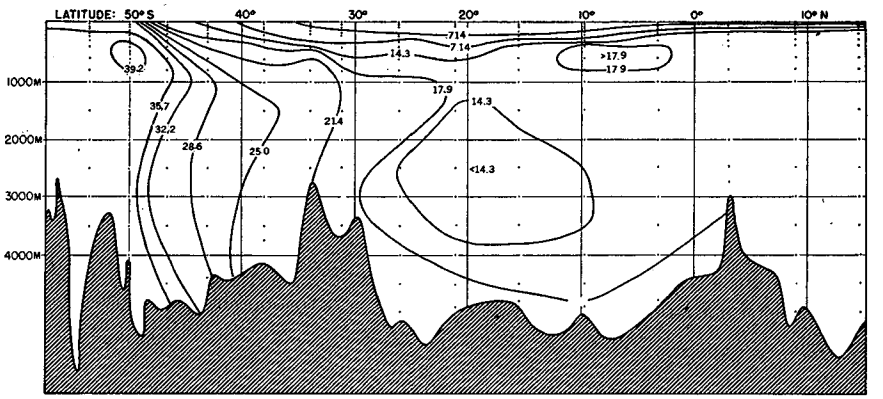

FIGURE 21.—*Distribution of nitrate (NO_3-N) in a section from Weddell Sea northward along 30°W., across Antarctic and subtropical convergences*
From Deacon (1933); *See* Figure 17.

There is less information on nitrates in this region because of analytical difficulties, but Deacon (1937a) has given a section shown in Figure 21.

The nitrate cycle is considered to be similar to the phosphate cycle, with high concentrations in the south (39.3 mg. at. N/m³), and in this section decomposition takes place principally south of the Rio Grande Ridge. Deacon remarks on the absence of nitrite from the deeper waters where decomposition is taking place, and this is presumably due to the rapid turnover from the first decomposition product, namely ammonia. Nitrite up to to 0.57 mg. at. N/m³ may be found in the surface, but once a discontinuity appears, preventing vertical mixing, more is found in the deeper layers.

NORTHERN INDIAN OCEAN

Reference has already been made to the high values of phosphate in the deeper parts of the northern Indian Ocean. Further widely scattered results for the northern Indian Ocean and for the water around the East Indies were obtained from the "Dana" survey (Thomsen, 1937). At some stations both nitrate and phosphate estimations were made, and the two nutrient values are closely parallel. However, the accuracy of the results is not high.

Between Madagascar and the southern tip of India, surface values were low—in many cases zero for both nutrients. Values increased steadily across the transition zone, the bottom of which lay at 400–500 meters off India, with 3.08 mg. at. P/m³ and about 36 mg. at. NO_3-N/m³ (Fig. 22). Further southwest, however, toward Madagascar, the surface layer of nutrients is in general thicker, and the transition layer is thicker (Fig. 22). A maximum nutrient layer is not evident everywhere, but this may be due to the lack of detail in the experimental results. The deep waters are fairly uniform, with 3.21 mg. at. P/m³ and 36 mg. at. NO_2-N/m³ off Madagascar and 3.31 mg. at. P/m³ and a similar quantity of nitrate off southern India. Near the East Indies the nutrient gradient is very steep (Fig. 23).

PACIFIC OCEAN

Particularly as a result of the "Carnegie" work there is a considerable amount of data, largely on phosphate, for the Pacific Ocean; the following summary is based on the papers of Graham and Moberg (1944). (*See* also Sverdrup *et al.*, 1944, for an account of the physical oceanography.) As in the Atlantic Ocean, distribution can

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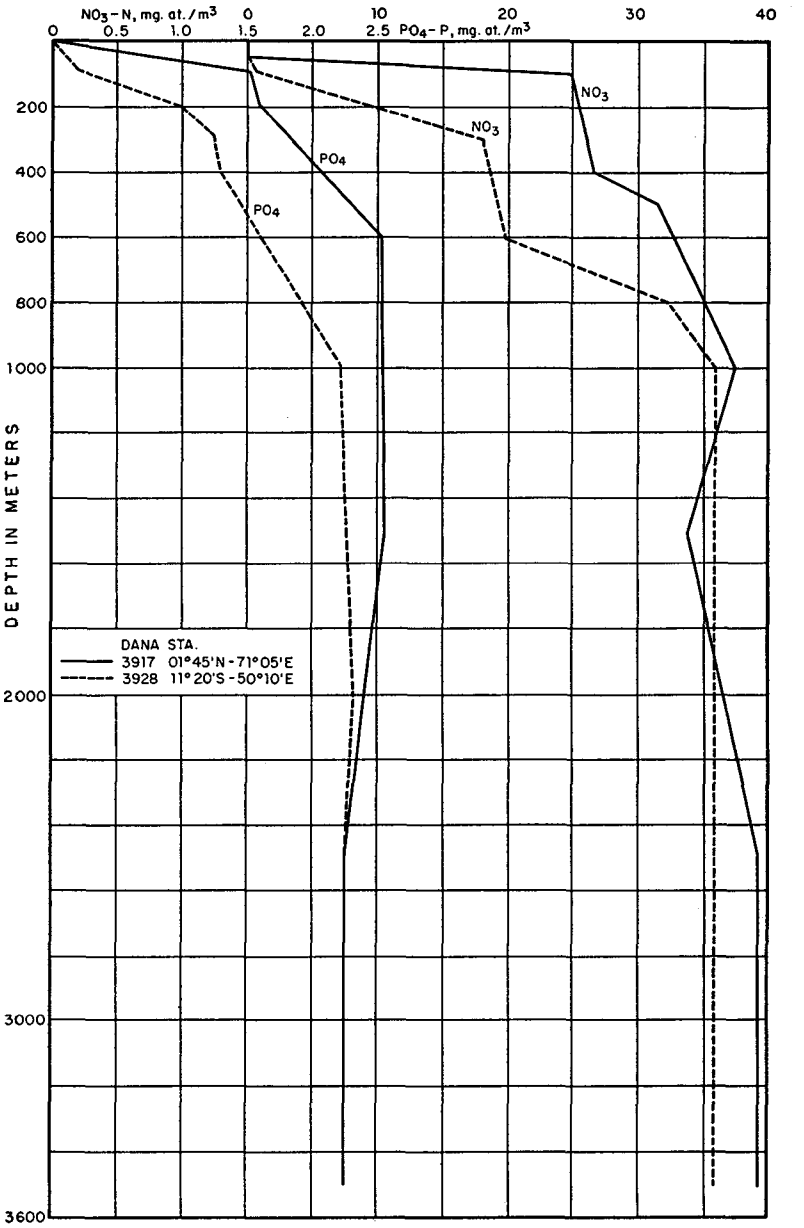

FIGURE 22.—*Distribution of phosphate and nitrate with depth in the Indian Ocean*

Off northern tip of Madagascar (Dana Station 3928) and southern tip of India (Dana Station 3917). From Thomsen (1937)

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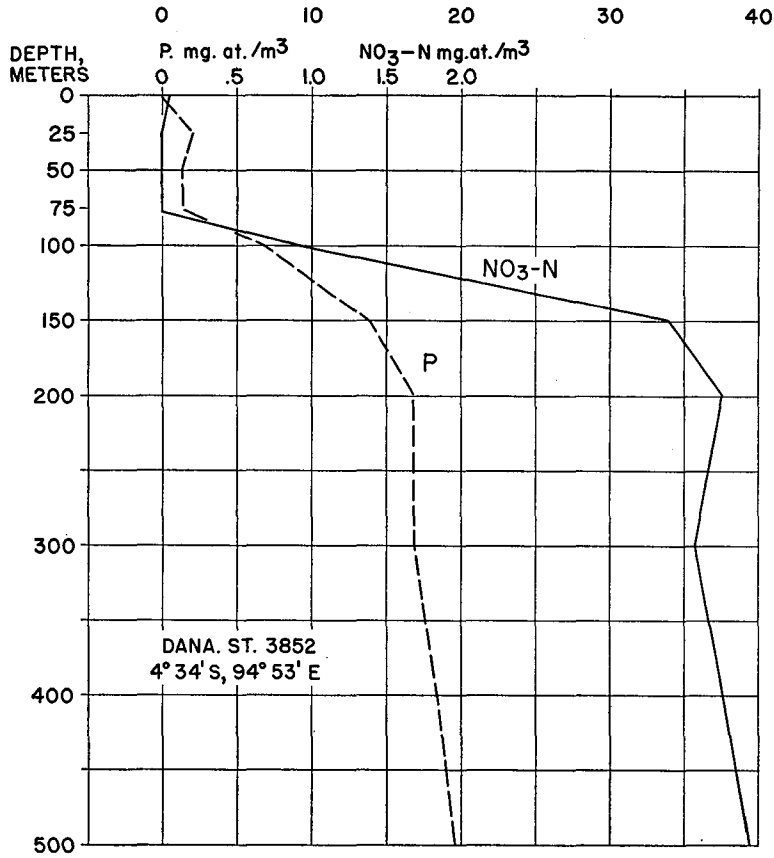

FIGURE 23.—*Distribution of phosphate and nitrate with depth off Sumatra*
Dana Station 3852, a little southwest of Sumatra. From Thomsen (1937)

be considered under the headings of surface values, the transition zone (where the phosphate values increase with depth), and the lower zones with high nutrient concentration. The concentrations of nutrient in these zones and the depths of the zones both vary from region to region, and the differences are intimately bound up with the current systems of the ocean.

At all stations north of lat. 40°N. the phosphate content of the surface waters is markedly high, usually ranging from 0.35 to 2.11 mg. at. P/m^3. An exception is station 117, just east of Japan. In the northwest Pacific there is a southward-flowing current which apparently originates in the Bering Sea, and the abundance of surface phosphate is no doubt due to the considerable mixing that takes place throughout the year. Apparently this phosphate-rich water flows southward until diverted eastward by the north Pacific West Wind Drift (commonly called the Japan Current). This drift carries the phosphate-rich water eastward and then southward by the California Current, which is formed in the area where the West Wind Drift

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reaches the Aleutians. In the area north of 40°N. there is considerable mixing due to convection during the winter months.

In this region the surface zone of phosphate was extremely thin. Where the surface phosphate zone was absent, the transition zone was considered to begin at the surface, as at Station 120 (Fig. 24), and it was thick, except at the station off the Aleutian Islands. The rich phosphate content of the upper layers in this region, 1.46–3.24 mg. at. P/m^3, is the combined result of the partial elimination of the temperature gradient and the addition of bottom water from the Bering Sea. The zone of maximum phosphate varies in this region; it is at higher levels in the central part and deeper in the

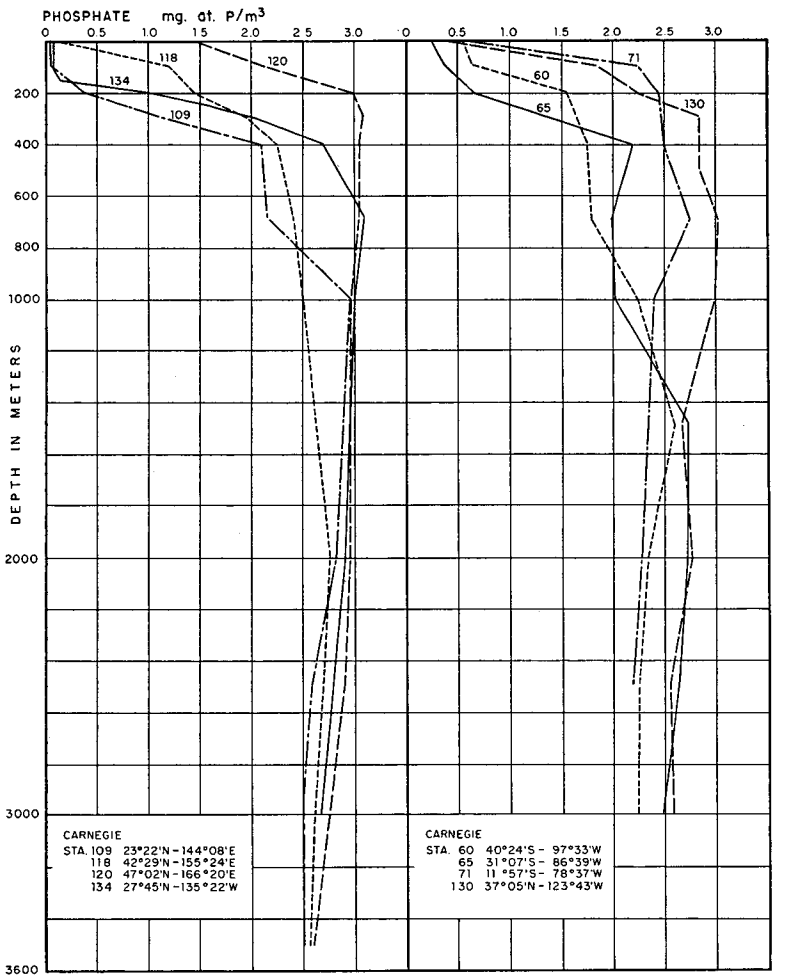

FIGURE 24.—*Left: Depth distribution of phosphate at various Carnegie stations in the north, central, and west Pacific*

Right: Depth distribution of phosphate at various Carnegie stations in the eastern Pacific

Showing different development of surface and transition zones. Note position of surface and transition layers at stations 60 and 65 and the effect of upwelling at stations 71 (off the coast of Peru) and 130 (off California coast). From Graham and Moberg (1944)

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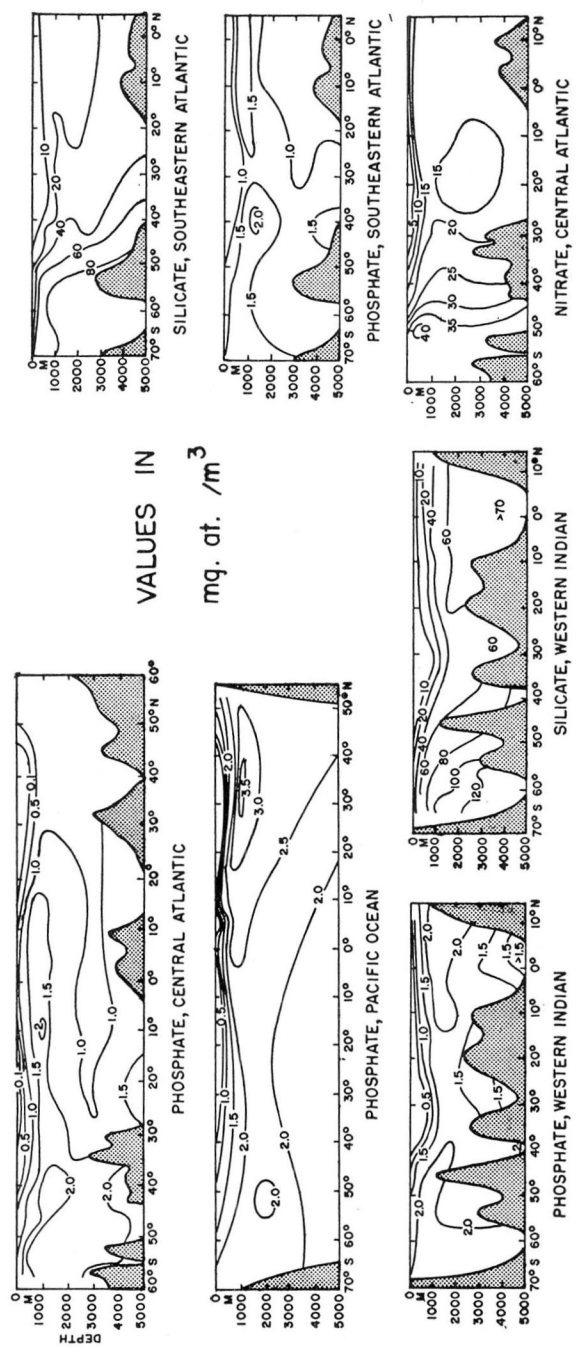

FIGURE 25.—*Distribution of nutrients in various oceanic regions*
From Sverdrup, Johnson, and Fleming (1942)

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eastern and western parts, where it occurs at depth of 1000–2000 meters. (Compare stations 120 and 118 in Figure 24.) The deep-water values are high, as is usual in the Pacific; they reach 3.92 mg. at. P/m^3 in the central region and not lower than 3.38 mg. at. P/m^3 elsewhere.

Between lat. 10° and 40°N., with the exception of a few stations near the California coast, the phosphate content was extremely low, nowhere exceeding 0.15 mg. at. P/m^3 and commonly half this quantity; further, these low values extended to 100 meters or more, as can be seen from station 134 (Fig. 24). The reasons for this paucity of phosphate seem to lie in two hydrographical features: first, a steep density gradient results in little vertical turbulence; second, there are no well-developed current systems except near the coasts of California and Japan. The relatively high phosphate values off the California coast (Fig. 25, station 130) may be attributed to upwelling from intermediate depths and possibly also to transport of phosphate-rich water from the north by the California Current.

The transition zone is relatively thick here, so that the increase in phosphate with depth is relatively slow. North of Hawaii and in the Western Pacific between Guam and Japan the transition zone extended to extremely low levels—even to 1000 meters (Fig. 24, station 109). The actual content of the transition zone was variable but nowhere reached the high values of the more northern regions—varying from 1.13 to 1.55 mg. at. P/m^3. As the California coast is approached, in addition to a gradual thinning out of the surface layer already mentioned, the transition zone narrows, and the phosphate content is greater (*see* Fig. 25, station 130) just off the coast. Again values in the deep water are high, reaching 6.56 mg. at. P/m^3 in waters just north of the Hawaiian Islands.

South of lat. 10°N. the surface phosphate content is in general intermediate between the above extremities. High values off the coast of Peru (Fig. 24, station 71) are due to upwelling, and the possible influx of nutrients in the Peruvian Current. (Gunther, 1936). However, the moderately high values in the tropical regions westward off Peru cannot be attributed to the westward flow from the Peruvian coast, because there is not a regular decrease in passing westward. The great variability in this tropical region is due to the very complicated hydrographical conditions, for Sverdrup has shown that the currents in southern tropics at depths of 200 meters are irregular and intermittent and that eddies are formed which bring about mixing of water at various depths.

Carnegie sections V and VIII cross the Equatorial Current and countercurrents; the former runs from the Samoan Islands northeast, and the latter runs from the Samoan Islands northwest. In these regions both the surface and transition zones are relatively thin, particularly in the vicinity of the countercurrent. Since the effects of high insolation would normally result in a thick surface layer as well as a transition zone and cause a low concentration of phosphate in the upper layers in the Equatorial region, the effects of circulation far outweigh the effects of insolation. The explanation is no doubt to be found in horizontal water movements, which according to Sverdrup produce eddies and possibly other forms of vertical circulation.

The line of stations from Samoa to Peru (Carnegie section II) also lies in the tropics, and here the transition zone in general extends to somewhat greater depths, since the stations are probably in a region of less disturbed hydrographical conditions. In general, both the surface and transition zone deepen toward the west; off the Peruvian coast the lower boundary is at 75 meters, but at long. 120°W. it reaches 650 meters. The narrow transition zone in the eastern part of the section is probably caused, in part at least, by the Antarctic intermediate current.

In the southeastern Pacific (Carnegie section X) the surface values increase from northwest to southeast (station 51 to station 60), and the surface layer and the depth of the transition zone increase as the distance from the shore is increased. (Compare stations 71, 60, and 65 in Figure 25).

Comparison of the deeper waters (for example, 2000 meters) over the whole area shows considerable variation from station to station, but any distinct progressive change is difficult to discern. There is in general, however, an increase from south to north: the mean values are 3.15 mg. at. P/m^3 between lat. 20° and 40°S. and 3.71 mg. at. P/m^3 north of 40°N.; this is in accord with the origin of the deep water in the Antarctic and with the fact that it is slowly moving toward the north.

SUMMARY OF REGIONAL VARIATIONS IN THE OCEANS

To understand better the relations between the different regions it would be necessary to discuss more fully than is here possible the numerous variables affecting the

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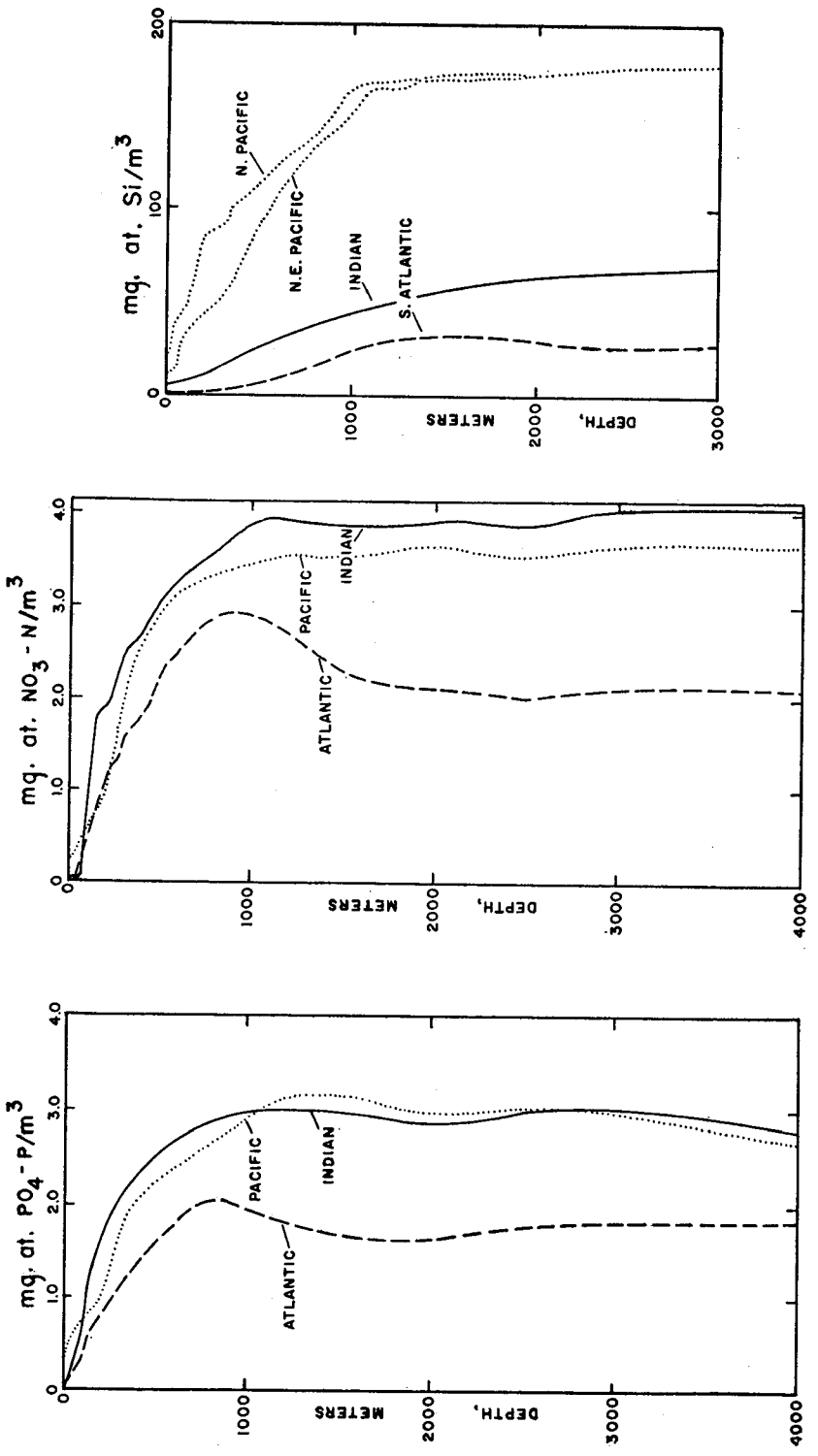

FIGURE 26.—*Longitudinal sections in the major oceanic regions, showing distribution of nutrients*
From Sverdrup, Johnson, and Fleming (1942)

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different oceans. Nor is there space to discuss adequately a recent attempt by Riley (1951) to correlate all the known facts with regard to one ocean—the Atlantic; in view of the lack of data on many of the important variables, such a synthesis must at the present time be speculative. However, an attempt will be made to summarize the general relations of the larger oceanic regions, with attention again concentrated on records of phosphorus data. Approximate values from widely scattered observations, some of which have been discussed in the preceding sections, have been computed by Sverdrup, Johnson, and Fleming (1942); longitudinal sections (Fig. 25) and vertical sections (Fig. 26) of the Atlantic, Pacific, and Indian oceans were taken from their work.

Nutrient concentrations in general are characterized by four layers:

(1) A surface layer in which concentrations are in places low and relatively uniform with depth
(2) A layer in which the concentration increases rather rapidly with depth
(3) A layer of maximum concentration that is usually located somewhere between 500 and 1600 meters
(4) A thick bottom layer in which there is relatively little change of phosphate and nitrate with depth, although silicate may increase considerably below 2000 meters

The nutrient-poor surface layer is thickest in mid latitudes in both hemispheres, and in these regions the layer of increasing concentration is clearly defined. In the regions of divergence, however, at and near the equator, the surface layer becomes thin and the underlying gradient steep.

In high latitudes the surface layer of low concentration may be absent, so that high values of nutrient concentration appear at the surface. In the Atlantic, maximum phosphate content (2 mg. at. P/m^3) is found in an intermediate layer extending northward from the Antarctic and centered at depths of about 1000 meters. At all depths greater than 1000 meters there is a gradual decrease in phosphate concentration from south to north. In the Pacific Ocean the distribution in the Antarctic region is similar, but maximum amounts (3.5 mg. at. P/m^3) are found north of the Equator, compared with 2.0 mg. at. P/m^3 in the Antarctic. Further, there is no layer of minimum phosphate content below the maximum layer in the Pacific Ocean.

The amounts of phosphate in the Indian Ocean are intermediate between those of the Atlantic and the Pacific, and an intermediate maximum in the southern latitudes corresponds to that in the Atlantic; the maximum in Equatorial regions corresponds to that in the North Pacific, since it is related to the low oxygen content of the water.

These facts are all related to differences in the deep-water circulations of the two oceans. Exchange of deep bottom water across the Equator takes place only in the Atlantic Ocean. It is present only to a slight extent in the Indian Ocean and is virtually absent in the Pacific. Thus the low concentration of nutrients in the North Atlantic is directly related to the exchange of water between the North and South Atlantic. The water that flows into the North Atlantic is low in nutrients. The net transport of these nutrients across the Equator must be nearly zero, and the southward-flowing deep water of the North Atlantic must therefore have low concentra-

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tions. Admixture with Antarctic intermediate water and Antarctic bottom water, with their high nutrient contents, increases the nutrient content maintained in the South Atlantic. North Pacific deep water contains great amounts of nutrients, but there is little exchange between the Northern and Southern hemispheres, so that dilution with northward-flowing water does not take place. Further, the circulation of deep water in the North Pacific is considered to be so slow that the concentrations of nutrients are maintained by further decomposition of organic matter. In the Indian Ocean conditions appear to be similar to those in the Pacific.

Data for nitrate and silicate are much more difficult to obtain, but some figures for silica have been computed (Figs. 25, 26). As would be expected there is no marked intermediate maximum; the concentration always increases with increasing depth. In the Atlantic Ocean the silica content of the deep water is much less in low latitudes than in the far south, but in the Indian Ocean the contrast is not so great (Figs. 25, 26). The waters of the North Pacific are extremely rich in silicate (170 mg. at. Si/m^3), comparable with the waters of the Antarctic region. Cooper (1952b) recently discussed the factors affecting the distribution of silicate in the North Atlantic Ocean. He points out that in the deep water, whereas the variations with depth of salinity, density oxygen, phosphorus compounds, and nitrate are small, the silicate content is doubled in a descent from 2000 to 4000 meters depth. There is considerable evidence that the tundra drainage may be an important factor in increasing the silicate content. Under a tundra climate, there is considerable solifluction during the summer thaws, and, with a climate favorable to rapid weathering and comminution of the rock particles, conditions lead to much soluble silica. The North Polar Sea receives a large amount of tundra drainage; this may escape into the East Greenland Current, which in turn contributes to the mixing areas south of Greenland, where the North Atlantic deep water may be formed. Direct observations on the silicate content of northern waters are needed.

ACKNOWLEDGMENTS

In this account of the nutrient elements an attempt has been made to cover all the most important aspects of this branch of marine biology. It is a wide field, but the difficulties in covering it have been lightened by the critical comments and helpful suggestions of a number of friends. I wish to acknowledge this assistance most gratefully, but at the same time these friends must be absolved from all responsibility for inaccuracy of statement or for the inadequacies in the presentation. Drs. L. H. N. Cooper and H. W. Harvey of the Plymouth Laboratory, Dr. G. E. R. Deacon of the National Institute of Oceanography, Prof. K. Kalle of Deutsches Hydrographiches Institut, Hamburg, and Dr. J. Tait of the Scottish Home Department, have all contributed.

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Chapter 12

Biogeochemistry of Trace Metals*

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Chemical studies on the ultimate composition of plants, animals, and sediments of the marine environment have revealed the existence of high concentrations of such minor oceanic constituents as zirconium, titanium, and thallium. The fact that some of these elements have not yet been detected in sea water has made these observations all the more striking. It is inviting, therefore, to explore the paths of trace metallic elements through the various geospheres of the earth's surface.

The task of delimiting chemically the marine *milieu* is beset with complexities. First of all, although more than 90 per cent of marine waters exists at depths greater than 1000 meters, the vast majority of chemical investigations have been concerned with waters of shallower depths. For example, in a recent survey of published iron analyses of oceanic waters undertaken by the author, only 4 of the 39 investigations presented data for waters taken at depths greater than 1000 meters.

The concentration of certain elements appears to vary by factors greater than two orders of magnitude. In the analyses cited above, the iron content in Japanese coastal waters shows a range of 0 to 800 mg/liter.

Finally, many reported concentrations fail to differentiate elements between the solid phases of either organic or inorganic origin and the dissolved phase. Although the experimental separation of the solid and liquid phases is arbitrary, as it is somewhat dependent upon the porosity of the filter employed, such distinctions are of utmost importance.

Table 1 presents the marine abundances compiled critically from the original literature. Although the values probably do not reflect truly characteristic marine concentrations—*i.e.*, from waters of depths greater than 1000 meters—the table is useful as a first approximation of the marine environment. For present purposes a trace metallic element is defined as an element of groups IA, IB, IIA, IIB, IIIA, IIIB, IVA, VB, VIB, VIIB, and VIII, whose marine abundance is less than 1000 atoms per 1,000,000 atoms of chlorine.

DISPOSITION OF ELEMENTS WITHIN THE MARINE HYDROSPHERE

The chemical elements of marine waters may exist either in the liquid phase or in a solid phase. The types of particulate matter can be defined by the geosphere in which the solid phase was formed. Lithogenous material arises from the continental or island areas and from submarine volcanic eruptions and remains in oceanic waters unchanged chemically. Biogenous matter includes the living organisms, their remains, and metabolic waste products including the hard, inorganic material such as

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TABLE 1.—*Chemical abundances in the marine hydrosphere*
Compiled by Edward D. Goldberg and Claude Michaux

	mg/l	atoms/10^6 atoms Cl		mg/l	atoms/10^6 atoms Cl
H	108,000.	202,000,000.	Ag	0.0003	0.005
He	0.00005	.0004	Cd	0.00011	0.002
Li	0.2	50.	In	<0.02	<0.3
Be			Sn	0.003	0.05
B	4.8	830.	Sb	<0.0005	<0.008
C	28.	4,300.	Te		
N	0.5	70.	I	0.05	0.7
O	857,000.	100,000,000.	Xe		
F	1.3	130.	Cs	0.0005	0.005
Ne	0.0003	0.03	Ba	0.0062	0.008
Na	10,500.	850,000.	La	0.0003	0.004
Mg	1,300.	100,000.	Ce	0.0004	0.005
Al	0.01	0.7	Pr		
Si	3.	200.	Nd		
P	0.07	4.	Pm		
S	900.	52,000.	Sm		
Cl	19,000.	1,000,000.	Eu		
A			Gd		
K	380.	18,000.	Tb		
Ca	400.	19,000.	Dy		
Sc	0.00004	0.002	Ho		
Ti	0.001	0.04	Er		
V	0.002	0.08	Tm		
Cr	0.00005	0.002	Yb		
Mn	0.002	0.07	Lu		
Fe	0.01	0.3	Hg		
Co	0.0005	0.02	Ta		
Ni	0.0005	0.02	W	0.0001	0.001
Cu	0.003	0.09	Re		
Zn	0.01	0.3	Os		
Ga	0.0005	0.01	Ir		
Ge	<0.0001	<0.003	Pt		
As	0.003	0.07	Au	0.000004	0.00004
Se	0.004	0.1	Hg	0.00003	0.0003
Br	65.	1,500.	Tl	<0.00001	<0.00009
Kr			Pb	0.003	0.03
Rb	0.12	2.2	Bi	0.0002	0.002
Sr	8.	160.	Po		
Y	0.0003	0.006	At		
Zr			Rn	9.0×10^{-15}	8.0×10^{-14}
Nb			Fr		
Mo	0.01	0.2	Ra	3.0×10^{-11}	2.0×10^{-10}
Tc			Ac		
Ru			Th	0.0007	0.006
Rh			Pa		
Pd			U	0.003	0.02

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siliceous or calcareous shells. Solid matter produced by oxidation, hydrolysis, or decomposition processes from dissolved constituents is classified as hydrogenous. Two minor categories include the cosmogenous matter originating from the rain of extraterrestrial particles upon the oceans and the atmogenous matter which results from the formation of insoluble substances from the components of the atmosphere.

The chemical characterization of the dissolved metallic ions can be developed in certain cases on the basis of modern structural theory derived from quantum mechanical considerations. Metal ions in water are co-ordinated with water molecules. However, in the presence of complexing groups or ligands such as chloride ion, the ammonia molecule, etc., the waters can be partially or completely replaced by such groups. Equilibrium constants can be determined to describe such processes. If equilibrium is established, all energetically and sterically possible ionic complexes will exist in amounts determined by their equilibrium constants (Bjerrum, 1950).

Although data for such calculations are scant, the following calculation is given to illustrate the fact that electrical charge and the size of an ion are dependent upon the factors of hydration and complex formation.

In the case of copper the equilibrium constants with chloride ion have been determined by Bjerrum (1946). For sea water the chloride concentration is taken as 0.7 M with a total dissolved copper content of 10×10^{-8} M. Concentrations rather than activities are utilized in order to approximate the distribution of ionic species of copper:

$$k_1 = (Cu(H_2O)_3Cl)^+/(Cu(H_2O)_4)^{++}(Cl^-) = 10^{-0.2}$$

$$k_2 = (Cu(H_2O)_2Cl_2)/(Cu(H_2O)_3Cl)^+(Cl^-) = 10^{-0.7}$$

$$k_3 = (Cu(H_2O)Cl_3)^-/(Cu(H_2O)_2Cl_2)(Cl^-) = 10^{-1.5}$$

$$k_4 = (CuCl_4)^{--}/(Cu(H_2O)Cl_3)^-(Cl^-) = 10^{-2.2}$$

Summing the total number of ionic species of copper to obtain its total content:

$$(Cu(H_2O)_4)^{++} + (Cu(H_2O)_3Cl)^+ + (Cu(H_2O)_2Cl_2) + (Cu(H_2O)Cl_3)^- + (CuCl_4)^{--} = 10 \times 10^{-8}\ M.$$

Solving the five simultaneous equations in five unknowns, the following concentrations are found: $(Cu(H_2O)_4)^{++}$, 6.5×10^{-8}; $(Cu(H_2O)_3Cl)^+$, 2.9×10^{-8}; $(Cu(H_2O)_2Cl_2$, 0.4×10^{-8}; $(Cu(H_2O)Cl_3)^-$, 0.9×10^{-10}; and $(CuCl_4)^{--}$, 0.6×10^{-13}. Thus more than 99 per cent of the copper in sea water is in a neutral or positively charged form, assuming that chloride, the most abundant anion, is the only ligand in equilibrium with the solvated cupric ion.

A further disposition of metallic ions in sea water is found in the scavenging of ionic species by finely divided solid phases. The activity of such scavengers is involved mainly in surface adsorption, and the process depends upon the relationship between the charge and the size of the adsorbed ionic species, as well as upon the charge and topographical character of the adsorbing surface.

DISPOSITION OF ELEMENTS BETWEEN THE HYDROSPHERE AND BIOSPHERE

Two general processes are evident for the uptake of trace metallic elements from the marine environment. The first encompasses those mechanisms in which there is a direct transfer of ionic species or dissolved substances from the hydrosphere to the

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organism. The uptake of particulate matter, including the adsorbed surface ions, constitutes an alternate method of transfer.

Lehninger (1950) has approached the problem of the biological specificity of metal ions for such organic substances as proteins and substrate molecules upon the physical basis of ion structure and properties. Four independent parameters taken from his list appear to be pertinent: (1) the mass of the ion, (2) ionic charge, (3) ionic radius, and (4) the oxidation-reduction potentials of the ion. Derivable from these properties are such characteristics of an ion as rate of diffusion, mobility in an electrical field, etc., which with other factors must influence ionic behavior of metals.

An additional factor may be the relative availability of the elements in marine waters. This involves not only the relative abundances but also the chemical states of the elements in question. The extensive association of iron and magnesium rather than other elements in porphyrin complexes in living organisms may be related to this factor of availability. Iron is significantly more abundant than cobalt, nickel, and manganese, whose chemical properties are similar to those of iron. Iron is also unique in that it occurs in particulate forms in the oceans. Thus, the widespread prevalence of hemoglobin in the biosphere may be related to this factor of availability. Similarly, the position of magnesium as the second most abundant cation in the oceans and its chelative ability may contribute to the explanation of the evolution of chlorophyl.

Lehninger also considers the two types of chemical bonding between metals and organic molecules—ionic and covalent. Although the first type is manifested more generally in crystal lattices, the electrostatic binding between positively charged metal ions and dipole molecules, either permanent or induced, is of more direct interest. This phenomenon accounts for the hydration of metal ions as well as the formation of iron hemoglobin. Ions of the transition metals (*e.g.*, Ni, Co, Zn, etc.) show a remarkable ability, as compared with the alkali and alkaline earth metals, to complex with both organic and inorganic molecules.

In the formation of covalent linkages, the ions of the transition metals, by the filling of the *3d* electronic orbitals, form strong bonds with complexing groups through the sharing of paired electrons—the covalent bonds. There is a continuous transition between the purely ionic and the purely covalent bond, yet it is clear that the transition metals display a remarkable ability to co-ordinate with other molecules.

Little work has been done on the physiologically important substances, such as proteins and carbohydrates, with regard to their specificity to complex metal ions and the strength of the formed complex under the chemical and physical variables of biological systems (Williams, 1953). However, this brief survey of the properties of metal ions may serve as a background for the observations of metal-ion concentration by members of the marine biosphere.

Spooner (1949) treated specimens of marine algae with carrier-free radioactive strontium and radioactive yttrium. The brown sea weeds, especially *Fucus serratus*, extracted strontium from the sea water medium by factors of 10 to 40. The red and green algae assimilated the strontium to a small or negligible extent.

Inasmuch as the concentration of strontium in marine waters is rather high (ca. 10 mg/1), Spooner pointed out that uptake by surface adsorption can be ruled out.

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First of all, the radiostrontium, diluted by the inert strontium, would be found on surfaces in but small amounts compared with that in solution. Again, the surfaces capable of such adsorption were undoubtedly saturated before the radiotracer was added, and any transfer of the radiostrontium to the surface by ion exchange was probably negligible.

However, this interpretation merely places back in time the real problem. How do the Sr-fractionating brown seaweeds initially remove the Sr from the sea water? Since Sr is present as an ionic species, a combination of the Sr with a component of the plant protoplasm suggests itself. Such a process may well be one of either ion exchange or chelation.

Radioyttrium ions were observed to be concentrated to such an extent by the red algae (*Rhodymenia*, *Gigartina*, *Chondrus*) and a diatom (*Nitzschia*) that in some cases the sea water was essentially depleted of this element. Again, an organic chemical grouping with a specificity for Y appears responsible for the removal of Y from sea water.

Ionic vanadium was concentrated directly from sea water by the tunicates *Ciona intestinalis* and *Ascidia ceratodes* with an efficiency of assimilation of 2½ per cent for unfed animals (Goldberg, McBlair, and Taylor, 1951). The instantaneous uptake of radiovanadium was found to be proportional to the amount in solution (Fig. 1). Radioautographs of sacrificed animals indicated that the initial site of uptake was the branchial basket. Chemical analyses localized vanadium concentrations in the gut wall, ovary, and oviduct.

Since the uptake of vanadium occurred uniformly for periods of 6 days, an adsorption process would demand that the adsorbing surface be in an unsaturated state with respect to the adsorption of vanadium at all times or that it be maintained in such a state by the constant regeneration of the surface. The mucous sheet of the branchial basket fulfills the latter requirement. The autographs indicated that there were high concentrations in the mucous material. The extraordinary biological specificity of the mucous of these tunicates is undoubtedly related both to the unique ionic structure of vanadium and to the chemical character of the mucus.

Fretter (1953) studied the uptake of Sr^{90} by *Mytilus edulis* and postulated two routes of Sr from the sea water to the animal. Strontium made direct entry into the ciliated epithelium of the gills within 40 minutes when the mantle cavity was given access to radiostrontium-activated sea water by a slight opening of the shell. Further, no activity was found in the gut regions. It is unlikely that the ions entering through the gut could have been circulated in the blood stream and taken up by these cells.

Further investigations showed that after 2 hours in sea water containing the radioisotope the mussel showed Sr accumulations in the lumen of the gut, the digestive glands, and the tissues of the gill filaments. It was concluded that the gut is the more important area for the ingress of ions into the tissues, the ions having been directed there by the feeding currents.

Fretter took counsel from Korringa (1952) and suggested that mucus is the agent by means of which ions in solution are collected from the sea-water environment and transported to the gut. Korringa had proposed that positive polyvalent ions like aluminum, copper, iron, zinc, mercury, and manganese are accumulated by the mu-

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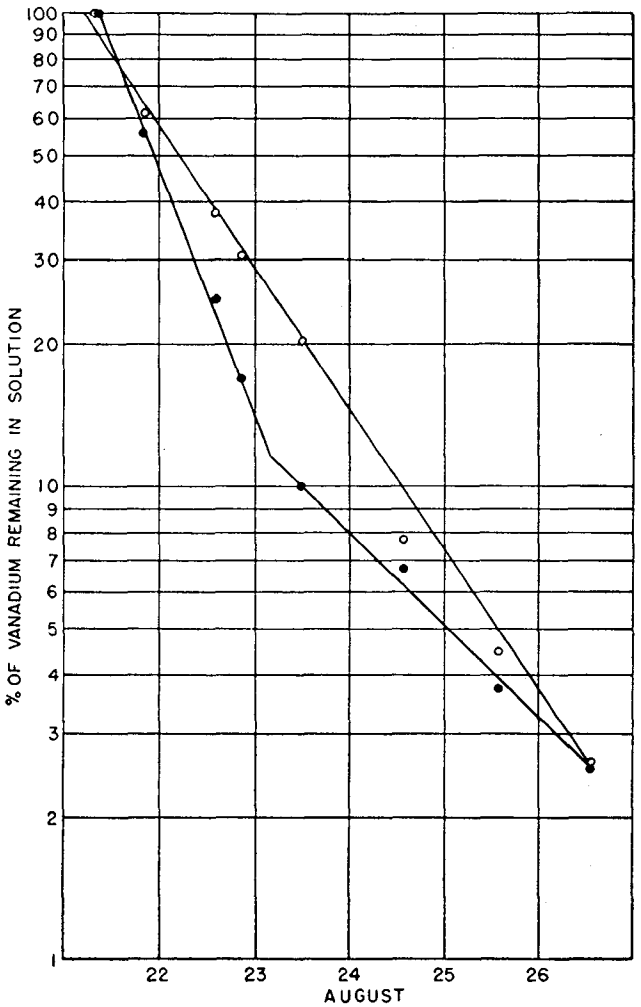

FIGURE 1.—*Uptake of* V^{48} *by two specimens of* Ascidia ceratodes

The change in slope of the uptake curve in one specimen (closed circles) probably reflects a change in mucus production

cous sheets of oysters as a result of the electrical properties of the ions and the feeding sheets. Fretter also observed that the nudibranch *Acanthodoris pilosa* collected strontium relatively rapidly from the surrounding water. Again it is likely that the mucous coating the body concentrates the ions which then pass through the general surface of the body while a smaller number pass into the lumen of the gut.

The direct uptake of the Sr into the ciliated epithelium of the gills finds a parallelism in the work of Jodrey (1953) who observed that calcium was deposited directly on the mantle of the oyster *Crassostrea virginica*. Utilizing the radioisotope Ca^{45} Jodrey observed that this direct assimilation occurred at a rate one-ninth as rapidly

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as the total deposition of Ca by the whole oyster. The Ca in the mantle is inert and apparently is not mobilized therefrom.

Rao and Goldberg (1954) maintained freshly collected specimens of the tunicates *Ciona intestinalis* and *Styela montereyensis*, the mussel *Mytilus edulis*, and the anemone *Anthopleura xanthogrammica* in filtered sea water containing Ca^{45}. After a few hours, mucus was collected from each animal and assayed for radioactivity. The tunicate *Styela montereyensis* accumulated significantly more calcium than any of the other organisms although all of them concentrated Ca in the mucus to about the same order of magnitude. These results were confirmed in investigations with mucus removed from the body and exposed for 15 minutes to a radiocalcium-activated sea-water samples. Radioautographs indicated that the initial transfer of calcium from the sea water to the mussel occurs at the mucous surface of the gill.

The ability of all the intertidal organisms examined to concentrate calcium (as well as other possible ions) points to a rejection mechanism for nonutilizable substances. Since there are many naturally occurring glycoproteins (mucins), there are in the digestive tracts of various invertebrates probably specific enzymes capable of disintegrating the mucous and extracting only the required components, and of discarding the rest.

In studies on the intake of Ca^{45} by marine molluscs Bevelander (1952) had previously shown that calcium ions are ingested by the organisms. Further, such ions are later incorporated into the mineral component of the shell.

A second form of accumulation of trace elements by members of the marine biosphere is the uptake of the particulate matter of the oceans. Armstrong and Atkins (1950) have analyzed the suspended solid matter of sea water and report that the ignited residue contained 17–55 per cent silica, 3–25 per cent ferric oxide, <1–20 per cent alumina, and 9–70 per cent calcium carbonate. These particles can enter the marine biosphere via the filter-feeding organisms and their predators, as well as by direct transfer through adhesion to the outer surfaces of plants or animals. Since all these substances except calcium carbonate can exist as colloidally dispersed species, it may be expected that the scavenged ions with charges opposite to that of the colloidal species will accompany these particles.

A marine diatom, *Asterionella japonica*, utilizes only particulate and/or colloidal iron as a growth nutrient, whereas ionically complexed ferric ion such as the citrate, ascorbate, or artificial humate are not available for uptake (Goldberg, 1952). Colloidal iron in marine waters is positively charged (Rankama and Sahama, 1950). In studies of manganese nodules and certain pelagic sediments, Goldberg (1954) postulated that titanium and zirconium, existing as anions in marine waters, are scavenged by the hydrogenous hydrated oxides of iron. Thus, in the natural growth of phytoplankton the existence of the scavenged ions should manifest itself.

Griel and Robinson (1952) found significant amounts of titanium in the ashes of diatoms collected in the Puget Sound area. Although iron analyses were not made on the samples, the results (0.0052–0.12 per cent Ti in the ash) are nevertheless encouraging since any Ti present is highly diluted by the silicon oxides from the tests.

During a bloom of a naked dinoflagellate, *Gymnodinium brevis*, near the west coast

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of Florida in October and November, 1952, Collier (1953) collected samples of the water and subjected them to semiquantitative spectrographic analyses. Titanium and zirconium were found in the "red-tide" waters at concentrations of 0.01–0.1 per cent and 0.001–0.01 per cent of the total solids, respectively, whereas neighboring waters outside the bloom area contained Ti and Zr in amounts less than the sensitivity of the method (0.001 per cent for either element). The water was not apparently separated from the organisms. Thus, there is no indication as to the location of these elements either in the water or in the organisms. These results emphasize the desirability of separating the particulate from the nonparticulate phases of natural waters. Although the results are suggestive of a particulate uptake of titanium and zirconium, there is no way of distinguishing between a rejection of either of these two elements into the solution by the plant and uptake by the plant.

Black and Mitchell (1952) spectroscopically assayed 15 elements in some common brown algae collected off the British Coast. In the 14 samples collected in January and May of 1949, where there was no danger of iron contamination in the treatment of the specimens, the iron-titanium ratio varied between 8 and 28 in all but two rather questionable samples. Similar correspondences appear between iron and vanadium and molybdenum. The author points out that soaking the plants in fresh water, although it removes a considerable portion of the mineral matter, does not elute the trace elements. He postulates that they are in an insoluble form and are possibly absorbed on the colloids present or combined with polysaccharides such as alginic acid or focoidin.

These Fe/Ti values are quite similar to those obtained by Correns (1937) and treated by Koczy (1950) for the sediments of the equatorial Atlantic Ocean. Thus, if iron is accompanied by titanium in the hydrogenous portion of the suspended matter of marine waters, the brown algae apparently do not fractionate one element in favor of the other.

In chemical analyses on five species of marine sponges—*Dysidea crawshyi*, *D. etheria*, *Chondrilla nucula*, *Terpios fugax*, and *T. zeteki*—Bowen and Sutton (1951) find values of Fe/Ti ranging between 9.2 and 22 in specimens where values for both elements were ascertained. Here again there is no preferential retention of either element.

Optical spectroscopic investigations of the ashes of nine species of marine animals from a Swedish fjord by Noddack and Noddack (1939) yielded iron-titanium ratios ranging from 25 in the jelly fish *Cyanea capillata* to 658 in the shark *Squalus acanthus* (intestines removed). The value for the sponge *Halichondria* was 298, greater by over an order of magnitude than the highest value of Bowen and Sutton. Since the organisms ranged from the lower to one of the highest members of the evolutionary sequence, some fractionation of the titanium is apparently greater in the more complex organisms.

Extensive analyses of the reported values of elements in marine organisms is usually limited by two factors: (1) Often only one or a few elements are analyzed, and parallelisms in biogeochemical paths are difficult to detect. (2) Many of the investigations have utilized spectroscopic methods with accuracies hardly exceeding factors

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TABLE 2.—*Enrichment factors for some chemical elements in marine organisms over sea water*
Dry weights of organisms were used. From Noddack and Noddack (1939).

Element	Enrichment factor
Ti	>10,000
V	>280,000
Cr	1,400
Mo	6,000
Mn	41,000
Fe	86,000
Co	21,000
Ni	41,000
Cu	7,500
Ag	22,000
Au	1,400
Zn	32,500
Cd	>4,500
Ga	800
Tl	>700
Ge	>7,600
Sn	2,700
Pb	2,600
As	3,300
Sb	>300
Bi	1,000

of 2 or 3 at best. Nevertheless, in summation certain generalizations appear from the published data.

(1) In general the concentration of heavy metals is greater in the marine biosphere than in the hydrosphere (Noddack and Noddack, 1939; Black and Mitchell, 1952; and references in this paper). On an average V shows the highest concentration factor, while Sb shows the lowest for the elements examined (Table 2). Further, the organisms of lower levels of organization seem to accumulate the trace metals to a greater extent than do the vertebrates.

(2) The trace metals are retained by fairly strong chemical bonds by the organisms and are not readily eluted (Noddack and Noddack, 1939; Black and Mitchell, 1952).

(3) Differences in concentration factors for a given element in organism over sea water exist not only among families but among species. Bowen and Sutton (1951) found that the sponge *Dysidea crawshayi* accumulated Ti, while *Dysidea etheria* did not. *Chondrilla nucula* concentrated copper. *Terpios fugax* and *Terpios zeteki* strongly take up Ti, while *Terpios zeteki* apparently accumulated Mn, Sn, and V in addition. The rather striking concentration of zinc by the brown algae (Black and Mitchell, 1952), up to factors of over 1000, deserves further experimental study since no other trace metal besides titanium shows such a high level of accumulation in these seaweeds.

(4) In general the relative concentration factors for metals in the marine biosphere

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as compared to sea water closely parallel the order of stability of metal ions with ligands. Schubert (1954) has summarized the stability orders of the complexes formed by metal ions and a variety of ligands. The stability increases with increasing basicity of the metal ion. The general order found for the divalent ions is: Pd > Cu > Ni > Pb > Co > Zn > Fe > Cd > Mn > Mg > Ca > Sr > Ba > Ra. In the case of the seaweeds reported by Black and Mitchell (1952) nickel and zinc are 550 and 900 times more concentrated in the plants than in sea water, whereas the value for strontium is but 23. The fractionation factors for the sponges studied by Bowen and Sutton (1951) are: Cu, 1400; Ni, 420; Co, 50; Mg, 0.07; and Ca, 3.5. This agreement is quite remarkable considering the fact that the stability order does vary depending not only upon the ligands but also upon whether the atom is attached to oxygen, nitrogen, or sulfur. The governing factors then in the competition among ions for uptake are the equilibrium constants of the reaction. Further, parallelisms in the assimilation of ions with similar stabilities exist. Both copper and cobalt were significantly higher in the sponges in which extraordinary nickel accumulations were found. Such a result is not unexpected, if the uptake process involved chelation or ion exchange.

PALEO-ECOLOGICAL ASPECTS OF MARINE BIOGEOCHEMISTRY

An environment may be defined as the loci of points in space which are delimited by given ranges of chemical composition and physical variables. It is of interest then to investigate the potential reflection of the composition of the hydrosphere in the hard parts of marine organisms that become a part of the fossil record.

The deposition of metals other than calcium in calcareous structures is determined not only by the composition of the water habitat but by temperature. Clarke and Wheeler (1922) called attention to the fact that the proportion of magnesium carbonate in the shells of crinoids and alcyonarians is dependent upon temperature. The percentage of magnesium carbonate increased with increasing temperature of the water. Analyses of Foraminifera, crustaceans, and algae also suggested this relationship.

Chave (1954), in more extensive studies of the biogeochemistry of magnesium, concluded that the most important factor controlling the distribution of magnesium in calcareous skeletons is the mineralogy of the carbonate. In the calcitic forms larger amounts of magnesium occurred in solid solution, while lesser amounts appeared in the aragonitic forms. The type or phylogenetic level of the organisms and the temperature of the water in which they lived influenced the calcium-magnesium ratio. Such factors as salinity, age or size of the sample, and depth at which the organism lived apparently exerted no measurable influence.

The aragonitic forms seldom contained more than 1 per cent of magnesium carbonate, while few of the calcitic shells assayed less than this amount, and many attained values of 20–30 per cent. The algae displayed the highest dependence of magnesium content upon temperature, followed in order by the sponges, Foraminifera, Alcyonaria, ostracods, echinoids, asteroids, ophuroids, crinoids, decapods, and barnacles. All the organisms examined showed a positive correlation between the magnesium content and the temperature of their habitat.

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Odum (1951) through the laboratory culture of aragonitic mollusks found that the Sr/Ca ratio in the shells was proportional to the Sr/Ca ratio in the environmental medium. These results lead to the inference that the Sr/Ca ratio of unaltered shells reflects the Sr/Ca ratio of past waters. A comparison of these ratios in fossil materials and their modern counterparts indicates that the Sr/Ca ratio of marine waters in the early Paleozoic and following times is the same as modern-day values. In experiments in which the snail *Physa* was raised in waters with a high Sr/Ca ratio, X-ray-diffraction studies showed that the shells contained crystals of both aragonite and strontianite instead of an isomorphous intermediate of a substitution series.

Kulp, Turekian, and Boyd (1952) in experiments paralleling those of Odum reach the same conclusion—that the primary factor determining the Sr/Ca ratio in a shell is the Sr/Ca ratio of the water in which deposition takes place. The second influence upon the ratio is the type of crystal lattice of the calcium carbonate. Aragonite more readily accepts strontium atoms than does calcite. The pelecypod *Crassatellites melinus* and the scaphopod *Dentalium attenuatum* show strong strontium enrichment and possess the aragonite structure. On the other hand the pelecypod *Pecten madisonius* and the gastropod *Epitonium pachypleura* show a lower strontium content than the average of the mollusks and have the calcite lattice. Since some mollusks have varying amounts of both aragonite and calcite in their shell structure, many observations lie between these two extremes. Further, Kulp and coworkers point out that the ratio is apparently independent of the age of the animal, the season of the year of shell deposition, and the biological processes. Inorganically deposited calcium carbonate from sea water (both from laboratory precipitation and from studies on oölites made in our laboratory) shows an aragonitic structure and contains more strontium relative to calcium than does sea water. The Sr/Ca ratio in sea water is higher than the ratio in most aragonite-depositing organisms. Again, Odum (1951) reports that recrystallizations always lowers the Sr/Ca ratio. Apparently, his observations refer to interactions of the calcium carbonate in nonmarine environments. Clearly, altered fossils cannot be used as an index of conditions in which the shell was laid down.

The differences in the deposition of magnesium and strontium in calcareous shells are undoubtedly determined by the degrees of difference of these elements from calcium. The ionic radius of calcium ion is 0.99 Å, while strontium and magnesium have values of 1.12 Å and 0.66 Å respectively (Ahrens, 1952). Since the ionic radius of strontium is within 15 per cent of that of calcium, strontium may be expected to follow a biogeochemical path similar to that of calcium. If the initial uptake process for these elements into the marine biosphere is a chemical chelation or ion-exchange mechanism, steric considerations of the elemental uptake by the organic functional group, as well as the activities of the ions in the water, will be the determining factors. Further fractionation during shell formation is apparently related to the type of crystal lattice.

Magnesium has a radius one-third smaller than that of calcium. It is more than three times more abundant in sea water than is calcium on a weight per cent basis. The lack of any correlation between the Mg/Ca ratio in marine waters and shells can be attributed not only to the difference in chemical properties, which arises from

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their dissimilar radii, but also to a difference in the physiological tolerance of magnesium and calcium by marine organisms.

In conclusion the doubly charged ions of cadmium, tin, and manganese with radii 0.97, 0.93, and 0.80 Å respectively may show a similar substitution pattern to that of strontium and may be of use in characterizing environments where these ions differ in differing water masses.

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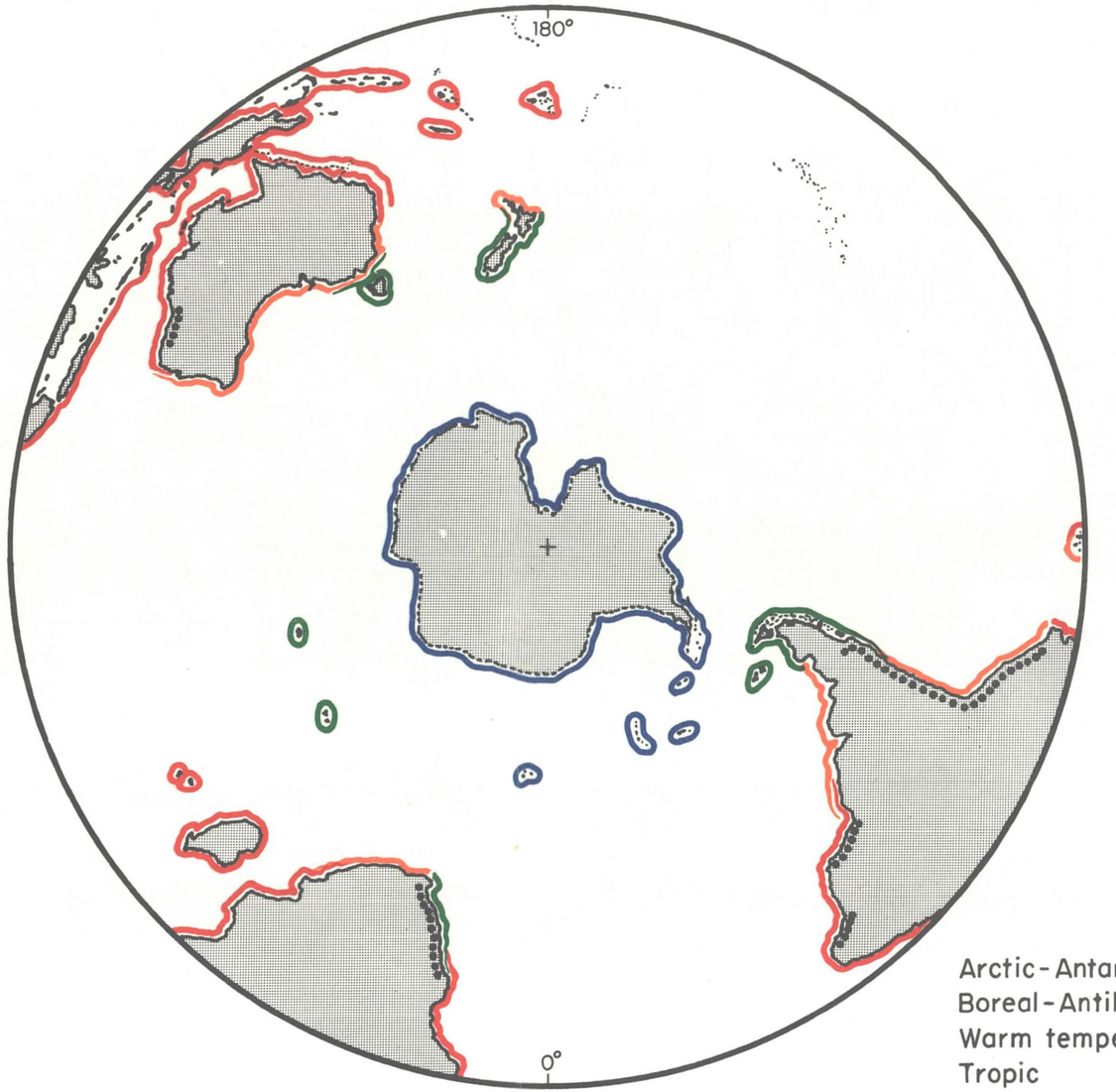

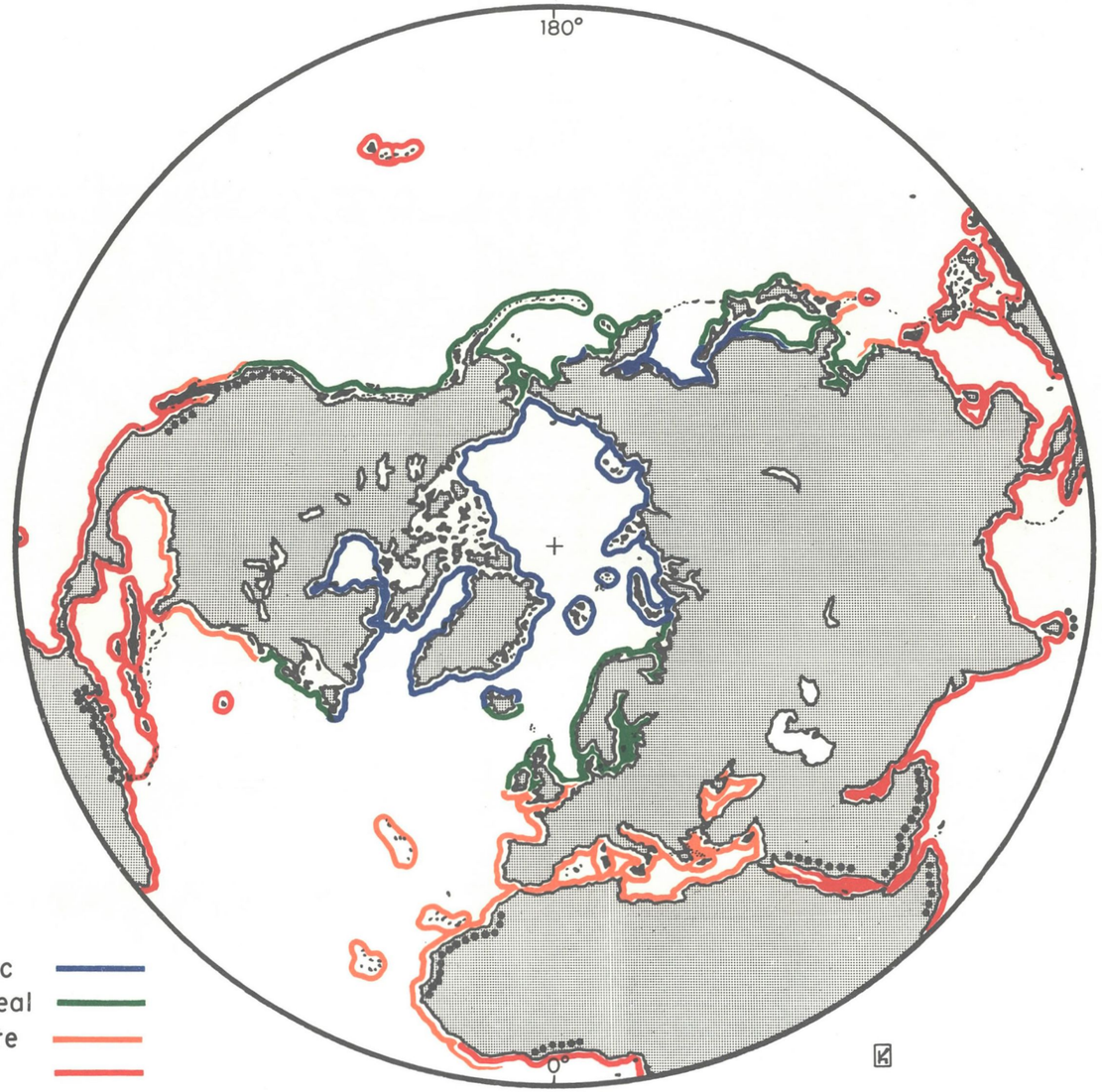

Arctic-Antarctic
Boreal-Antiboreal
Warm temperate
Tropic

Regions of coastal upwelling

LITTORAL PROVINCES OF THE WORLD

Compiled principally from Ekman

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Geol. Soc. America
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Chapter 13
Marine Biogeography*

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The student of history follows, with intense interest, the march of a conqueror, or the migrations of a nation. . . . Yet, absurd as it may seem to those who have not thought of such things before, there is a deeper interest in the march of a periwinkle, and the progress of a limpet.

EDW. FORBES

INTRODUCTION

While many ecologists apparently consider biogeography to be that branch of ecology concerned with describing in somewhat static terms the systematic distribution of plants and animals, some biogeographers evidently consider ecology a minor branch of biogeography; Dansereau (1951), for example, regards ecology as simply one of the "integrative levels" of biogeography. Neither extreme is tenable, for the distribution of organisms in time and space is an essential facet of ecology, and biogeography is intimately dependent on the findings of ecology; studies of evolution, in turn, rely heavily on the findings of biogeography. The study of the biogeography of ecological units (communities) is, however, a comparatively recent development, and much of the current literature of biogeography is still concerned with the classic problems of the distribution of species, genera, and families—*i.e.*, it is systematic and historical rather than ecological in its approach. It must be emphasized, however, that the distribution of systematic units must be analyzed before that of ecological units. Indeed, the biogeography of marine communities, first attempted in a comprehensive manner by Clements and Shelford (1939, p. 313–353), is still a pioneer subject. For example, the summary provided by Thorson in Chapter 17 of this volume is the first attempt to catalogue the bottom communities of the sea on a worldwide basis.

Marine biogeography, as a comprehensive and independent subject, is barely a hundred years old; the first summary was provided by Forbes and Godwin-Austen in *The Natural History of European Seas* (1859). Such a summary, even at that time, could not have been possible without a large body of published observations about the distribution and dispersal of organisms in the sea.

In those halcyon days the most important task of the biogeographer was to chart the provinces of distribution. While such provinces might be called centers of creation even by Forbes, the possibility that they were the result of events far in the geologic past was not denied. Provinces exist in time as well as in space, and geology is an essential aid to the biogeographer:

In studying the geographical distribution of organized beings philosophically, it is absolutely necessary to call in the aid of geology; and the time is not far distant when no reasonable man will venture on that most interesting branch of natural history research without a grounding in geological science. (Forbes and Godwin-Austen, 1859, pp. 9–10).

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Nevertheless the major source of biogeographical data, today as then, is the record of distributions accumulated by specialists, and marine biogeography has been for the most part a by-product of studies of such easily collected organisms as mollusks, crustaceans, echinoderms, and fishes. Even before the publication of *The Natural History of the European Seas* the outlines of marine zoogeography had been provided by James D. Dana (1848) who postulated the broad distribution patterns of the sea in relation to isocrymes as a result of his observations of coral reefs, and by the conchologist S. P. Woodward (1856) who defined a province as an area in which 50 per cent of the species are endemic.

Although a vast amount of information has been published since these pioneer studies, efforts to provide a synthesis of marine biogeography have been few. The most noteworthy are those of Ortmann (1896), and Ekman (1935; 1953). In Ekman's work we have a comprehensive summary of the distribution of many groups, primarily systematic and regional in scope, rather than quantitative and synthetic; certain statistical approaches are suggested by Ekman (1940), although primarily with reference to terrestrial problems. Nevertheless, the task of bringing this information together is enough to ask of one man, and the further synthesis is up to future workers. The opinion of Nikolsky (1947) that this classic stage of biogeography is "mainly a thing of the past" seems, however, somewhat premature since the biogeography of faunistic and ecological complexes is, as indicated above, only in its bare beginnings.

LITTORAL PROVINCES

Of the various distribution patterns in the sea, the best known are those of the shore and shallow sea, the littoral and neritic regions. Many of the currently accepted patterns were recognized at the outset, and the general distribution of shore life as indicated on Plate 1 would be familiar to Forbes and Woodward; indeed, the color convention is the same as used in Forbes' map of European provinces in 1859. This does not mean that this diagram is perfect and needs no further change. We still know little about the character of the fauna of South America in particular (although some recent information has been provided for the west coast of South America by Mann, 1954), and on almost every coast changes in detail might be proposed by specialists. It may be significant that Ekman did not attempt to make such a map, although it would be difficult to find a more adequate source for it than his book. The major divisions recognized by Ekman are given in Table 1.

This distribution of major types of marine life roughly according to latitude may be still further simplified, as in the diagram (Fig. 1) by Zenkevich (1949a). This might be considered the sort of distribution pattern that could occur on a symmetrical globe with neatly defined continental masses according to the generalized conditions discussed in Chapter 5. But the continents are irregular, and the patterns of winds and currents are correspondingly irregular. As a result, transitions, exceptions, and anomalies of distribution seem to be more common than conformities. Forbes himself was not unaware of this when he referred to the Celtic province as a "neutral ground."

The smoothed abstraction of Zenkevich's diagram suggests, for example, a land mass shaped something like Africa. On the basis of incomplete information Ekman

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TABLE 1.—*Major divisions of the shore and shallow sea according to Ekman* (1953)

ARCTIC
BOREAL
- European Atlantic Baltic
- Atlantic North American

TEMPERATE
- Pacific

WARM-WATER
- Indo-West Pacific
- Atlantic-East Pacific
  - Tropical and subtropical America
  - Tropical-subtropical West Africa
- Mediterranean Atlantic
  - Sarmatic

WARM TEMPERATE of S. Hemisphere
- South Coast Africa
- South-west Africa
- Southern Australia and Tasmania
- New Zealand
- Peru and northern Chile

ANTIBOREAL
- South America
- Oceanic Islands
- Kerguelen

ANTARCTIC

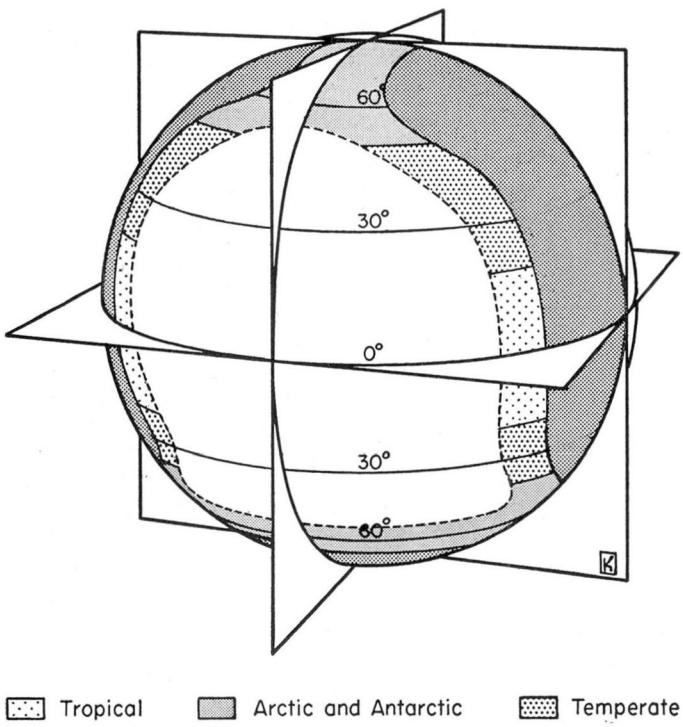

FIGURE 1.—*Generalized symmetry of the marine biosphere*

After Zenkevich (1949a)

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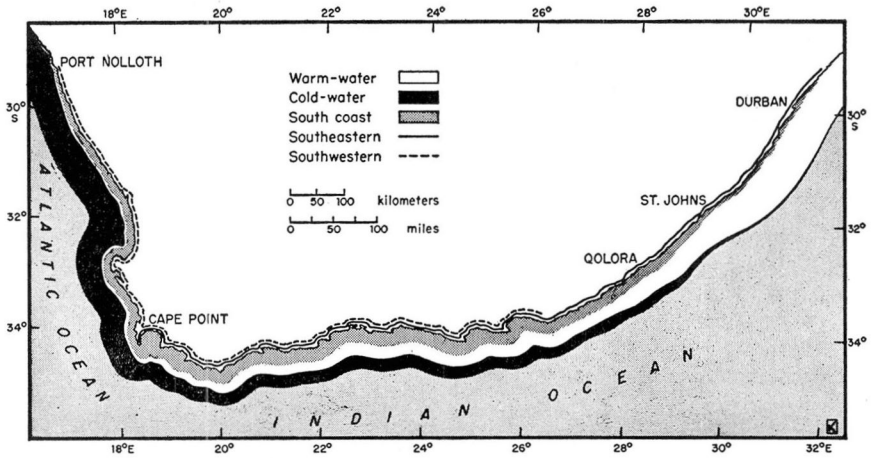

FIGURE 2.—*Faunal components of the shores of South Africa*
From Stephenson (1947)

classified the Cape region and part of the southwest coast of Africa as a unit in his first book (1935), but when more information became available he recognized the complex nature of this region in his revision (1953). An indication of this complexity may be gained from Figure 2.

A similarly complex situation exists along the southern coast of Australia, according to the recent studies of Bennett and Pope (1953), and is partly indicated on Plate 1. In both these examples the complexities in the patterns of shore faunas are reflections of complex hydrographic conditions in these regions. Conditions in the northern parts of the great oceanic basins are equally complex; in the North Pacific, for example, there are cold areas isolated from the Arctic, while northern Alaska is more boreal than Arctic (Fig. 3). These temperature differences are accompanied by several well-marked distribution patterns, especially of fishes, in this region. Figure 4 exhibits such distribution patterns within a single fish family.

On Figure 3 an attempt to assign more definite limits for the temperature characteristics of the various regions is indicated. Much uncertainty and confusion would be avoided if such definitions were more frequently provided. Such terms as "boreal," "cold temperate," and "temperate" may be used by different authors to refer to very similar temperature conditions. Among the better-known definitions of the major temperature regions are those of Vaughan (1940) and Stephenson (1947); these are indicated on Figure 5.

Traditionally these major temperature realms are divided into provinces. These provinces bear such names as Celtic, Lusitanian, and Mediterranean in European waters; Virginian and Carolinian on the east American coast; and so on. Although the limits of these regions may have been set according to isotherms, conspicuous geographic features, or Woodward's index of 50 per cent endemism, they have actually been determined by the subjective appraisals of the specialists.

There is little agreement, for example, on the limits of such provinces on the Pacific coast of North America south of Alaska. Granting that some of the discrepancies indicated on Figure 6 are due to

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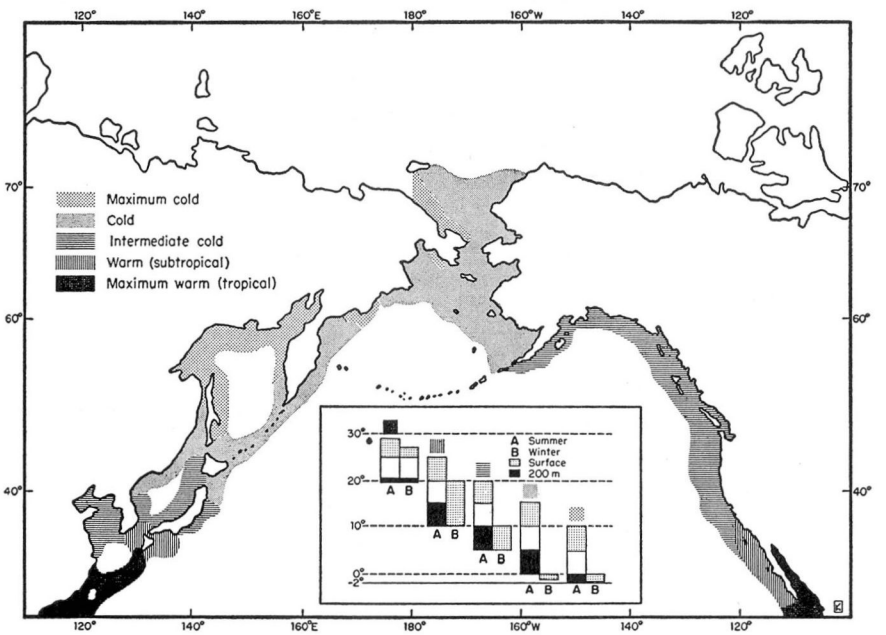

FIGURE 3.—*Temperature regions in the North Pacific and Bering Sea*
From Schmidt (1950) after Andriashev (1939)

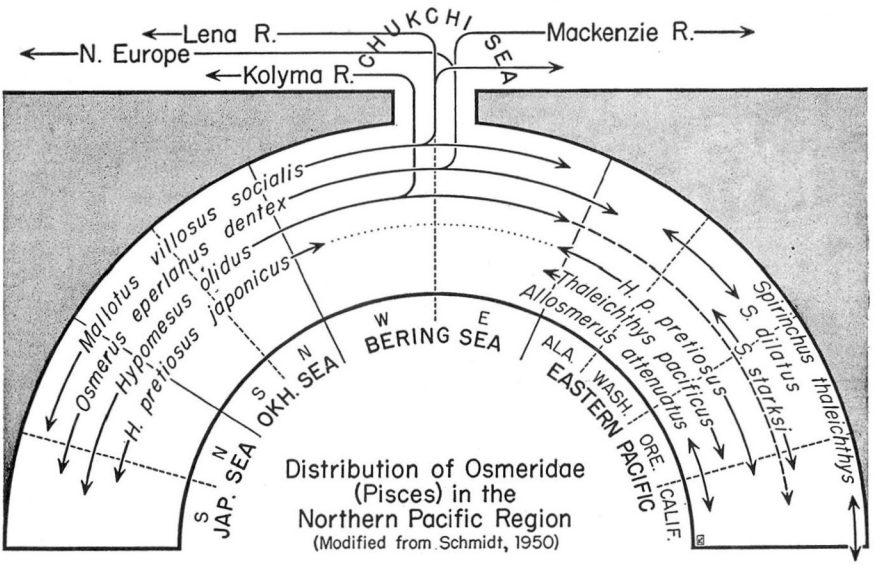

FIGURE 4.—*Distribution of osmerids in the North Pacific*
Showing their affinities with other regions (from Schmidt, 1950).

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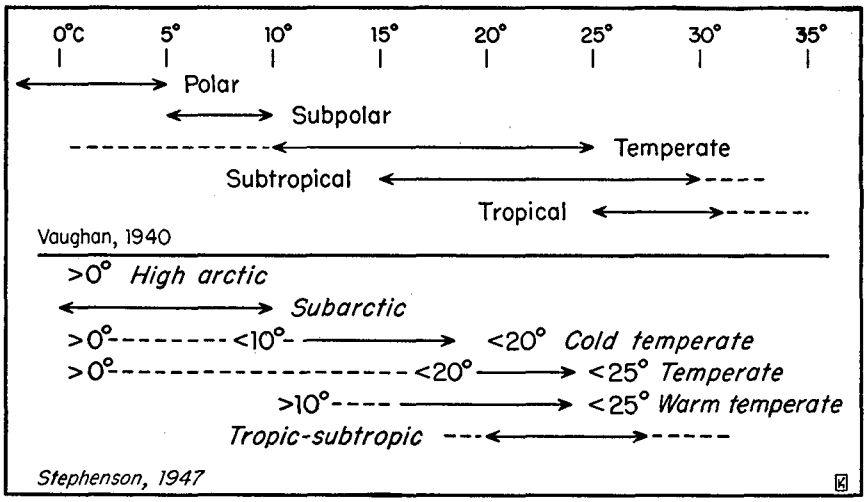

FIGURE 5.—*Temperature limits of various biogeographic zones*
According to Vaughan (1940) and Stephenson (1947).

inadequate data (and it should be noted that Ekman did not have sufficient information to recognize a warm-temperate fauna on the California coast as Garth [1955] has shown), this lack of agreement for the limits of provinces in the "temperate" regions suggests that each worker has used his own criteria. It may also suggest that there is perhaps not too much real difference along this coast—*i.e.*, that the resemblances between the mollusk faunas of British Columbia and California are more significant than their differences. This criterion of external differentiation has been discussed by Ekman (1947). (*See also* the discussion on recognition of bottom communities in Chapter 17 of this volume.) The basic philosophy is still that of Woodward's index, although the statistics may be more sophisticated or at any rate more detailed.

The divisions proposed by Schenck and Keen (1936) for western North America are based on an attempt to define provinces objectively with the aid of statistical analysis, a procedure which Ekman (1953, p. 152) considers "methodologically . . . a pioneer work." The data for this analysis consisted of the mid-points of the ranges of all species of mollusks between Alaska and San Diego, without reference to abundance, depth, or any other ecological factor. Species known from only a single locality or single collection were included.

On the assumption that the greatest number of such mid-points will indicate the center of a province—*i.e.*, that the species with short ranges will tend to occur near the center—Schenck and Keen have arrived at a somewhat different arrangement of provinces; in particular they consider their Californian province as extending from 42° to 23° N. Lat., with its center about at Pt. Conception, which most workers have considered an important faunal boundary (Fig. 6). In their later papers (1937; 1940) they recognize the importance of this geographical feature for the distribution of shore species but appear to distinguish between littoral districts and provinces.

Their reasoning has been criticized by Newell (1948). By analyzing the same data differently, Newell found substantial agreement with older concepts of provinces. He also found a coincidence between nodal points of ranges (admittedly a statistical abstraction but nevertheless falling at well-known faunal boundaries) and the occurrence of species with short ranges or known from single localities or collections. Newell suggested that this indicates the occurrence of hybrids and ecotypes near the borders of faunal provinces. This would seem to indicate that boundaries between provinces are like ecotones in providing a greater range and variety of habitats (Chapter 3).

When such habitat differences as substrate are taken into consideration, the mid-points method of Schenck and Keen is impractical because the real center of distribution within a given range may have no relation to the geometrical center. (*See* Hedgpeth, 1953, for examples.) The method also

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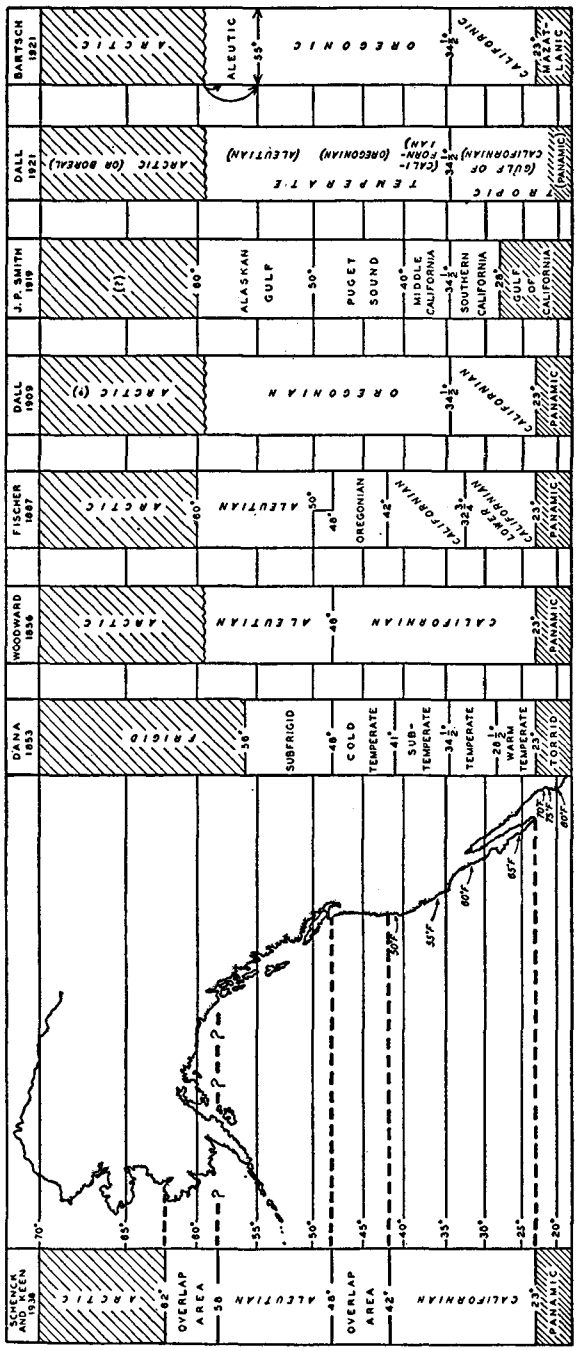

FIGURE 6.—*Faunal provinces of the Pacific coast of North America*
According to various authors (from Schenck and Keen, 1936).

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does not compensate for the occurrence of species in regions of upwelling far to the south of their present "normal" range. This phenomenon is especially pronounced on the Pacific coast of North America. In an implicit criticism of this method of giving equal statistical weight to the total range of all species without respect to their abundances, Ricketts (*in* Steinbeck and Ricketts, 1941, p. 293–297) points out the difficulties of defining a province on the basis of one group of organisms on a single criterion and emphasizes, from his extensive field experience in collecting and observing the invertebrate fauna as a whole, the value of recognizing provinces on the basis of the most populous and characteristic species of the region.

Another attempt to indicate distribution quantitatively has been suggested by Kuronuma (1942). According to this scheme a numerical value, the "latitudinal value", is obtained for the distribution of each species in the group considered (flatfishes in this example) by obtaining the algebraic sum of the total range in minutes for the region considered (4200 in the case of Japan) and the known ranges of the species. For northern forms this value is positive, and for southern forms it is negative:

$$(B - O) - (4200 - A); \quad or, \quad -((4200) - A) - B - O)$$

where A is the known northern limit, and B the known southern limit of the species, with the equator (O) as the southern limit of the region. It is assumed in these computations that the distribution data are reliable, that the given form occurs at all localities between its limits of range, and that the shore

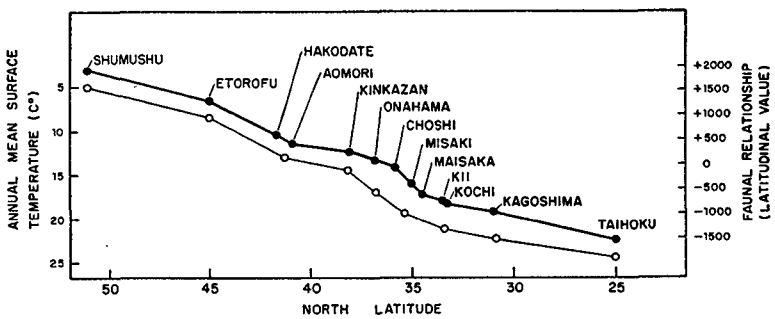

FIGURE 7.—*Correspondence between the latitudinal value for the flatfish fauna and average temperatures along the coast of Japan*

Kuronuma (1942)

line is linear along its north-south projection. Vertical range is not considered. The latitudinal value for the fauna of a given locality may be computed as follows:

$$\frac{\text{Sum of latitudinal value of each form at locality}}{\text{Number of forms at locality}}$$

Kuronuma concluded from his computations of the flatfish fauna that there was no evidence of sharply defined faunal divisions or provinces, but that each species or subspecies was distributed independently from the others in the group concerned. He also found a close correlation between the rate of change of composition of the flatfish fauna and change of mean temperatures along the Japanese coast (Fig. 7).

At the present state of our knowledge, the delineation of provinces, at least in its finer details, is a problem that is not amenable to strict statistical analysis. Schenck and Keen themselves, despite their attempt at statistical objectivity, propose a subjective definition for a province: "A marine molluscan province is a subdivision of a

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region, subregion, or realm, populated by a distinctive assemblage of species." (Schenck and Keen, 1936, p. 923).[1]

Nevertheless, the substantial agreement in the extent of the major biogeographic divisions of the shore provided by diverse and unrelated studies does indicate that elaborate statistical treatment may do little more than refine certain details. It is interesting to note, for example, the correspondence between biogeographic divisions based on faunistic and floristic studies and the distribution of characteristic types of marine fouling growth in harbors (Redfield and Ketchum, 1952).

DISTRIBUTION IN THE HIGH SEAS

Distribution patterns for the high seas, the bathypelagic regions and the great deeps, are still incompletely known, although the broad outlines of the major pelagic realms of the upper or photic layer may be drawn. Figure 8 shows that these major

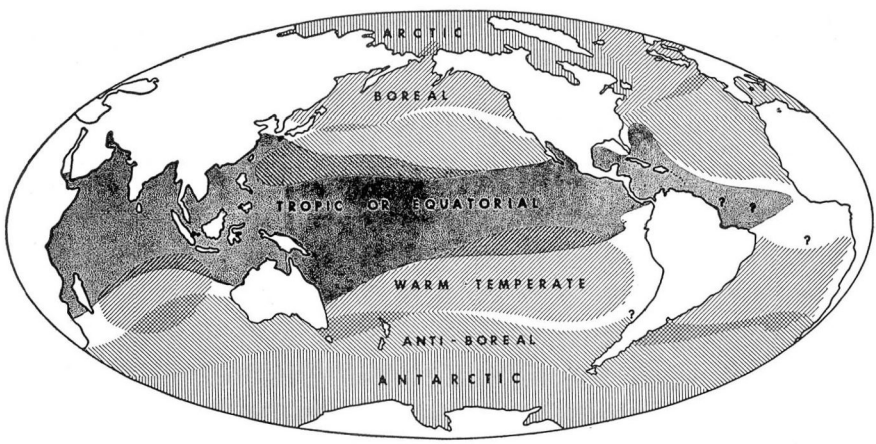

FIGURE 8.—*Generalized distribution of the major types of plankton*
Principally according to Steuer (1933).

divisions roughly correspond to the latitudinal climatic belts of the sea, with a number of broad transitional areas. The extent and location of these transitions may vary seasonally and are accordingly not simultaneous in both northern and southern hemispheres. For several regions such transitions have not been observed, or for which the data are inadequate; these have been left blank on the figure. There are preliminary indications that the region in the northeastern Pacific between the Boreal and Warm-Temperate regions harbors an endemic fauna. Nevertheless, this diagram is not essentially different from that drawn up by Steuer (1933) and suggests the still-incomplete status of plankton studies in the oceanic region.

It should be emphasized that this diagram refers only to the high seas or epipelagic plankton, omitting neritic faunas and the "displaced benthos" of the Sargasso Sea (Fig. 9). While the Arctic, Indo-Pacific tropic or equatorial, southern cool tempera-

[1] A corallary to the mid-points method is its application to fossil assemblages as a means of inferring possible temperature conditions in the past; (See Chapter 2 of Volume 2).

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ture or antiboreal divisions indicate regions with uniform faunal and floral assemblages, the boreal and northern warm-temperate regions are somewhat less uniform, and the affinities of the Atlantic tropical region with that of the Pacific seem to be even less pronounced. The boreal region lacks, according to Ekman, a truly epipelagic endemic fauna but is populated mainly by cosmopolites, Arctic-North Atlantic species, and occasional species from intermediate depths. Nevertheless, the planktonic biota in general is much more uniform than is that of the neritic regions or of the littoral benthos. As Ekman (1953, p. 319) has expressed it, "the main faunistic regions of the high-oceanic pelagic fauna are more weakly characterized taxonomically than the main regions of the shelf."

The bathypelagic regions, roughly from 500 meters to almost the bottom, constitute the greatest part of the biosphere. Of the total volume of the oceans, more than 75 per cent occupies the depths below 1000 meters. In this vast realm a host of curious and wonderful creatures move and have their being. Medusae, crustaceans, cephalopods, and fishes are among the more abundant animals, while bizarre nemerteans are less abundant but no less characteristic. The distribution of many of these animals is incompletely understood, but many of them are considered cosmopolitan at their depths in all the seas of the world, and the ranges of other species are being extended by further collections. This is to be expected because of the continuity of similar water masses at these depths (Coe, 1946). Some of the forms may be associated with certain

FIGURE 9.—*Displaced benthos of the Sargassum*

The examples illustrated are taken from Sargassum found near shore in the northern Gulf of Mexico, and include *Scyllaea pelagica*, *Portunus sayi*, *Histrio histrio*, *Anemonia sargassensis*, *Platynereis dumerili*, *Litiopa melanostoma*, *Latreutes fucorum*, Bryozoa, serpulid worms, and hydroids. Inset: details of hydroids, a caprellid, the pycnogonid *Tanystylum orbiculare*, a juvenile ophiuran, and a polyclad worm.

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water masses, best expressed in terms of density characteristics, as Pickford (1946) has suggested for *Vampyroteuthis*, and Haffner (1952) for fishes of the genus *Chauliodus*, although the data are not completely convincing in either case. In the latter example the picture is complicated by the diurnal migration of the animals from their daytime level of 500–2500 meters to less than 500 meters at night, although it appears that various populations have distinct distributions. Temperature alone does not have a useful correlation with distribution. The study of *Chauliodus* suggests that there may be distinct populations or races in other bathypelagic forms usually considered cosmopolitan.

It is difficult to infer much about the zoogeography of the deep-sea benthos, although recent expeditions by the Danes and Russians have added much to our knowledge of this life. Most of the species are still represented by single specimens or single collections, and such records are useless for zoogeographical purposes. Nevertheless there is slowly accumulating evidence that the commonly supposed cosmopolitan distribution of much of the deep-sea benthos may be essentially correct. Many deep-sea genera and families are cosmopolitan, although there are indications of distinct faunas in the Indo-Pacific and Atlantic basins. Here, however, the traditional picture may not be the correct one; Madsen (1953) suggests that the deep-sea echinoderms may be separated into Indo-Atlantic and Pacific elements, although this again may be an artifact of collecting. There are also some differences in the fauna of the trenches, Bruun's "hadal" zone. For some reason, most of the known Pogonophora have been collected in the Kurile-Kamchatka trench and in the Bering Sea, while anemones seem to be more characteristic of the South Pacific trenches. The evidence suggests that the great trenches have endemic subspecies and species in addition to these differences. The problems of distribution and origin of the deep-sea fauna are taken up in more detail in Chapter 22.

TEMPERATURE BASES OF DISTRIBUTION

From the outset temperature has been considered the most important single factor governing distribution; hence, the behavior of temperature as a factor in the environment and the relations of organisms to temperature have been of prime concern to biogeographers.

One of the earliest generalizations, for example, was made by Lamouroux (1816) who hypothesized that in the tropics the organisms found in the depths and on the bottoms were those found at the surface in polar regions, and those in the tropics at 100–200 fathoms were to be expected at the surface in temperate regions. Since the time of Lamouroux, at least, there has been a general feeling that biotic elements occur at lower levels toward the warmer latitudes. Gislén (1944), for example, found "a clear tendency to depression of the levels of the communities, usually amounting to 3–5 decimeters" along the Pacific coast of America. Knight (1947) observed that the levels of *Fucus vesiculosus* and *Fucus serratus* (immediately below) were below "Mid-tide level" on the Devonshire coast, but that on the Isle of Man, 3.5 degrees north, this mid-tide level occurs at the break between the two species. A similar shift was noted in the lower limit of *Fucus serratus* where it meets the *Laminaria digitata* population. Knight suggested that the fucoid zone at least "thus appears to emerge from the sea for longer periods with increasing latitude." Conversely, there may be a submergence of warm-water elements northward below the colder surface layers (Fig. 10).

Such variations in bathymetric distribution with latitude are familiar to marine biologists and are usually considered to be governed by the temperature tolerances

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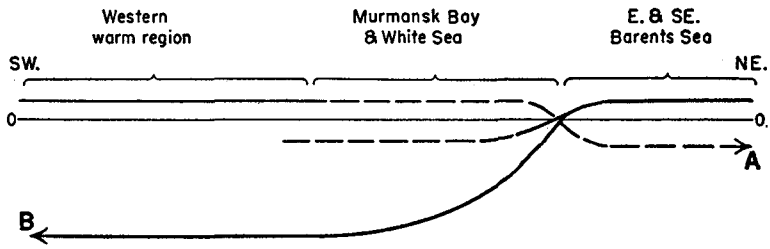

FIGURE 10.—*Latitudinal submergence in northern Europe*
Zenkevich (1947)

of the organisms concerned. This may involve, in the case of some intertidal organisms, the degree of exposure to air, so that an organism may occur intertidally in cooler waters where its exposure to air would provide the warmer temperatures necessary, for example, to sexual development (Southward and Crisp, 1954). Another aspect of latitudinal variation in distribution is the occurrence of species beyond the range of the main population in isolated patches, either in regions of upwelling, as documented for the coast of Baja California by Dawson (1951), or in pockets of colder or warmer water associated with topographic features. Forbes (1859, p. 222–224) attributed the occurrence of such extra-territorial patches of northern species in deeper waters around the British Isles (which he termed "outliers") to isolation by an elevation of the sea bed. Nevertheless, he emphasized (p. 17) the influence of existing physical factors on distribution:

> The distribution of marine animals is primarily determined by the influence of climate or temperature, sea-composition and depth, in which pressure, and the diminution of light are doubtless important elements.

Although we may grant that temperature is the most significant observable factor governing distribution in the shallow sea (where the quantity of light, which is simply another aspect of radiant energy, may complicate the picture), the exact manner in which temperature controls distribution is not always obvious. Many biogeographers are satisfied with knowing the annual mean temperatures for the regions concerned, others require the maximum and minimum means. A cursory examination of temperature data will demonstrate, however, that localities with the same mean temperature may have different extremes, or that a region with an equable temperature may have the same mean as one with a well characterized seasonal progression. The mean annual temperature will therefore tell us little about the essential ways in which one environment may differ from another. Thus the picture of littoral provinces shown in Plate 1, based on annual means and biotic similarities, is applicable only in a broad way.

It has long been known that organisms may have different temperature requirements or tolerances at different stages in their life histories (*see* Chapter 8 for discussion and documentation), but biogeographers have only recently attempted to synthesize these differentials in a general scheme. The most comprehensive statement is that of Hutchins (1947), although the germ of this is to be found in a paper by Allee

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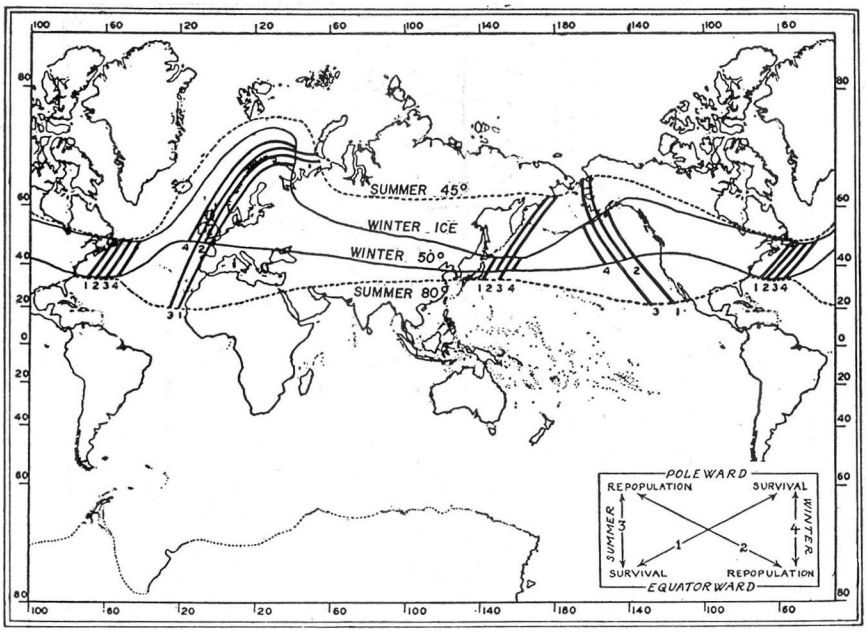

FIGURE 11.—*Four zonal types of distribution*

Extent of the four major zonal types based on the mean temperatures at Newfoundland and Cape Hatteras as limiting intensities (from Hutchins, 1947).

(1923); Hutchins, however, has provided documentation. He postulated four major types of distribution in the northern hemisphere in relation to the latitudinal distribution of a species. These are: (1) minimum temperature for survival; (2) minimum temperature for repopulation; (3) maximum temperature for repopulation; and (4) maximum temperature for survival. On this basis one would expect, *a priori*, the four types of distribution indicated in Figure 11 (inset). Type 1 would be representative of an organism of which the poleward limits of its range are established by the coldness of winter. In such a case it is expected that during the summer the water is warm enough to permit reproduction and replacement. In the case of this Type 1 organism its equatorward distribution would be limited by the warm summer temperatures, with winter temperatures cool enough to permit reproduction and repopulation. Type 2 would be regulated similarly by temperatures affecting the repopulating mechanisms of the species without inhibiting survival. Type 3 and Type 4 are the converse of Types 1 and 2 respectively.

An example of Type 2 is *Ascophylla nodosa*, which at its northern limit, Greenland, fruits in the summer and at its southern limit, New Jersey, fruits in the winter. This particular species has occasionally been washed in at Bermuda but has never become established there. It thus appears that farther north the summer temperatures do not permit reproduction or repopulation, nor do the winter temperatures fall low enough in the south to permit reproduction. Furthermore it appears (Setchell, 1932), since this species only "occasional washes in" at Bermuda, that *Ascophylla* is not limited by being killed by the summer temperatures at the latitude of New Jersey. It is known from measure-

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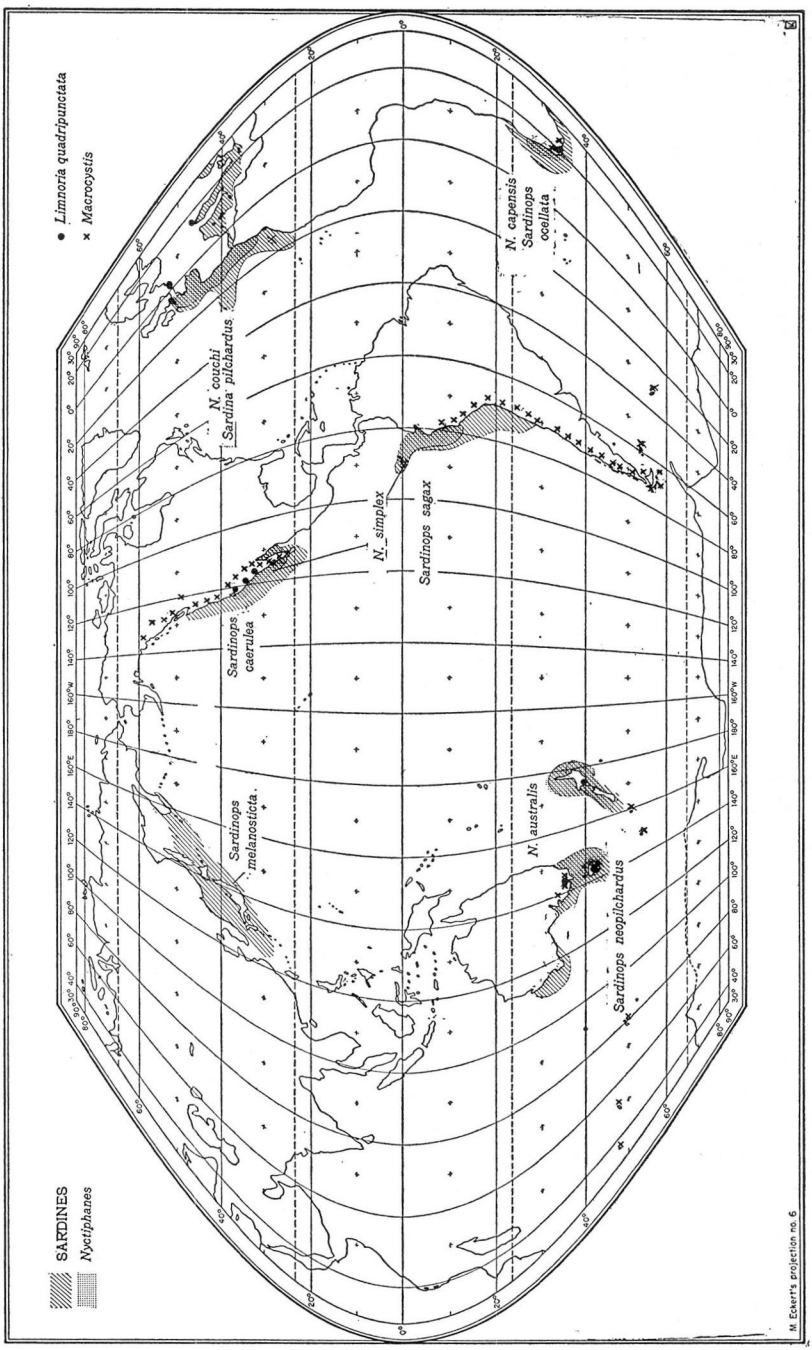

FIGURE 12.—*Patterns of longitudinal and latitudinal discontinuity as represented by certain species and genera*
(Compiled from various sources)

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ments of growth at Woods Hole that *Ascophylla* almost ceases to grow during the warm period of the year.

The ramifications of this scheme are brought out when the distribution of winter and summer maximal and minimal isotherms on the four northern hemisphere coasts are considered. Figure 11 shows the distribution of the winter minimal and summer maximal temperatures at Newfoundland and the winter minimal and summer maximal temperatures at Cape Hatteras. From this figure it is to be noticed that the maximum and minimum figures coinciding at Cape Hatteras or Newfoundland do not coincide on the other three major coasts involved.

Another type of limitation of range discussed by Hutchins is the possibility that on different coasts or in different years the zonation type of a given species may be different. He gives as an example *Balanus amphitrite*, which is limited poleward by inability to survive winter temperatures below 45°F. and is unable to reproduce unless the summer temperature reaches 65°F. On some coasts the positions of these extremes in latitude are different and thus the poleward distribution of this species would be limited by whichever of these factors occurred nearest the center of distribution (*i.e.*, the equator in this case).

Hutchins concluded that species occurring on the eastern coast of North America uniformly between Cape Hatteras and Newfoundland and also occurring on the other three northern hemisphere coasts would be segregated according to his four types on the other three coasts corresponding to the same extreme temperatures with which they are correlated on western Atlantic shores. Two such species, *Balanus balanoides* and *Mytilus edulis*, were cited as examples.

Implicit in Hutchins' system is another phenomenon, the longitudinal discontinuity of certain species. These are stenothermal forms which occur on the coast of Europe but are absent from the Atlantic coast of America presumably because the temperature ranges are too great. The example given by Hutchins is the hydroid *Syncoryne eximia*. There are a number of spectacular examples of such latitudinal and longitudinal discontinuity, involving both northern and southern hemispheres. The best known of these, at least to ichthyologists, is that of the sardines, discussed and mapped by Regan (1916); another is that of the giant kelp, *Macrocystis pyrifera* (Setchell, 1932; Womersley, 1954). Other examples are also known, involving both pelagic and littoral organisms (Menzies and Hedgpeth, in press). Some of these are indicated on Figure 12, which demonstrates the basic pattern of identical or closely related forms that live on the western sides of continents of both hemispheres but are absent from the tropics.[2] Some of these may occur in the Mediterranean region, where northern species are not uncommon below 60 m, and as relicts in the Adriatic (*see* Ekman, 1953, p. 86–87); others extend into southern Japanese waters. Although the data are as yet incomplete, enough are available to suggest that we are here dealing with reproductive stenotherms requiring not some minimum or maximum mean, but a narrower range within the extremes (as suggested by Hutchins' Type 1). This range must also be of some minimum duration—that is, the required temperature

[2] As will be noted from this figure, the sardines are given as belonging to several species in two genera. Recent studies by C. L. Hubbs (personal communication) suggest that the sardines are a more closely related complex than suggested by their separate names.

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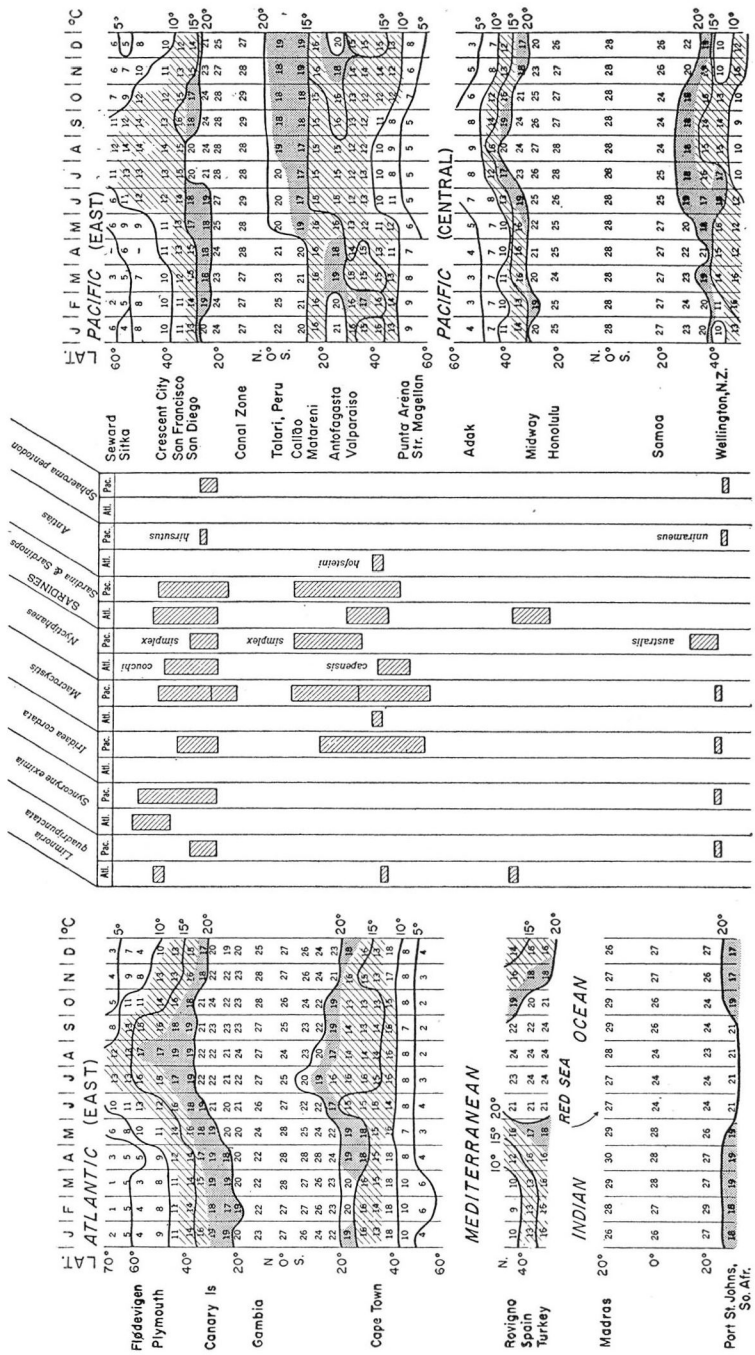

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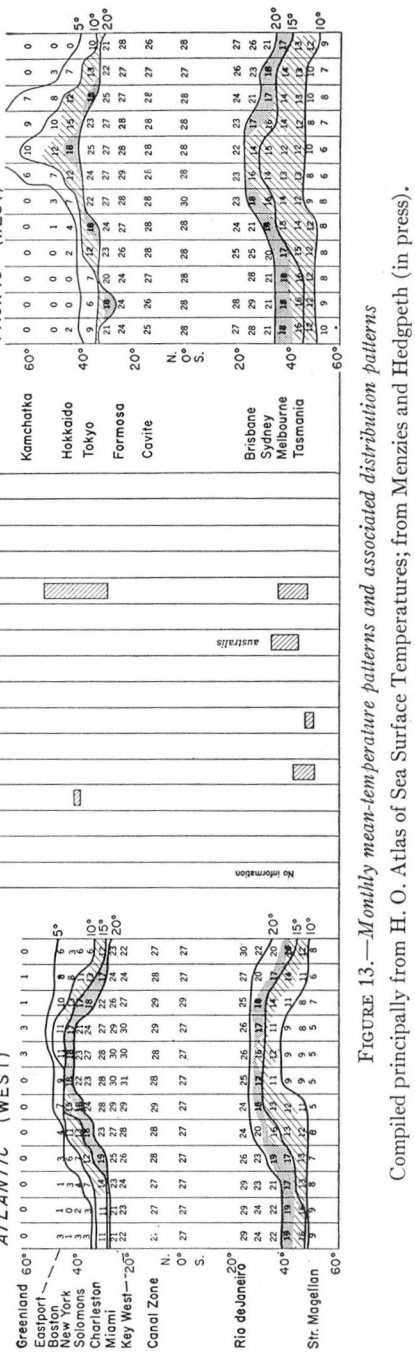

FIGURE 13.—*Monthly mean-temperature patterns and associated distribution patterns*

Compiled principally from H. O. Atlas of Sea Surface Temperatures; from Menzies and Hedgpeth (in press).

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for reproduction is quantitative as well as qualitative—and the duration of the temperature must also be taken into consideration. If an organism requires two successive months of a given mean temperature range for reproduction, it cannot, of course, reproduce in an otherwise favorable region where the 2 months may be separated by periods of higher or lower temperatures.

For some of the species indicated on Figure 13—*e.g.*, *Limnoria quadripunctata*—the required range is 12°–16°C, for 5 months of the year. For the main stock of the Pacific pilchard or sardine, the spawning range is given as 12.5°–16.5°C., with "only negligible amounts of spawning" at lower temperatures although some spawning may occur up to 20° (Ahlstrom, 1954); the required duration of the spawning temperature is not stated. A number of other examples are indicated on Figure 13, together with the temperature means for all months of the year. For the organisms examined, there seem to be two types of stenotherms, those falling between 12°–16° and those between 17°–19° or perhaps 12°–19°C. This figure (compiled from tide-station records and the U. S. Hydrographic Office Atlas of Sea Surface Temperatures) indicates that it would require relatively small changes in monthly means in some regions to permit the dispersal of reproductive stages or gravid females or, conversely, to affect seriously the spawning in a given year. It is to be remembered that, when the spawning or perhaps optimum range of a species is only 4°C., a 1-degree change is a matter of 20–25 per cent change in a given environmental factor; far less drastic changes in some environmental factors may alter the distribution of a species.

The identity and near identity of the forms considered in this study suggest that at some time in the past neritic temperatures in the tropics, particularly along the western coast of the Americas, were markedly lower than they are now, and that these conditions may have occurred sufficiently long ago to permit subsequent trends in speciation to occur in such groups as the euphausiids and perhaps the sardines, while other groups have retained their specific identity, perhaps because of slower rates of evolution or because of more recent dispersal. The occurrence of some of these discontinuous organisms in the Mediterranean, southern Japan, and the southern Galapagos suggests that such populations have recently become acclimated or that these records are for the most part of individuals or populations beyond their breeding ranges.

Furthermore, records of occurrences of species falling into this pattern in regions lacking the observed temperature requirements are suspect. This is also indicated by Hutchins' work, which demonstrated for example that *Balanus balanoides* should not occur along the northern coast of the Gulf of Mexico, despite published records to the contrary. This record has not been verified and is undoubtedly erroneous (Hedgpeth, 1953). Conversely it is possible that some species, considered distinct on geographical grounds, may be more closely related than indicated by their different names. Womersley's (1954) division of *Macrocystis*, for example, in which different temperature ranges for the same species are assumed in different hemispheres, has been questioned on these grounds by Menzies and Hedgpeth (in press).

There are, of course, exceptions. An example is apparently the barnacle *Elminius modestus*, a native of the Antipodes, whose recent colonization in Britain would suggest that it might be a reproductive stenotherm. Crisp and Davies (1955), however, found that this barnacle can reproduce at any season, in temperatures up to 25°C,

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as long as temperatures do not fall below 6°C. This is obviously one of those estuarine organisms which might be expected to occur all over the world (*see* Chapter 23), and in view of this eurythermy its comparatively limited distribution is something of a puzzle.

It may be that the hypothesis advanced by Moore (1952) of a dual-temperature control for planktonic organisms which undergo pronounced vertical migrations is applicable to other types of life histories as well. In attempting to assay the temperature relationships that may govern the distribution of an organism, we must agree with Bullock (1955, p. 333):

> Without further work we cannot assume that the monthly average, daily average or any given measure short of the complete curve of the temperature against time, is biologically appropriate, since we do not know how the organism weights equal departures from the average in the two directions or for different lengths of time.

BIPOLARITY

Latitudinal discontinuity has long been a favorite topic for biogeographers (Ekman, 1953, Ch. XI). Originally it was considered an indication of the former continuity of biota now widely separated at the polar regions; from this it followed that either the middle latitudes were once much cooler than now and the bipolar species had become separated by the gradual warming of the tropics, or that they were originally warm-water species now acclimated to cold regions after being forced out by newer species. The corollary to either hypothesis is that the fauna of the colder or polar regions is older than that of the tropics—that is, it is essentially relict in character.

The bipolar theory—or hypothesis—was first espoused with particular vigor by Théel (1886; 1911), although the systematic data were challenged by his contemporaries, notably D'Arcy Thompson (1898). Gradually the species considered to be identical fell before critical taxonomic examination, until there remained a few *bona fide* bipolar genera with closely related species. The most spectacular of these is the genus *Priapulus*, upon which Théel based much of his case for bipolarity (Fig. 14).

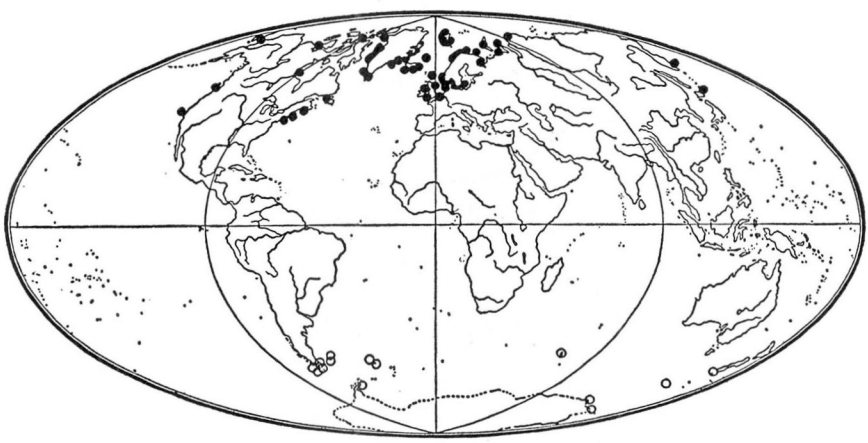

FIGURE 14.—*Bipolar distribution of the species-pair* Priapulus caudatus (●) *and* P. tuberculato-spinosus (○)
From Lang (1951)

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Other critics attacked the idea that the separated populations were relict in character, preferring the view that migrations at cooler depths in the tropics were in active process ("tropical submergence") or had taken place during comparatively recent periods of cooling. These various hypotheses were summarized by Stiasny (1935), who evidently felt that the problem was solved, since he concluded; "Es gibt kein Bipolaritätsproblem mehr." (*See* Figure 15). But, as Murphy (1928) remarked, the old theory always turns up in one way or another, and the present version is that of antitropicality—that is, there are many organisms on both sides of the tropics that once had continuous ranges during Pleistocene time (Berg, 1933; Hubbs, 1952). Even at the present time, however, the tropics are not an impassable barrier to some species, as indicated by the occurrence of many estuarine organisms in both hemispheres (*see* Chapter 23) and possibly the recent dispersal of the barnacle *Elminius modestus* from the Antipodes to the shores of Europe (Den Hartog, 1953). It is improbable, however, that such an extraterritorial establishment has been achieved on the basis of only a few individuals; a massive inoculation of larvae from breeding adults would be required, and in the case of *Elminius* the event evidently depended on a combination of circumstances that had not occurred previously. Since regular shipping has been going on for at least 100 years, and the time required for surface passage has probably not been greatly reduced in the decade before 1943 (when *Elminius* was first discovered in Europe), this particular dispersal may have been due to the massive shipping of the wartime years (H. Barnes, personal communication). Once the migration to a new region is accomplished, there still remains the problem of establishment, which requires some minimum population as well as ecologically favorably conditions:

> A critical distance must exist, related to the current system and the duration of free swimming stages, beyond which the rate of settlement of the larvae is normally insufficient to reach the minimal population density within the life-time of an individual. (Crisp and Southward, 1953).

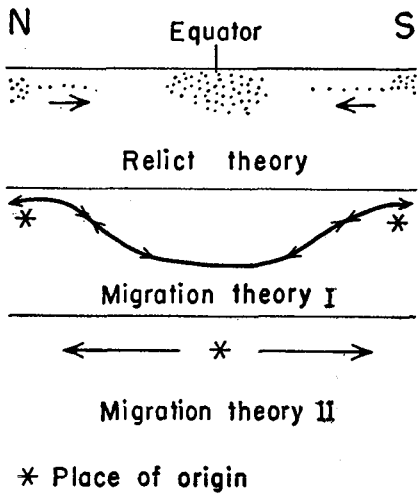

FIGURE 15.—*Summary of theories of bipolarity*
From Stiasny (1935)

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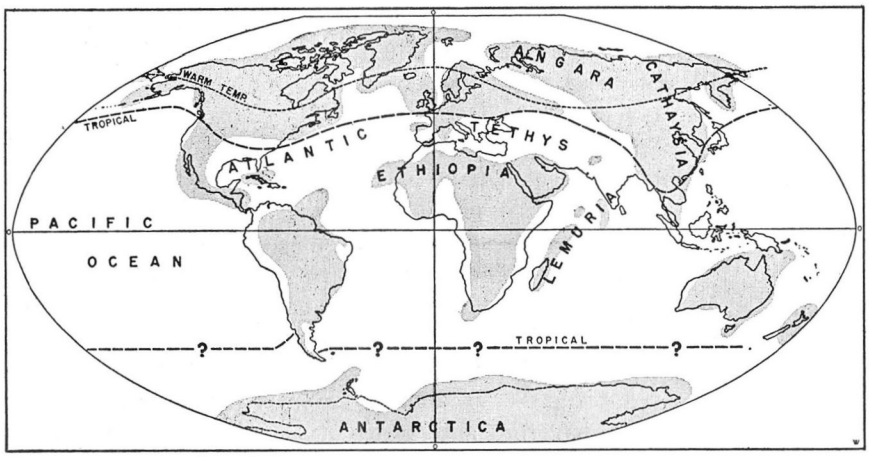

FIGURE 16.—*Relationship of land and sea and suggested temperature conditions in Eocene times*
After Oakley and Muir-Wood (1949) and Durham (1952) with modifications suggested by R. W. Fairbridge.

In the case of an ovoviviparous organism, such as *Limnoria*, migration of more than one gravid female probably is necessary to establish a new population.

The migration of an entire fauna poses even greater problems. Although the Chatham Islands are less than 600 miles from southern New Zealand, in the same biogeographic region (without pronounced temperature barriers and reached by currents which have successfully carried many forms from New Zealand) the biota is still an incomplete and possibly random sample of the parent assemblage, although migration has been apparently continuous through Pleistocene times. Many of the common New Zealand species (including *Elminius modestus*!) are absent (Knox, 1954). With such an example in mind we cannot assume that the observed distribution patterns of stenothermic organisms are the result of migration across the present temperature barriers as a common and easily recurring event.

While the discontinuous distribution of organisms in the northern and southern hemispheres suggests somewhat cooler temperatures in Pleistocene or early Recent times, or at least slightly reduced temperatures along the western sides of continents as implied in Figure 12, there is also a convincing amount of evidence for much warmer temperatures in earlier geological periods, particularly during Tertiary times (Durham, 1950); according to Emiliani (1954) the average temperature of abyssal water in the Oligocene was about 10.5°C., which would mean that the average temperature of the oceans in the Tertiary was much higher than today. (*See* Chapter 10.) During the Mesozoic and early Tertiary, tropical or warm-water faunas occurred at comparatively high latitudes (Fig. 16), and the present wide occurrence of tropical species is considered to be the heritage from a tropical Tethys of Cretaceous and Eocene times. This would imply that the tropical biota is relict in character, since there appears to be no evidence from the marine fauna, at least, to substantiate such

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notions as continental drift or the shifting of the poles (see Durham, 1952).[3] It may be that temperatures were more equable in Mesozoic and early Tertiary times, that strongly contrasting polar and tropical zones are comparatively recent phenomena in the history of the earth or at least are associated with major epochs of glaciation. On the other hand Zenkevich (1949b; 1949c) suggests that the cold-water biota is at least as old as the tropical, and that there have been uninterrupted cold as well as tropical zones in the seas for hundreds of millions of years. The greater variety of the tropical biota is attributed to the diversity of environments, which provides greater possibilities for evolution. This implies that the problems of distribution and dispersal are the same for the past as the present—i.e., that there has always been a considerable range of temperature in the seas and that there were stenothermic and eurythermic organisms in them. Nevertheless the evidence suggests that the colder regions have at times been greatly reduced or expanded in extent, and with this the patterns of temperature distribution have probably varied considerably in the past.

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[3] Polar wandering and continental drift are not, however, impossible according to W. H. Munk (1956). Recent geophysical reconsiderations would suggest wandering of the pole by almost any degree necessary to satisfy biogeographic requirements, but such movements may have occurred well back in the Paleozoic rather than in Mesozoic or Tertiary times.

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Chapter 14

Particulate Organic Detritus*

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Our hydrosphere, of which the oceans constitute by far the greatest portion, is far from being a clear, homogeneous solution of dissolved salts. Rather, it is a highly complex, heterogeneous system of particulate materials, ranging in size from macroscopic aggregates down to colloidal micelles of solid, liquid, and gaseous nature, dispersed in an aqueous saline medium. Furthermore, the content of dissolved salts ranges from a few fractional parts per million in fresh alpine lakes and in granite-floored streams which feed them, through somewhat more substantial concentrations near the mouths of large rivers and in estuarine waters, achieving values of 33.0 to 35.0‰ in the sea, and up to full saturation (ca 300 ‰) in natural or man-made, land-locked bodies of salt water.

Concentrations of leptopel (Fox, Isaacs, and Corcoran, 1952), the finely particulate organic and inorganic matter suspended in natural waters, are minimal in clear, blue mountain lakes, are probably highest in sluggish or stagnant waters of tropical or subtropical swamps, and occupy intermediate but widely varying values in the oceans.

The various colors of marine waters, from deep blue in oceanic areas through various shades of blue green, yellow green, or even ruddy or brownish in neritic or near-shore regions, reflect the general turbidity and corresponding amounts of responsible microplankton and particulate organismal products of decay or excretion.

Concentrations of organic (*e.g.*, protein, lipid, and polysaccharide) and inorganic leptopel (silicates, insoluble carbonates, phosphates, hydrous oxides, etc.) and proportions between these two classes of suspended matter are highly variable, even in temperate waters. Their disposition depends upon depth, temperature, light, relative densities, water movements, season, and proximity to land (Goldberg, Baker, and Fox, 1952).

An average general profile of organic leptopel concentrations in littoral and neritic waters may show wide ranges, *e.g.*, from a few fractional parts per million in mid-ocean regions and in deep-lying zones, through values of several milligrams per liter nearer the surface of neritic areas, to ten-fold or more such concentrations in or immediately beneath surface slicks. But, while concentrations are measured in parts per million in the waters themselves, the amounts of organic matter may rise by ten thousand-fold where the surface-active components have become adsorbed upon solid surfaces (*e.g.*, of beach sand, which may involve 1 per cent of organic matter) or may even reach a hundred thousand times their values when adhering to fine silt or to bottom muds (Fox, Isaacs, and Corcoran, 1952).

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The whole body of ocean water may be likened to a vast, loosely organized but actively metabolizing cell, its rather saline but organically dilute "sap" receiving some of its dissolved nutrients (*e.g.* NO_3^-, $PO_4^{\equiv}$) from terrestrial runoff, some from electrical storms via rain, and a considerable portion from bacterial action in the endemic biochemical cycle. If we carry the cellular analogy further, we may compare various metabolic features of living matter with processes applying to the ocean's fluid medium. There is a vast, complex circulatory system, involving many well-defined currents; by means of this system, nutrients and dissolved gases receive transportation, while water masses of different original temperatures and salinities are partially mixed. Closely related to the atmosphere is a "respiratory" exchange of O_2 and CO_2 through the sea surface, as well as an extensive "transpirational" exchange of water in its respective vaporous and fluid states as it evaporates from and is ultimately returned to the parent mass (Chapter 10). Photosynthesis proceeds on an enormous scale through chlorophyll-bearing planktonic cells, as well as through larger seaweeds of the lighted zones. Finally, the fluid medium bathes countless organized tissues, whose somatic integrity and reproductive faculties are assured by continuous supplies of finely divided food material, whose excretory and other osmotically expelled products are carried away. Some of the solid, more refractory wastes may gradually find their way to the floor of the sea.

The ocean has regions of high variability, not only with reference to the organic content of its water, but as regards intensity of metabolism. There may be minimal values of the total organic carbon and organic nitrogen budget, for example, at equatorial latitudes, and in deep waters of the Pacific, while total metabolism may well be maximal in temperate latitudes at and near shore lines; finally, they may vary highly with season in polar regions, where they are relatively low with the winter freeze and high with the spring thaw. It is with the nature, measurement, distribution, and metabolic utilization of organic matter, in both its suspended (leptopelic) and adsorbed (pelogloeal) condition, that this chapter is primarily concerned.

The water is drawn through microfiltrational membranes of cellulose acetate and nitrate, whose pores retain bodies of diameter no greater than 0.5 μ (often 0.2 μ). The filtered residue is stained, washed, and dried *in situ*, and the membrane is finally rendered microscopically transparent with a medium of suitable index. Thus one may gain a clear, qualitative idea and much quantitative information regarding the numbers, size distribution, and total estimated volume and weight of cellular material present. Ashing of sufficiently large collections made in this manner will provide values of total inorganic leptopel per unit volume (Goldberg, Baker, and Fox, 1952).

To determine the total organic matter present, the water is passed instead through finely divided inert, inorganic powder (*e.g.*, MgO and refined Celite) capable of retaining even the finest colloidal micelles by adsorption. Complete oxidative digestion of the sample, as collected upon the pad of inert powder, will yield corresponding amounts of CO_2 or ammonia, either of which may be measured chemically, or will involve a commensurate reduction in the amount of the carefully measured, standard oxidant, such as chromic acid. Alternatively, total ether-soluble lipids may be ex-

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tracted and determined from such samples, or measurements may be conducted on total diagnostic natural pigments (*e.g.*, carotenoids) similarly extractable.

Whatever may have been the complex biochemical nature of the first true living, reproducing cellular entities, their common parent was the hydrosphere, this vast, relatively unorganized "cell" with irregular boundaries, and with a great diversity of raw organic and inorganic materials from which the newly formed organized units selectively drew their nutritional supplies (Oparin and Morgulis, 1953). The ratio between organized and unorganized organic matter was necessarily greatly in favor of the latter, and unorganized organic materials still predominate over living matter. But, with the evolution of living matter, there have been great qualitative changes in the kinds of nonliving organic compounds which persist in the environment. It is extremely doubtful whether living matter is still being formed *de novo* in today's world, for there now exist countless species of potential consumers among our microflora (Oparin and Morgulis, 1953). The unorganized matter of the environment is composed largely, if not entirely, of biochemical detritus—*i.e.*, derived from catabolic wastes, undigested, partially resolved residues, or whole bodies of dead organisms.

It is naturally to be expected that regions of high organic content will support extensive and diversified populations of organisms. The two manifestations are inseparably associated environmental units; the organized and unorganized organic matter exist in a kind of dynamic equilibrium or state of flux, until or unless outside influences bring about local changes. Still, in any reasonably stabilized locus, or considering the marine world as a whole, the mass of the accumulated, standing crop of unorganized, detrital organic matter must exceed considerably that of the aggregate living organisms. Such a condition is a cumulative heritage from the primary marine producers—*i.e.*, the photosynthetic phytoplankton—and is indispensable if life as we know it is to be assured of continuance.

Concentrations of organic matter in true solution can hardly exceed a small, fractional part per million in most marine waters (Fox, Oppenheimer, and Kittredge, 1953). The material is thus inaccessible to animals, even those of the filter-feeding classes and, at such low concentrations, is doubtless used but slowly and incompletely by bacteria, fungi, or other plant cells (ZoBell, 1940; ZoBell, and Grant, 1943). But organic matter in suspension itself, or adsorbed as it inevitably is in considerable part to inorganic suspensoids, is readily utilized as potential food, since suspension feeders are equipped to resolve the disperse phase of a fine "puree" from its continuous medium, while they cannot similarly resolve a tea or "consomme" of true solutes.

Let us consider briefly the metabolic features of a few marine species, which depend upon suspended or adsorbed organic detrital matter for their nutrition. The sea mussel, *Mytilus californianus*, may be taken as representative of suspension-feeding pelecypods or lamellibranchs; the polychaete worm, *Thoracophelia mucronata*, will typify the wholesale swallowers or "shovelers," while the intertidal gastropod, *Littorina planaxis*, exemplifies the large class of "scrapers," which remove adsorbed pelogloea by means of their radulae.

A community of a million mussels (*e.g.*, on a moderate area of rocky coast), during their second year of life, remove the finely suspended matter from at least

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22,000,000 tons of water—*i.e.*, from a volume of ocean water about 1 mile square and 25 feet deep. From such water, containing on the average 5 mg of suspended organic matter per liter, the animals may filter about 121 tons of potentially nutritive material. They augment their own combined weight of organic matter by some 4.1 tons, thus demonstrating a ratio of filtered organic matter to that incorporated in tissues of about 3.3 per cent. Not all the material filtered from the water is actually ingested by the mussel however; some is rejected by the gills and palps as pseudofeces. Moreover, a considerable portion of even the organic matter swallowed is not digested by the mussel—*e.g.*, humus and other refractory materials, as well as many living, cellulose-enveloped dinoflagellates (Coe and Fox, 1944; Coe, 1945; 1947; Fox, 1950).

Obviously these factors will combine to favor a greater efficiency on the part of the consumer. In order to derive an alternative, conservative figure for this efficiency, we may refer to the figures estimated by Fox and Coe (1943) for a community of mussels, 50 per cent of which are in their first year of life, 30 per cent in their second, and the remaining 20 per cent in their third. A hundred such animals have been estimated to void a total of 1960 g of feces in 1 year and to produce some 210 g of gametes, while laying down a total of about 139 g of somatic tissue (all figures calculated on an ash-free, dry-weight basis). Thus the quotient of $(210 + 139) \times 100$ divided by 1960 amounts to 17.6 per cent "efficiency." Even this can hardly be a maximum figure.

Manifestly, lamellibranchs such as mussels and their kin—*e.g.*, oysters, clams, scallops, etc.—as well as allied suspension-feeding forms including tunicates, sponges, and the like are responsible for removal of vast quantities of finely particulate organic matter from the sea; they incorporate significant fractions of it into their own tissues and void still greater portions of it, as large fecal aggregates, which may find their way to the sea floor, there to enrich the supply of food for benthic animals and their associated microflora. Pelagic suspension feeders, including many copepods, euphausiids, and salps, are beyond doubt responsible for the principal role in marine biochemical cycles, of which suspended organic matter is an indispensable part.

Considering next the polychaete worm *Thoracophelia mucronata*, we may gain a roughly quantitative idea of the role occupied by the large class of animals which subsist, as does this species, by ingesting the particulate substrate of their natural habitat. *Thoracophelia* inhabits damp sand along the shores of Western North America, where it continuously cycles sand through its alimentary tract, deriving its nutrition mainly from the relatively small quantities of colloidal or otherwise finely particulate material adsorbed from the water to the siliceous surfaces.

A typical worm bed may be 10 feet in width and may extend for indefinite distances along the sandy foreshore, limited only by rocky barriers.

A worm bed 1 square mile in area (*i.e.*, 500 miles long by 10 feet wide) and 1 foot deep contains some 2.64×10^7 cubic feet of damp sand, which, when dry, would weigh about 1.41×10^6 tons. Using the average figure of 3000 worms per square foot, as derived from counts, there should be nearly 8×10^{10} of the animals resident in the bed, weighing an aggregate 3500 tons. Since each worm may swallow about 2100-fold its own (wet) weight annually, these animals are capable of cycling at least 7.3×10^6 tons of sand per year, and of converting 700 tons of the 7×10^4 tons of

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available organic matter into living tissue, if one assumes an annual life cycle. The animals thus demonstrate a value of about 1 per cent for the ratio of ingested to incorporated organic matter. While perhaps not completely typical, they may be regarded as generally exhibiting the nutritional picture of loose sand- or mud-eating invertebrates (Fox, Crane, and McConnaughey, 1948).

Taking as a final example a typical radulate feeder, the common periwinkle or intertidal littorine snail, *Littorina planaxis*, we may gain some idea of the metabolic activity and eroding behavior of these rock-scraping forms and their allies. The so-called gray or flat littorine, obtaining its nutrition from the small quantities of organic matter (algae and adsorbed particulate detritus) associated with impacted siltstone, is a major factor in the erosion of this material and its return to the sea as finely comminuted particles. A roughly quantitative survey of this snail's activities should yield some conservative information. The data are derived from Wheeler J. North (1953; 1954) who conducted his researches in the Division of Marine Biochemistry at the Scripps Institution of Oceanography.

Populations of *Littorina planaxis* on tidally exposed areas of siltstone in the vicinity of La Jolla, California, have been estimated to amount to about 1 snail per 30 cm^2. The annual increment of tissue (dry weight) achieved by a snail whose shell length is 8 mm (the predominant size) is 7.2 mg. The snail's intake of siliceous material (output of feces) is 2336 mg per year. Since the siltstone contains about 2.6 per cent organic matter, the snail's efficiency or ratio of assimilated to ingested organic matter, amounts to $(100 \times 7.2)/(2336 \times .026) = 11.9\%$.

While feeding at this fairly efficient rate, the snails in an area of 1 square mile of wet siltstone, amounting to calculated populations of some 8.6×10^8 individuals, will erode approximately 2200 tons (ca 3×10^4 cubic feet) of the substrate, involving 57.2 tons of organic matter, of which 6.82 tons (dry weight) are fixed as tissue materials. The operation of this biological agency does not naturally produce a homogeneous removal of 0.3 mm per year but results instead in the excavation of many roundish basins in the impacted silt; these basins are of many different circumferences and depths. Furthermore, not all of them are eroded in horizontal areas of the substrate, such that they are filled with water at low tide, but some of the smaller excavations, especially in the more seaward localities, appear in slanting or even vertical faces of the stone. These erosion basins, familiar to all who have inspected areas of the shore at low tide, tend to deepen and to become intercommunicating from their surfaces as the years pass. It has been calculated that a theoretical standing population of 100 *Littorina planaxis*, of an average shell height of 8 mm, are capable of excavating a 1-liter volume of siltstone every 11.5 years (North, 1953).

The foregoing examples of metabolic processes in the sea will serve, it is hoped, to illustrate the magnitude of but three diversified physical and chemical operations, proceeding incessantly, and on a vast scale, at the agency of countless species of marine animals which depend in large measure upon finely particulate materials in a suspended or an adsorbed condition.

In summarizing, let us consider a relatively conservative value of 1 ppm as the concentration of particulate organic detrital matter in ocean waters. Let the density of this material be taken as approximately equal to that of water. If we then apply

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the figure of 1370 million km^3 (Sverdrup, Johnson, and Fleming 1942), or about 330 million cubic miles, as representing the total volume of the world's oceans, we arrive at a product of $(5280)^3 \times 330 \times 62.4 = 31 \times 10^{14}$ lbs. or 1.5×10^{12} tons. This is suggestive of the mass of finely particulate organic detritus which is available as food for marine scavengers, and which is hence continuously returned by them to the vast biochemical cycles of carbonaceous matter in the sea

The realistic value of the foregoing figure is fortified by some estimations by Riley (1944; 1953) and others. Adopting a relatively high value of 200 g of organic carbon (equivalent to about 400 g of organic matter) as representing the annual production by marine phytoplankton underlying each square meter of ocean surface, and applying to this the factor 360×10^{12} m^2 as that of the total water surface, gives a value of 14.4×10^{13} kg, or about 1.3×10^{11} tons of organic matter produced each year. Augmenting this figure by the estimated productivity of the world's terrestrial plants—*i.e.* about 3×10^{10} tons per year (Riley, 1944)—would yield a total of 1.6×10^{11} tons of organic matter produced annually by marine and land plants combined.

The estimated minimal standing crop of marine organic leptopel exceeds by at least ten-fold the value for annual productivity. Since the figure presented for total annual phytoplankton productivity may be somewhat excessive, and the estimated value for marine organic leptopel rather conservative (since it omits sedimentary organic matter) the standing reserves may exceed the annual synthesis by more than one, perhaps even by two orders of magnitude.

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Chapter 15

Interrelations of Organisms

A. Commensalism

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Every organism is related in some way to other individuals of the same species and to individuals of other species living in the same area. With dioecious organisms, for example, a relationship must exist between the two sexes, at least at some time of the year, to ensure the continued existence of the race; among predators, recognition factors exist where by the predator preys principally on individuals of other species, although many predators attack and eat the young and weak of their own kind. Molting Crustacea, for example, receive no quarter from their hard-shelled kind.

Some of the most striking associations among different organisms are between animals and plants (Chapter 15C). In the present chapter we are concerned with certain relationships, usually distinct from parasitism, which exist between animals of different species in the sea.

Although there is a certain amount of competition among most organisms for food and living space, many species have become closely associated, often to mutual advantage. Where the association is clearly to the advantage of one of the members without seriously inconveniencing or harming the other, the relationship is referred to as commensalism. This is to be distinguished from inquilinism, which is a particular kind of commensalism in which one organism lives within another, usually in some part of the alimentary tract or respiratory chamber, without being parasitic on it or causing it any serious harm. It should be pointed out that the alimentary canal is, morphologically, not really inside the animal. This kind of relationship is relatively rare, but the habit of living in burrows or nests formed by a host is common and is considered by many to be a form of inquilinism. Among colonial or social animals such as ants and termites there are many examples of complicated inquiline realtionships for which counterparts are unknown in the sea. In some other cases the partners are associated to mutual advantage. They are often called symbionts, and such partnerships are referred to as instances of mutualism (the "symbiosis" of English workers). Parasitism, on the other hand, may be defined as a partnership in which the advantage is wholly on one side, usually at the expense of the other partner; many parasites live in the tissues of the partner. The distinction between parasitism, inquilinism, and some instances of commensalism is thus not always very clear, and the terms are of use mainly as stepping stones in helping us to understand the real relationships in any particular association. In commensal relationships the partner which derives the benefit from the association is often referred to as "symbiont" or "the guest," the other as "the host."

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TABLE 1.—*Host relationships of some symbiotic hydroids*
Compiled by Cadet Hand

Host	Hydroid	Locality	Remarks	Reference
GORGONIANS *Anthoplexaura dimorpha*	*Hydrichthella epigorgia*	Japan	Three types of zooids; nutritive, generative, protective (of two types). Some of the protective zooids have eight tentacles, all other individuals are tentacleless	Stechow (1909)
PENNATULIDS *Ptilosarcus sinuosus*	*Ptilocodium repens*	Dutch E. Indies	Dimorphic colonies; tentaceless nutritive zooids and tentacled protective zooids	Coward (1909)
POLYCHAETES *Potamilla torelli*	*Proboscidactyla stellata*	England	Hydroid first described as *Lar sabellarum* by Gosse (1857). This two-tentacled hydroid utilizes the feeding currents of the polychaete in obtaining its own food	Gosse (1857)
Potamilla myriops *Pseudopotamilla ocellata* *Schizobranchia insignis*	*Proboscidactyla flavicirrata*	Japan, Puget Sound, Oregon coast	Found on *Potamilla myriops* in Japanese waters and on the other two polychaetes in American waters	Uchida and Okuda (1941)
Pseudopotamilla ocellata *Pseudopotamilla intermedia*	*Proboscidactyla circumsabella*	Central Calif.	All the species of *Proboscidactyla* for which the hydroids are known are found living in the hydroid stage as commensals on the tubes of sabellid polychaetes	Hand and Hendrickson (1950)
Pseudopotamilla intermedia	*Proboscidactyla occidentalis*	Southern Calif.		Fewkes (1889) Hand (1954)
HERMIT CRABS *Eupagurus gracilipes* *Pagurus arrosor*	*Hydractinia epiconcha*	Japan	Symbiotic species of *Hydractinia* may have as many as four types of zooids: nutritive; generative; sensory; protective. Free-living colonies do not possess the protective (spiral) zooids so characteristic of the symbiotic forms. *H. epiconcha* overgrows original snail shell and enlarges living space so that the pagurid does not have to seek a larger shell as it grows.	Balss (1924) Summarizes all literature to 1924 on hydroids and pagurids
Eupagurus bernhardus *Eupagurus excavatus*	*Hydractinia echinata*	North Sea, N. Atlantic to New England		Schijfsma (1935) One of few experimental studies of *Hydractinia* and symbiosis
Eupagurus constans	*Hydractinia sodalis*	Japan		

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Eupagurus pubescens *Pagurus* sp.	*Podocoryne carnea*	Mediterranean, N. Atlantic to New England; S. Africa, Chile.	*Podocoryne* grows on shells with hermit crabs or on living snail shells. Four types of zooids may occur on a colony (Fraser, 1944)	Kramp (1952) Records *P. carnea* var. *chilensis* and refers to other symbiotic species
PARASITIC COPEPODS				
Sarcotretes scopeli	*Ichthyocodium sarcotretis*	Northeast Atlantic	Tentacleless hydroid found only on parasitic copepod which is known only from the fish, *Scopelus glacialis*	Jungerson (1911) Debouttéville and Nunes (1951) Review of literature on hydroids associated with parasitic copepods; most hydroids involved are facultative, not obligative, commensals and are calyptoblasts
PELECYPODA				
Donax gouldi *Tivela stultorum*	*Clytia bakeri*	Southern California	An unmodified form which lives on *Donax* in the surf on sandy beaches; a similar hydroid lives on species of *Donax* on Texas and Louisiana coasts	Torrey (1904)
Axinopsis sericatus	*Monobrachium parasitum*	Puget Sound, S. Calif., White Sea	A one-tentacled hydroid living on small bivalves. A species of *Monobrachium* also occurs in about 100 fathoms off coast of Baja and Southern California	Mereschkowsky (1877) Fraser (1918) Hand (1957)
Nuculana pustulosa *Nucula nucleus* *Nucula tumida*	*Perigonimus abyssi*	Arctic and N. Atlantic	A minute *Perigonimus* with reduced numbers of tentacles. Also found on *Dentalium* sp.	Ritchie (1913)
Crassostrea rhizophorae	*Eugymnanthea ostrearum*	Puerto Rico	A solitary hydroid which lives as a commensal in the oyster's mantle cavity. Produces only one medusa at a time	Mattox and Crowell (1951)
Tapes decussatus	*Eugymnanthea inquilina*	Italy	A commensal in the mantle cavity	Palombi (1936)
Mytilus galloprovincialis	*Eugymnanthea polimantii*	Italy	A commensal in the mantle cavity	Cerruti (1941)
GASTROPODA				
Ilyanassa obsoleta	*Stylactis hooperi*	New England	On shells of living snails; an obligate relationship for the hydroid	Sigerfoos (1899); Fraser (1944) for literature
Hyalaea trispinosa	*Kinetocodium danae*	North and South Atlantic, Indian Ocean	Large, few-tentacled, naked polyps. Gonophores produced from hydrorhizal net	Kramp (1921); also with remarks on 3 others of 5 known species found only on pteropods
Phyllirhoe bucephala	*Mnestra parasites*	Atlantic and Mediterranean	This medusa is commonly considered to be on the nudibranch. However, evidence indicates the opposite—that the nudibranch begins as a commensal inside the bell of *Mnestra*, and when this habitat is outgrown it attaches itself to the manubrium of *Mnestra*	Ankel (1952) proposes *Mnestra* is the victim of the nudibranch; good illustrations

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TABLE 1.—*Continued*

Host	Hydroid	Locality	Remarks	Reference
TUNICATES				
Halocynthia aurantium *Halocynthia igaboja* *Ascidia callosa* *Ascidia paratropa*	*Endocrypta huntsmani*	Puget Sound	A commensal in the branchial basket of tunicates.	Fraser (1937)
FISHES				
Minous inermis	*Podocorella minoi*	India to Japan	An obligate commensal. Hydroid not modified.	Alcock (1892) as *Stylactis* Stechow (1909) as *Podocoryne* Komai (1932) as *Podocorella* Gudger (1928)—general review Heath (1910)
Hypsagonus quadricornis	*Perigonomus pugetensis*	Puget Sound	An obligate commensal. Hydroids not modified.	
Erosa erosa	*Stylactis pisicola*	Japan	*Minous*, *Hypsagonus*, and *Erosa* are all bottom-dwelling scorpaenids.	Komai (1932)
Monocanthus tomentosus	*Nudiclava monacanthi*	Andaman Sea	Highly modified, tentacleless hydroid; perhaps a parasite	Lloyd (1907)
Seriola zonata	*Hydrichthys mirus*	Narraganset Bay, Rhode Island	Tentacleless, highly modified, parasitic (?) hydroid	Fewkes (1887); *see* Gudger (1928) for illustrations
Ambassis natalensis *Mugil* sp. and a glyphidodontid	*Hydrichthys boycei*	South Africa	This species is reported to feed upon the blood of the fish host. Both species of *Hydrichthys* are found on pelagic fish.	Warren (1916)
Acipenser ruthenus	*Polypodium hydriforme*	Volga River	A parasite of ovarian eggs of the sturgeon. Free-living stages and life history unknown	Gudger (1928); review of literature and knowledge of this species

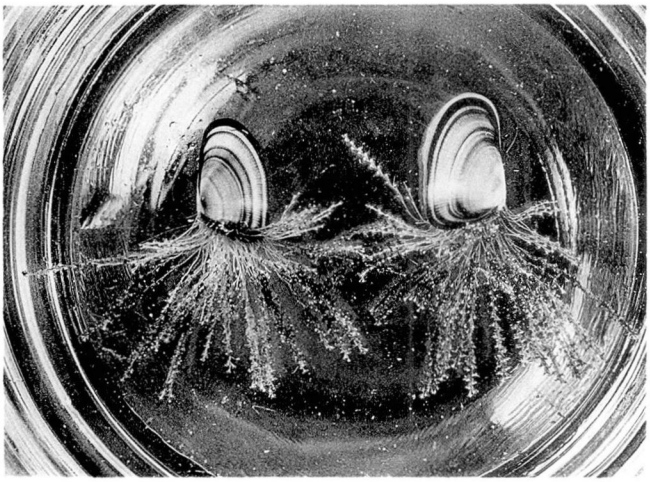

FIGURE 1. Hydroid *Clytia bakeri* on *Donax gouldi* (Photograph courtesy Cadet Hand).

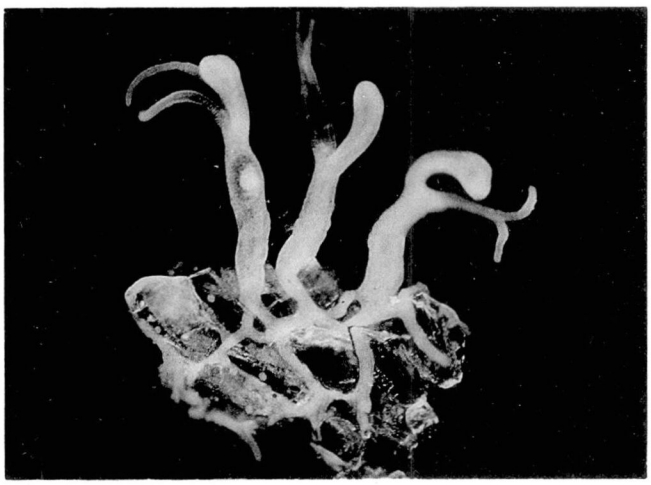

FIGURE 2. Hydroid "Lar" (*Proboscidactyla circumsabella*), a commensal on sabellid worms. (Photograph by John R. Hendrickson, courtesy Cadet Hand)

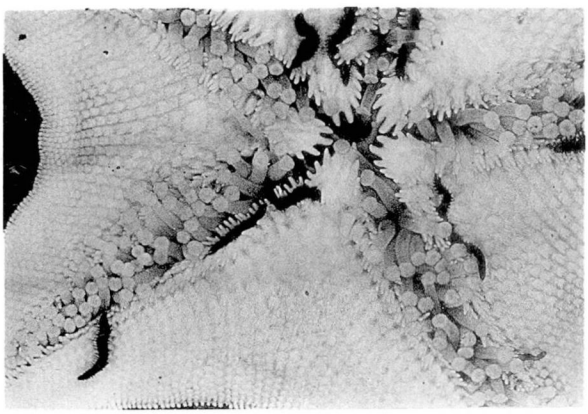

FIGURE 3. Commensal polychaetes, *Podarke pugettensis*, in the ambulacral groove of the bat star, *Patiria miniata*. (From MacGinitie and MacGinitie, Natural History of Marine Animals, 1949; courtesy George E. MacGinitie and the McGraw-Hill Book Company, Inc.)

EXAMPLES OF COMMENSALISM

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There is some danger, in considering the various types of symbiosis, to lapse into teleological expressions if not thought, and it is more profitable to consider symbiosis as an example of specialized behavior, grading from casual association to relationships in which the symbiont makes an active search for its host (Davenport, 1955).

Many sedentary marine animals are epizoic on other animals, and some of these are restricted to a few or even to a single species of animal. Many of these epizoites are Protozoa, coelenterates, and Bryozoa, found on the shells or exoskeletons, and sometimes on the softer parts of other organisms. For example, among Protozoa, *Zoothamnium* is often found between the parapodia of such polychaetes as *Glycera robusta*, and a species of holotrich (*Heterocineta*) occurs on the tentacles of a phoronid (Kozloff, 1945). A more specialized example is that of the vorticellid, *Ellobiophrya donacis*, which occurs on the gills of the clam, *Donax vittatus* (Chatton and Lwoff, 1929). Unlike other vorticellids, *Ellobiophrya* has two stalks which wrap around the interfilamentary junctions of the gill of the clam so that it is literally "padlocked" onto the host. The folliculinids or "bottle animalcules" form curious flask-shaped tests, attaching themselves to various hard substances including mollusk shells. Some species are epizoic on the telson of species of *Limnoria;* another is known from the soft abdomens of hermit crabs (Andrews and Reinhard, 1943). Certain positions on the body of another animal may, indeed, often be the most advantageous habitat for sedentary animals, which may benefit especially from the feeding or respiratory currents of the host. Many such epizoites may be found on other animals only in such positions. The hydroids in particular exhibit all degrees of relationship from fortuitous association (Gudger's "feeble and unpurposeful inquilinism," 1937) to true parasitism, with accompanying structural modifications (Table 1).

Among the Entoprocta, *Loxosoma minuta* is usually found growing on sipunculids, and *Barentsia discreta* on the carapace of *Upogebia* and chitons. Many species of Bryozoa grow on shells of mollusks and on crustacean carapaces, leaving behind them tests which may be of use to the paleoecologist as indicators of past environmental conditions. Sometimes the host may present the only available substratum, but often the association is a loose one. On the other hand, the hard surface of the host may actually be superior to a fixed object such as a rock, since by the movements of the host the epizoite may benefit by moving from one place to another while having the advantages of a sedentary life.

Another example is the association of the hydroid *Clytia bakeri* with certain mollusks. On the surf-swept beaches of Southern California, the wave action does not usually permit the growth of delicate hydroids on exposed surfaces in the intertidal zone. *Clytia bakeri*, however, may be found growing on the tip of the shells of the small clam *Donax gouldi* as well as on the larger Pismo clam (*Tivela stultorum*), or more occasionally on the spire of the olive shell (*Olivella*) (Pl. 1, fig. 1). A similar association between a hydroid and *Donax* occurs on the Gulf coast of the United States. The hydroids probably benefit from their position near the feeding currents of the clam, while in the case with *Olivella* the hydroid gains mobility, and its usual position near the siphon may further improve the chances for food.

An especially interesting association is that between the peculiar hydroids known as "lars" and sabellid worms. This was first observed by Gosse (1857); related species

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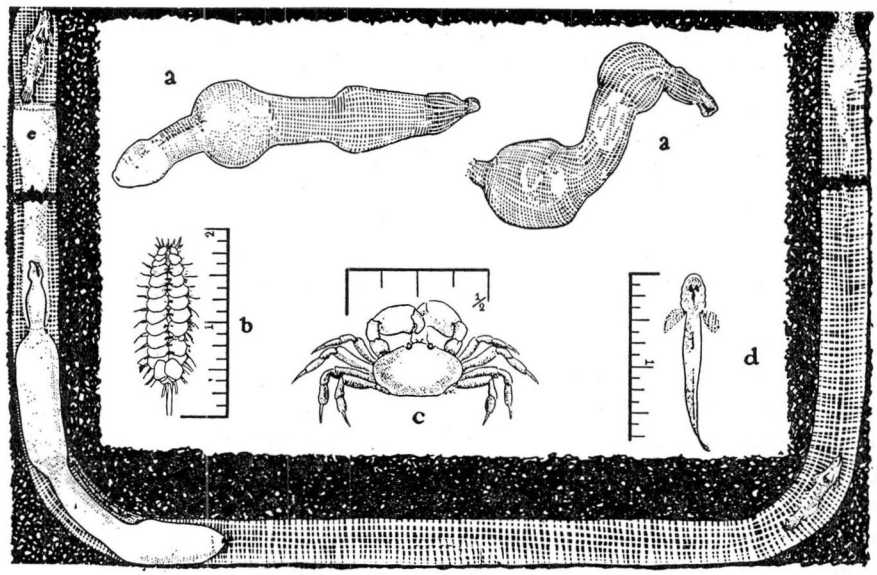

FIGURE 1.—*The innkeeper* Urechis caupo, *in its burrow with its guests*

a. The innkeeper *Urechis caupo*; b. *Hesperonoe adventor*; c. *Scleroplax granulata*; d. *Clevelandia ios*; e. mucus net made by *Urechis* (After Fisher and MacGinitie, 1928).

have since been found on the coast of California and in Japan. (*See* Table 1 for names and literature.) The two-tentacled gastrozoids of these hydroids are extremely active; they remove food particles from the various parts of the crown of the sabellid and from the worm's feeding currents (Pl. 1, fig. 2).

Another category of commensalism is shown by animals forming a burrow or permanent tube. These tubes or burrows often harbor various guests which live by snatching the surplus or rejected food or waste materials from the host. Fisher and MacGinitie (1928) named the large Californian *Urechis*, which has a motley assortment of such guests in its burrow, *caupo*, meaning "the fat innkeeper" (Fig. 1). This creature feeds with the aid of a mucus bag, drawing the water through the bag by peristaltic movements of the body, thus trapping food particles on the mucus. In front of this bag there are often several small gobies, *Clevelandia ios*, which use the burrow mainly for protection and emerge to feed. Alongside the *Urechis* there is usually a polynoid worm, *Hesperonoë adventor*, which snatches part of the mucus bag when the host is eating the bag and its trapped food particles. This scale worm is obliged to move back and forth along the wall of the burrow to avoid the peristaltic swellings of the host, and can reach the bag only when the host is itself eating it. Behind the host is a pinnotherid crab, *Scleroplax granulata*, which usually occurs in pairs. A small clam, *Cryptomya californica*, is often embedded in the wall of the burrow. Other boarders live with the burrowing shrimps, *Upogebia* and *Callianassa*. Often all three of these burrowing hosts will be found on the same mud flat, and, while many of the commensals occur impartially in the burrows of all three hosts, some are found with only one (Fig. 2). A similar complex of interrelated commensals and hosts has been studied

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in the Salcombe estuary by various workers at the Plymouth Laboratory (Fig. 3). Another well-known "innkeeper" is *Chaetopterus*, which secretes large U-shaped parchmentlike tubes (Enders, 1905). Other animals commonly found in burrows and tubes are the crabs belonging to the genus *Pinnixa*, which are usually much flattened and elongate, fitting the burrow and causing the host little inconvenience. They are found all over the world with various worm and crustacean hosts, and often are restricted to a single species.

While commensals living with hosts forming permanent tubes or burrows are common, few examples are known of commensals associated with active burrowers. Probably the most spectacular example is that of the small clam *Entovalva semperi* Ohshima (1930) which attaches itself to a burrowing sea cucumber, *Protankyra bidentata*, by means of a highly modified foot that functions like a suction cup (Fig. 4). This association is found in Japan and Philippines; a similar but less highly modified species, *Entovalva perrieri*, is associated with synaptids on the French coast (Anthony, 1916).

In most of these examples it is quite clear that one of the partners—the host—

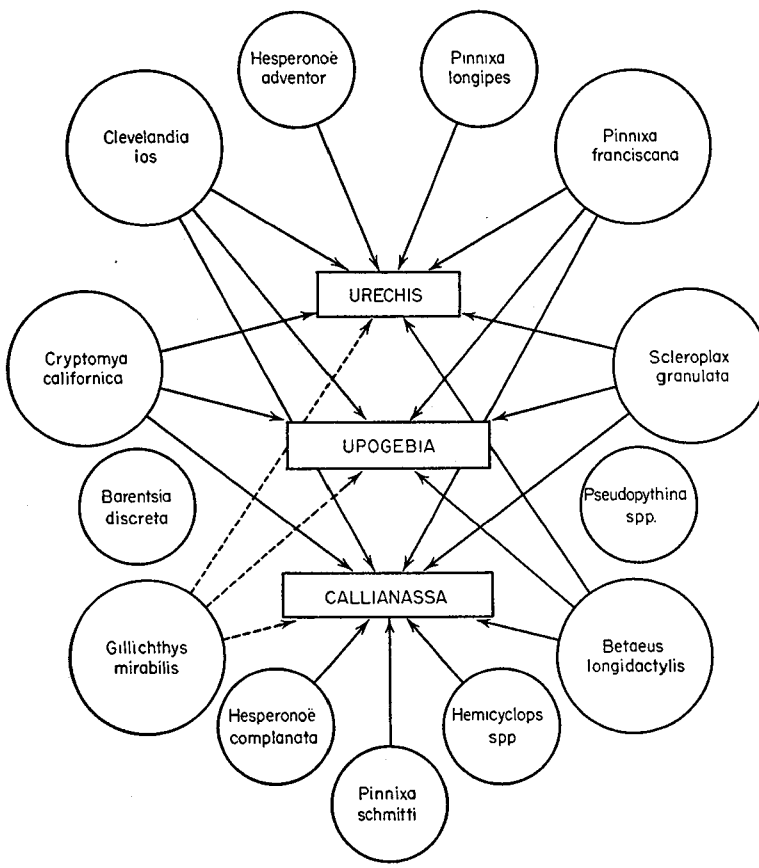

FIGURE 2.—*The commensals of* Urechis, Upogebia, *and* Callianassa

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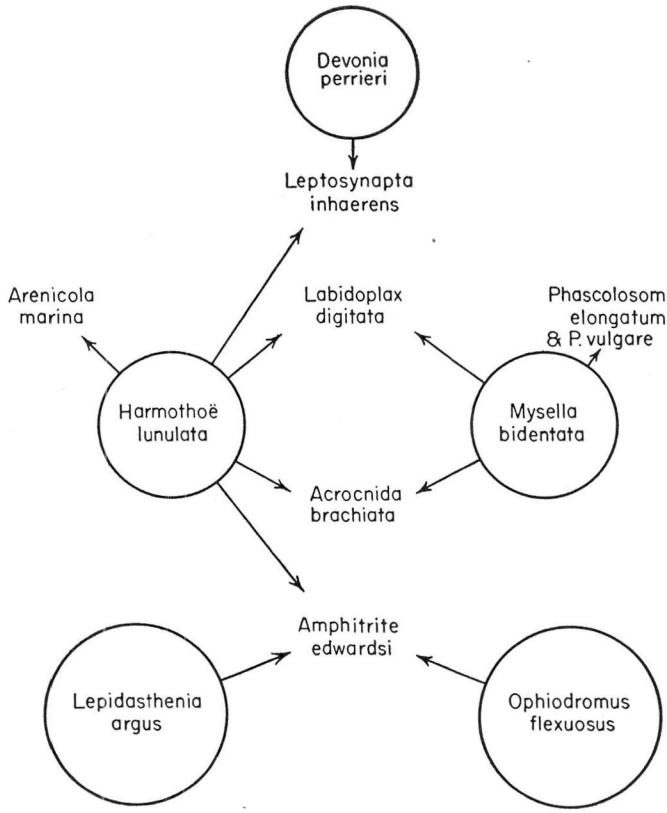

FIGURE 3.—*Commensal relations at Plymouth*

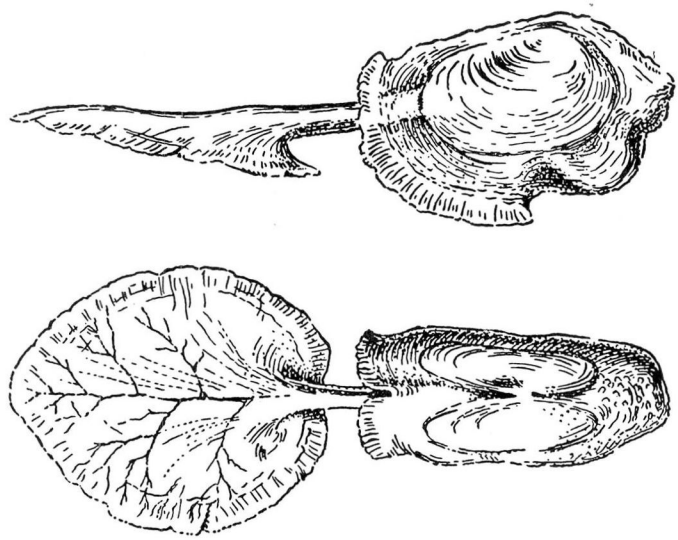

FIGURE 4.—Entovalva semperi, *a bivalve commensal on synaptid holothurians*
After Ohshima (1930)

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provides one or more of the conditions necessary for the life processes of the commensal. In many instances, such as the growth of some hydroids on the shells of mollusks, the host is apparently merely providing a suitable attaching surface; in others, the feeding currents set up by the host may be used by the commensal, and, while in most cases such commensals may be found with a variety of hosts, some have become specific—that is, confined to a single host.

Some curious relationships exist between crabs and actinians. Several of these have become familiar constituents of zoology textbooks and popular natural history works since Gosse first observed the transfer of an anemone to a larger shell by a hermit crab in 1859. The most detailed account of this performance has been provided by Cowles (1919). The series of crab-actinian relationships may be summarized in tabular form (Table 2). Many hermit crabs carry anemones on the shells they inhabit, and they are careful to transfer the anemones when they are obliged to change shells. Other crabs may bear the anemones on their own bodies (*Hepatus*) or carry them in their chelae (*Lybia* or *Polydactylus*). In all these examples there must be at least a passive co-operation on the part of the guest; if the anemone carried about by *Lybia*, for example, did not open to feed, the crab would be unable to use them as food gatherers as they are reported to do, and the anemones removed by hermit crabs submit to treatment which would, if applied by an investigator, result in injury. The observations of Burger (1903) suggesting that the anemone is the active partner in bringing about the association with the calappid crab, *Hepatus*, have apparently not been repeated, but the replacement of the hermit's shell by the specialized pedal disc of *Adamsia* is certainly a step beyond the relationship shown by *Calliactis* or *Antholoba* on the carapace of *Hepatus*. Also, the occurrence of certain actinians on living gastropods is not rare (Fig. 5), and Balss (1924) and Carlgren (1928) agree that this habit of anemones may indicate the manner in which the association between hermit crabs and actinians arose. Other commensals are often found with hermit crabs; in Europe, *Nereis fucata* is commonly found with *Eupagurus bernhardus* in some regions (Fig. 5), while in others the scale worm *Harmathoë coeliaca* may be found more commonly with the hermit. Such examples could be multiplied almost indefinitely.

That the crabs have also played their part in setting up these associations with actinians is not to be denied, and the habits of various "masking" and decorating crabs suggest the manner in which their participation originated, although these masking crabs are not related to the calappids and pagurids. Many dromiid crabs such as *Dromia vulgaris*, collect and attach such sponges as *Suberites domunculus* to their carapace, and other sponges, particularly hexactinellids, are appropriated by other crabs. *Dromia vulgaris* also attaches simple ascidians to its back (Carlisle, 1953). Oxyrhynchous crabs adorn themselves with a variety of objects from algae to hydroids and compound ascidians as well as sponges. Experiments with these crabs (mainly with *Maia*) have been performed by Minkiewicz (1907; 1909), who found that the crabs have the ability to select rags of different colors to match the tone of the background, and that having done so they do not move into areas where their adornments would render them conspicuous.

Further examples of relationships involving coelenterates are those in which fish

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TABLE 2.—*Synopsis of commensal relationships between crabs and actinians**
Compiled by Joel W. Hedgpeth

Crab	Actinian	Locality	Character of association	Remarks	Principal reference (usually to detailed accounts)	Illustrated (* = color) *photographs* in italics
GRAPSOIDS						
Lybia tesselata	*Bunodactis* sp.	Indo-Pacific; Seychelles to Hawaii, on reefs.	Crabs holds small anemones in each claw for defense (?) or food gathering (?)	The species of anemones involved have not been adequately identified.	Moebius (1880) Borradaile (1902) Duerden (1905)	Borradaile's drawing is source of most later figures; Edmondson (1946, *fig. 181*[b])
Polydactylus cupulifer	?*Bunodeopsis* sp., *Actinothoe pugna*	Indo-Pacific; Seychelles to Hawaii, on reefs.				
CALAPPIDS	ACTINOSTOLIDAE					
Hepatus chilensis	*Antholoba achates*	Chile, shallow water	Anemone attached to carapace; usually one individual in anterior median location	Bürger found the anemone was active partner, but not subsequently confirmed	Bürger (1903)	
	HORMATHIIDAE					
Hepatus epheliticus	*Calliactis tricolor*	N. Gulf of Mexico, shallow water		*Calliactis tricolor* is common on the gastropod *Rehderia georgiae* off South Atlantic, U. S. A., about 100 fathoms.	Carlgren and Hedgpeth (1952)	Carlgren and Hedgpeth, (1952, Pl II*)
PAGURIDS	ACTINIIDAE					
Paguristes oculatus	*Actinia equina*	Mediterranean	Accidental		Brunelli (1913)	

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	HORMATHIIDAE					
Eupagurus bernhardus	*Calliactis parasitica*	No. Europe-Med., shore and shallow water	Anemone attached to shell carried by hermit; on large shells there are often several individuals. The anemone is not structurally modified. The transfer of the anemone by the crab as it moves to a larger shell has been observed.	Anemone attached dorsally but bends down to feed off bottom; most of the well-known figures made from aquarium specimens which do not usually behave as wild individuals.	Stephenson (1935)	Yonge (1949, *Pl. 30**)
Eupagurus excavatus	*Calliactis parasitica*				Chevreux (1908)	
Clibanarius misanthropus	*Calliactis parasitica*				Faurot (1910)	
					Brunelli (1913)	Brunelli (1913 Pl. 1*) (as *A. rondeletti*)
Pagurus arrosor	*Calliactis parasitica*			*P. arrosor* also reported with *Hormathia coronata*; accidental	Faurot (1910)	
Pagurus arrosor	*Calliactis japonica*	Japan		Of the 15 known species of *Calliactis* 8 reported as hermit commensals; other species probably also		
Eupagurus sp.	*Calliactis japonica*					
Pagurus arrosor	*Calliactis algoaënsis*	So. Africa			Carlgren and Hedgpeth (1952)	
Pagurus floridanus	*Calliactis tricolor*	Southeast and Gulf, U. S., Philippines, Great Barrier Reef				
Petrochirus bahamensis	*Calliactis tricolor*					
Dardanus deformis	*Calliactis miriam*				Cowles (1919)	Cowles (1919, Pl. 1); Roughley (1947, *Pl. 27**)
Dardanus asper	*Calliactis armillatus*	Hawaii				
Unidentified pagurids	*Calliactis variegata*	Gulf of California		*C. variegata* introduced accidentally (as larvae) into Scripps Aquarium, summer, 1953, osberved attached to carapace of *Cancer anthonyi*, Jan. 1954		
	Calliactis polypus	S. Africa				
Parapagurus bicristatus	*Paracalliactis valdiviae*	East Africa, 628–741 fathoms	Apparently a more obligate relation than with species of *Calliactis* as a carcinoecium is developed by the anemone	The anemone may be attached either dorsally or ventrally.	Carlgren (1928)	
Parapagurus andersoni					Carlgren (1928)	Carlgren (1928, *Fig. 2*)
Parapagurus pilosimanus	*Paracalliactis stephensoni*	off Ireland, 982 faths.				

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TABLE 2.—*Continued*

Crab	Actinian	Locality	Character of association	Remarks	Principal reference (usually to detailed accounts)	Illustrated (* = color) *photographs* in italics
Undetermined	*Paracallicatis michaelsarsi*	Bay of Biscay, 4708 meters		On shells (with hermits?)	Carlgren (1928)	Carlgren (1928, *Fig. 3*)
Eupagurus prideauxi	*Adamsia palliata*	Europe and Mediterranean 11–182 meters.	The original shell of the hermit crab is retained as the anemone grows a carcinoecium with the aid of its specialized pedal disc to accommodate the growing crab.	Anemone so attached that disc is on under surface. *Eupagurus prideauxi* reported immune to *Adamsia's* poison	Faurot (1910)	Faurot (1910, Fig. 2)
Eupagurus excavatus	*Adamsia palliata*				Stephenson (1935)	Stephenson (1935, Fig. 86)
Catapagurus sharreri	*Adamsia sociabilis*	Northeast America, 145–888 meters				Verrill (1883, Pl. VIII.2)
Undetermined	SAGARTIIDAE *Sagartiogeton californica*	Gulf of California	Similar to *Calliactis*?			
Parapagurus armatus	ACTINIIDAE *Isadamsia cancrisocia*	Pemba Strait, 818 meters	Anemone specialized as in *Adamsia*.	A remarkable example of convergence; the anemone belongs to the young group lacking acontia, whereas the Adamsias are acontiate.	Carlgren (1928)	Carlgren (1928, *Fig. 1*)
Undetermined	ACTINOSTOLIDAE *Antholoba australiensis*		On shells of hermits		Carlgren (1930)	

* Nomenclature of the actinians according to Carlgren (1949); that of the crabs mostly after Balss (1924).

† References merely indicating occurrence of the association omitted.

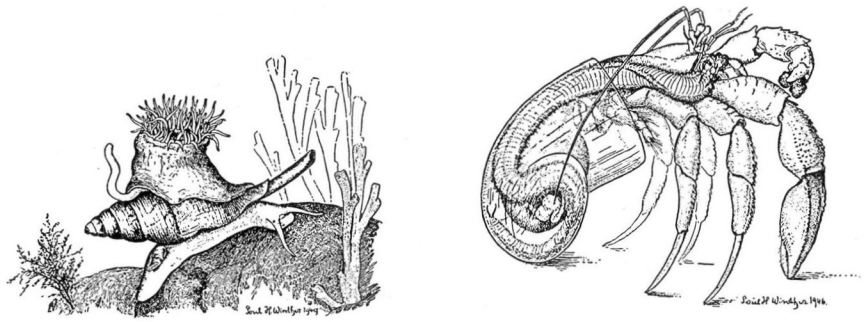

FIGURE 5.—*Examples of commensalism*

Left: The commensal sea anemone, *Allantactis parasitica*, on the gastropod *Sipho curtus*, with a commensal nemertean, *Nemertopsis actinophila* (From Christmas card by Gunnar Thorson, drawn by Poul Winther). Right: The commensal polychaete *Nereis fucata* and its host, *Eupagurus bernhardus* (From Christmas card by Gunnar Thorson, drawn by Poul Winther)

are the guests. Either the fish are immune to the nematocysts of their coelenterate hosts, or in some way the discharge of the nematocysts is inhibited in the presence of the guest. The Portuguese man-of-war fish (*Nomeus gronovi*) finds shelter among the trailing tentacles of the *Physalia* which may catch and eat much larger fishes than the *Nomeus*. Some large medusae are also known to provide protection for small fishes: *Caranx* often forms small shoals under a large *Crambessa* and other small fish, and fish of genera not associated as adults with jellyfish may be seen with *Cyanea* and *Chrysaora* (Pellegrin, 1905).

The association between small pomacentrid fishes (*Amphiprion* and *Premnas*) and large anemones (*Stoichactis*) in the Indo-Pacific waters has received attention from naturalists, especially Verwey (1930), since first reported by Collingwood (1868). The literature on this unique example of mutualism has been summarized by Gudger (1947); *see* Schultz (1953) for a review of species of *Amphiprion*. These small fishes are colored in striking patterns, conspicuously different from the colors of their anemone hosts, and they live in the shelter of the anemone's tentacles, allegedly taking refuge in the enteron of the host (Fig 6). The damsel fish are apparently immune

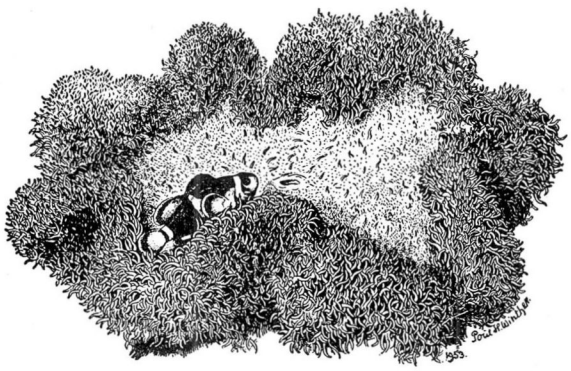

FIGURE 6.—*Anemone fish,* Amphiprion, *nestling among the tentacles of* Stoichactis
Drawing by Poul Winther from Galatheas Jordomsejling, courtesy A. Fr. Brunn.

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to the anemone's nematocysts. Gudger suggests that this immunity may be acquired as a result of the observed habit of the fishes in mouthing and nibbling the tentacles of the anemones. The fishes carry food to the disc of the anemone, lure predatory fishes within reach of the host, and have been observed in at least one instance to catch and bring other species of fish to their host (Gohar, 1934). They also drive other fishes away from their hosts (Gohar, 1948), but it is not plain whether this habit is actually part of the commensal relationship or is simply a defense of territory by the fish. The observations of Verwey and others indicate that the anemones do not prosper without their guests, at least in the environment of an aquarium. In some way or other the anemones recognize their commensals and have been observed to turn their tentacles away as the damsel fish swim among them. The small shrimp *Periclimenes* and certain crabs are found in the same association, but their relationships with the host have not been investigated.

Mention may be made here of some other examples of commensalism in fishes. *Apogonichthyes strombi* remains within the pallial cavity of the large conch *Strombus gigas* during the day and emerges to feed at night (Plate, 1908). Another, probably the best-known example of this inquiline habit, is that of the carapid *Fierasfer* (or *Carapus*) which finds refuge in the cloacal chamber of holothurians, and also (more rarely) in the stomach of large starfish such as *Culcita*. Frequently the holothurian ejects its viscera as a result of the invasion of the fish which surely indicates that the holothurian is not a completely willing partner in the arrangement. Indeed, the recent investigations by Arnold (1953) indicate that *Carapus* is, at least in its juvenile stages, an obligate parasite of the holothurian, attacking the gonads and respiratory trees, and that even the adults, although less dependent, do not leave their host voluntarily, but emerge only when the host eviscerates. Another *Fierasfer* occurs in the mantle cavity of pearl oysters in the Gulf of Panama, hence the name "pearl fish" sometimes applied to these fishes. Occasionally this fish enters an inhospitable mollusk by mistake, with fatal results.

The association between fishes and sharks is well known. One of these involves large sharks and small carangids (*Naucrates ductor*, the pilot fish) which form small schools beneath and in front of the sharks. The scombrids pick up food dropped by the shark and possibly warn their host of the presence of prey or other organisms. Pilot fish often follow small boats for long distances, and one of the interesting observations made during KON-TIKI expedition was that pilot fish often adopted the raft after the host had been killed. The school remained with the raft and reacted to it in much the same way as to a shark. A more specialized example is that of the Remora (*Echeneis remora*) associated with large sharks, whales, or sea turtles, to which it attaches itself by means of a special dorsal sucker (Fig. 7). Remoras have been reported to enter the mouths or gill cavities of such fishes as *Xiphias*, *Istiophorus*, and *Mola* where they gain both protection and food (Norman, 1932). Recent observations by free divers, documented by excellent motion pictures, indicate that the cleaning of large fish (picking off parasites and diseased flesh as well as unconsumed food particles) by small fish and also certain shrimp, which are permitted to enter the buccal cavity and pass freely between the gills as well as roaming over the surface of the host, is more widespread than previously suspected. It would appear that some clean-

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ing organisms may occupy regular stations where they are immune from predation, and large fish have been observed to wait their turn for service. (Conrad Limbaugh, personal communication).

Many polychaetes, especially the scale worms, are commensals. Some live in the burrows or tubes of other polychaetes or of Crustacea; others are associated with various echinoderms, especially starfish (Pl. 1 fig. 3). Some of these partnerships are specific, and the commensals occur with a single host; others frequent several hosts. Many are facultative, and both free-living and commensal individuals are found with a variety of hosts; in many of these cases the individuals found with the hosts are larger or show slight morphological differences from those which are free living. A few of the more familiar examples of polynoid commensals are summarized in Table 3.

Experimental examination of the way in which commensals recognize their hosts, using polynoids, has been made recently by Davenport (1950) and Davenport and Hickock (1951) with the aid of an arrangement of Y tubes (Fig. 8). The experiments demonstrated that the polynoid *Arctonoë fragilis* was attracted by water from the tank occupied by the host starfish *Evasterias troschelii*, but not by that from another starfish, *Pisaster*, with which the worm is not commensal. Also, *Arctonoë*, commensal with *Stichopus*, was similarly attracted by water coming from its host, but not by water from another cucumber, *Cucumaria*, with which it is not commensal, but which is common in the same habitat. In cross experiments Davenport was able to show that the attracting substances were not the same in each case, since the commensals were not attracted to each other's hosts. Negative results, however, were obtained with the *Arctonoë-Luidia* partnership. This may have been due, as Davenport suggests, to injury of these delicate starfish before the the experiment. In later experiments with *Arctonoë fragilis* and *Evasterias*, it was shown that the attracting substance had no effect some hours after the removal of the host, and that, if the host is contained in a dialysing bag, the water from the host aquarium does not

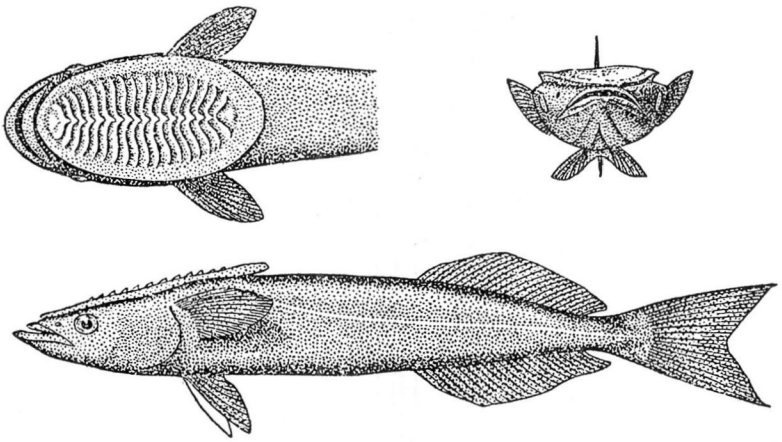

FIGURE 7.—*Pilot fish*, Echeneis remora
(Redrawn from J. R. Norman's *History of Fishes*, New York, Frederick A. Stokes [n.d., 1932?]).

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TABLE 3.—*Host of the genus* Arctonoë *on the Pacific coast of North America*
From Davenport (1950)

	A. fragilis	*A. pulchra*	*A. vittata*
Asteroidea	Evasterias	Solaster	←→Solaster
	Luidia	←→Luidia	Dermasterias
	Stylasterias	Pteraster	←→Pteraster
	Orthasterias		Henricia
	Leptasterias		Crossaster
	Pisaster*		
Holothuroidea		Stichopus	←→(Stichopus)
Gastropoda		Megathura*	Diodora
			Puncturella
			Acmaea
			Cidarina
			Argobuccinium
Amphineura		Cryptochiton*	←→Cryptochiton
Polychaeta		Loimia*	Neoamphitrite

* Not recorded as hosts in Puget Sound.

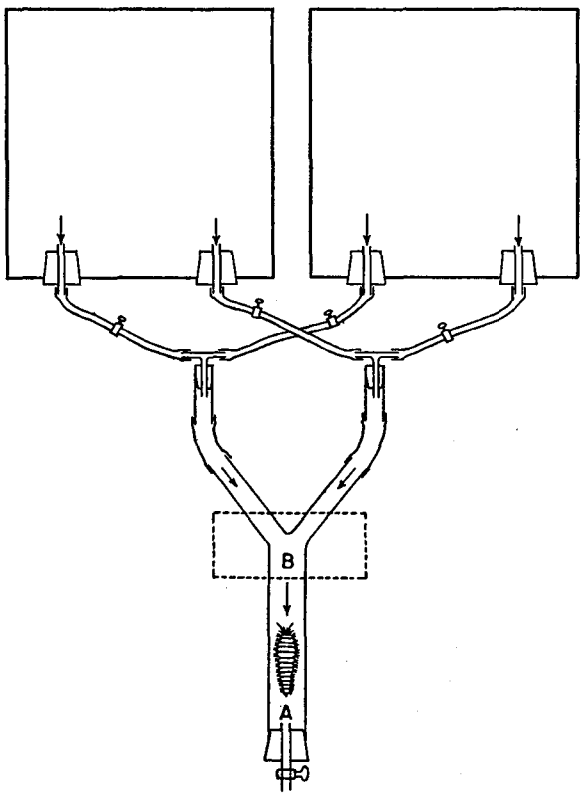

FIGURE 8.—*Apparatus used in experiment on host preference in commensal polychaetes*
from Davenport (1950)

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attract the commensal. Also, commensals are not attracted if the host is disturbed or injured in any way. On the other hand, no attracting substance could be demonstrated for *Amphitrite robusta* and its commensal *Halosydna brevisetosa*. This is interesting since this scale worm is also commonly found with other hosts and in the free-living state.

In some cases it appears to be the nature of the substratum that attracts the commensal. In the small clam *Modiolaria*, which is found attached to ascidians, Bourdillon (1950) could find no evidence of an attracting substance and demonstrated that the clam has a preference for settling on the tunic of the ascidian only when it has come into contact with it. He found that the clam also attached itself to the tunic of a freshly eviscerated and washed *Ciona*, and to the inside surface of a tunic of another *Ciona* which had been eviscerated and turned inside-out. Evidently the substance that stimulates the settlement is in the tunic itself, and this view is supported by the fact that *Modiolaria* larvae may be induced to settle on sheets of cellulose nitrate. The investigations of Wilson (1952) indicating the influence of the substratum upon the metamorphosis of planktonic larvae of certain bottom-living invertebrates suggest that commensals in the larval state may similarly be able to postpone their metamorphosis until the host is found.

In many examples of such partnerships the border line between commensalism and parasitism is very faint. This is especially true in the case of certain crabs that form galls on their hosts or invade the mantle cavity of bivalves. Many pinnotherid crabs living in crabs and mussels apparently do not harm their hosts, but at least one, the oyster crab, *Pinnotheres ostreum*, injures its host in a way that justifies calling it a parasite (Stauber, 1945). A stage beyond the lesions caused by the oyster crab on the gills of its host is the gall-forming habit of such crabs as *Eumedon convictor* on the sea urchin *Echinothrix turca* (Bouvier and Seurat, 1905), and *Harpalocarcinus marsupialis* on the coral *Pocillopora caespitosa* (Potts, 1915). In this latter case the young female crab settles in a small growing fork near the tip of the coral. With the continued growth of the coral, the crab becomes enclosed in a small chamber between the two young branches, altering their growth by its respiratory currents. The branches of the coral at first grow parallel and finally coalesce, leaving a row of apertures along the line of fusion of the coral branches (Fig. 9). The female remains incarcerated for the rest of her life in this chamber, feeding on the plankton drawn into the chamber through the apertures by the respiratory currents and movements of the highly specialized mouth parts. The minute, unmodified male is appar-

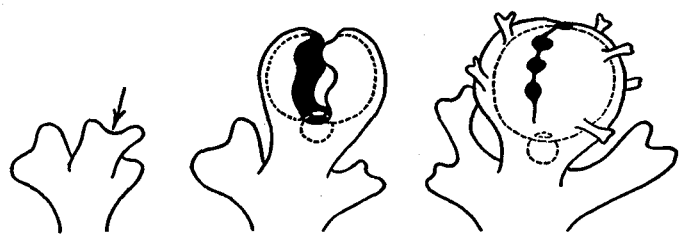

FIGURE 9.—*Stages in the development of the coral gall*
Redrawn from Potts (1915)

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ently able to get inside the chamber, at least in early life, to fertilize the eggs produced by the female. A similar condition is found in the genus *Cryptochirus*, although in this case the crabs live only in pits; in one species the male lives commensally with the female, and in another the sexes live in separate cavities. In the latter species the pits made by the sexes are very similar, and the crabs leave their pits to moult and breed and may then make new pits or occupy an abandoned pit (Hiro, 1937).

Among the myzostomids, a group of curious worms of rather uncertain phylogenetic position which are found on crinoids, various grades of commensalism and parasitism have been observed; some species form galls. Galls and scars caused by myzostomids have been observed on fossil crinoids in Paleozoic rocks.

A curious borderline case between commensalism and parasitism is that of certain small pyramidellid snails which live in association with sedentary polychaetes and bivalve mollusks. Some species live near the end of the tube of their polychaete host, and when it is feeding they insert a long, prehensile proboscis into the alimentary canal and rob the host of food (Fretter and Graham, 1949). Most of these snails are clearly parasitic and feed directly upon the tissues of their hosts.

It is not pretended that the foregoing discussion does more than present a few of the many interesting examples of commensal relationships encountered among marine animals. An entire book might be written on this subject alone, and the interested reader might turn to such summaries as those of Caullery (1952), and Baer (1951), which are devoted to problems of commensalism and parasitism in general.

While explanations of the origin of such intricate relationships as those between damsel fishes and anemones, and hermit crabs and anemones, are for the most part speculative, a few generalizations as to the origin of commensalism may be made. Some facets of this subject have most recently been discussed by Davenport (1955; see also earlier papers, 1953a; 1953b).

In the first place, many of the associations have their origin in the crowded conditions of the littoral and sublittoral zones. The food supply is abundant, and the major competition is often for space. Hence many associations are, at least in their origin, fortuitous, and even the most intimate associations must clearly have originated more or less by chance. But if individuals of a species commensal with some other animal gain some advantage over solitary individuals of the same species, then natural selection can act in favor of the commensal individuals. At the same time, any factor which enables the commensal to find or to remain with the host will become important. Factors such as irrigation or feeding currents are obviously a less certain means than a substance which is released by the host, and which could be highly specific. If one species is found with another in numbers greater than would be expected by pure chance, there are probably some recognition factors which enable one of the partners to find and remain with the other. In most instances where a species is found with a number of different hosts in the same area, or both with hosts and in the free state, the factors are likely to be of a general nature, such as water currents, excretory products, common chemical substances, or, in the case of commensals found in burrows and tubes, simple negative phototaxis.

On the other hand, in associations of a highly specific kind, the factor or factors

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attracting and keeping the commensal with the host might be expected to be highly specific. It is not difficult to see that if there is in fact a distinct advantage to a commensal to live with some other animal and that the attractant seems to be a specific one, then the partnership itself may become strictly specific. Lucas (1947), in his review of the ecological significance of external metabolites, has discussed the significance of what he terms "ectocrine" substances to the establishment of commensal and symbiotic relationships, either by the tolerance of one species for the metabolite of another, or in more specific relationships, possibly as a result of a guest species being adapted to utilize such an external metabolite. In some mutual partnerships we may find attracting factors, not necessarily the same for each partner, acting in both directions.

As already mentioned, in unilateral relationships accessory factors which tend to keep the guest with the host become important. Many commensals assume the same odors as their hosts, and, if the host should have different color phases, the commensal may have corresponding phases; many very remarkable instances of this are known, especially between polychaetes and echinoderms. On the other hand the pigmentation of some commensals becomes reduced, since the color may not have the value it had to the free individual. In the case of the blind goby (*Typhlogobius*) living with *Callianassa* in Southern California, Hubbs (1927) has suggested that the fish originally had a tendency for the reduction of the eyes and favored dark refuges; gradually it became adapted to this habitat and lost its sight and body pigmentation in the process. Other fish such as *Gallichthys* and *Clevelandia* seem to be developing along similar lines.

Because of the difficulty of applying the experimental method to such complex problems, we know little about the true nature of most commensal relationships. Their interpretation is peculiarly susceptible to anthropomorphic bias, and the complexity of the relations cannot usually be satisfied by simple explanations which reduce the behavior patterns to simple reflexes, though many particular instances may prove to have a relatively simple foundation. It is, perhaps, a field in which exceptions should be noted particularly.

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B. Parasitism

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Parasitology is, at least in part, a branch of ecology. In the first place, parasitism, symbiosis, commensalism, inquilinism, and mutualism are all among the different types of relationships among the organisms of a community, the study of which is a major phase of ecology. In the second place, parasites play an important part in the control of host populations, and in fluctuations of populations, which must be understood in any study of the dynamics of a community. In the third place, the study of parasites often furnishes knowledge of the habits and movements of the hosts which could be learned only with great difficulty, if at all, if nothing were known of the parasites. Unfortunately, few ecologists know enough parasitology to understand the role of parasites in communities, and many community studies ignore them, although they give adequate attention to more obvious relationships such as predation and competition for food. It is the purpose of this chapter to point out some of the ways in which parasites affect marine communities, and some of the ways in which an ecologist can use parasites as aids in understanding community relationships. The discussion is confined to a few general principles. A full account of "Parasitism in the sea" would require almost as much space as "Life in the sea," for the parasites are as numerous and as varied as the free-living organisms.

The words "parasite" and "parasitism" have been used in so many different ways that each author must define them according to his own usage. For the same reason the related terms "symbiosis" and "commensalism" must be defined in so far as they border on or overlap parasitism. Parasitism in its broadest sense is the type of symbiosis in which one organism, the parasite, lives in or on the host and receives benefit from the host in the form of food, with or without harming the host. In this usage, some cases would be both commensalism and parasitism; the two terms are not mutually exclusive, but they are not synonymous because commensalism also includes many cases in which one organism does not live in or on another. Thus one may speak of "commensal parasites" if the parasites do not harm the host, and of "pathogenic parasites" if they do injure the host. The two human intestinal amoebae *Entamoeba coli* (commensal) and *E. histolytica* (pathogenic) are classic examples. Attempts to limit usage of the terms parasite and parasitism to cases of pathogenicity are foredoomed to failure, for it is well known that the same species may be pathogenic at certain times, under certain conditions, or to certain individuals, but harmless in all other cases; a parasite is still a parasite, regardless of the host's condition or reaction. As in other biological terminology, it must be expected that definitions will not neatly pigeonhole all cases; organisms and their relationships vary too much for that, and the pigeonholes should be conceived as having partitions in a bad state of repair so that some of the contents may project into neighboring compartments. In the case of parasites, the neighboring compartments will include one labeled "predators,"

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for some cases lie on the border line between the two (*e.g.*, so-called parasitic insect larvae and nematodes which begin as tissue parasites of insects and end by completely devouring the host).

As noted above, many parasites normally have no harmful effect on the host, or at least none that is detectable without very careful study. It might be supposed that an organism which robs its host of nourishment must be harmful in some degree, even if the host shows no apparent effect, but under favorable conditions it is probably not difficult for the host to compensate or even overcompensate for the loss by ingesting more food. Under conditions of food scarcity the same parasite might become harmful. It is possible for parasites to affect host populations without injuring the health of parasitized individuals; parasitic castration is a common and widespread phenomenon among marine organisms, and in these cases the destruction of gonads sometimes causes the castrated hosts to grow to unusually large size, and apparently increases the life span, but the next generation is affected to the extent that the number of progeny is reduced in proportion to the incidence of infection of the parent generation. Rothschild and others have described a number of cases of giantism and prolonged survival of marine snails castrated by the precercarial stages of trematodes.

Mass mortalities caused by heavy parasite infections are known to occur in many land and fresh-water animals (and plants) and in a few marine organisms. It is suspected that other mass mortalities of marine organisms are due to the same cause. Such mass mortalities, though spectacular, are probably not the most important effects of parasites upon host populations. Epidemics which kill most of the host population are usually followed by periods of scant populations which are even worse for the parasite than for the host species; until the host population regains normal density, the parasite has much less chance of finding a host at the proper time to complete its life cycle, and the parasite species may even disappear for a time, until reintroduced from another population. Such lethal epidemics are not uncommon in artificial populations maintained by feeding, as in hatcheries, aquaria, fish ponds, or poultry yards. They probably occur in natural populations, on a scale which could be called a mass mortality or "die-off," only under exceptional conditions. Mass mortalities may occur when a new parasite is introduced into a nonimmune population under conditions especially favorable for the parasite, or when an aquatic population becomes crowded into a small volume of water in a drought period, or when temperatures are abnormally high for a considerable period, or when the host population has reached a peak density as a result of a period of unusually favorable conditions for reproduction and survival, or when the population of an alternate, intermediate, or reservoir host is unusually dense because of some exceptional condition. An example of the last is a mass mortality of trout in some Idaho lakes, caused by a very heavy infection by pseudophyllidean cestode larvae, following an unusually dense concentration of the fish-eating birds which carried the adult tapeworms.

Less spectacular mortalities, which result in a decrease of the host population without reaching the point of a "die-off" or mass mortality, are a more common phenomenon and often cause fluctuations in populations. The dynamics of these phenomena has been studied under both field and laboratory conditions in some animals, especially insects, and is now fairly well understood by entomologists. The literature is

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reviewed by Allee *et al.* and by Solomon (1949). It has been claimed that the fungus *Ichthyosporidium* (= *Ichthyophonus*), formerly considered a sporozoan, causes fluctuations in the population of sea herring in the North Atlantic. Many other marine animals, including a number of mollusks, have notably fluctuating populations for reasons unknown but have not been investigated by parasitologists. The little surf clam *Donax* is an especially interesting case; in several places it is parasitized by trematodes, which in turn are infected by sporozoans, and it has been claimed that the violent fluctuations in *Donax* populations may be due to the interactions of this triple relationship.

Probably the most important, as well as the commonest, effect of parasites upon host populations is a slight decrease in the health, vigor, or escape reactions of infected individuals so that they are more likely to fall victims to predators or other natural hazards. Most parasites, even the pathogenic ones, do not normally kill their hosts. In fact, parasites which do kill their hosts are sometimes considered "imperfect parasites" on the theory that this indicates an imperfect adaptation to parasitization, at least of that particular host. The death of the host usually results in the death of the parasites, and those parasites which build up large populations without destroying their own homes should have the advantage in the struggle for existence. On the other hand, a great many parasites require two or more different hosts in order to complete their life cycle, and in most cases this means that the first host must be eaten by another animal. Some studies on prey-predator relationships, such as the very thorough studies on muskrat populations, indicate that most of the individuals eaten by predators (except under abnormal conditions, as in times of drought or flood, or when the natural conditions have been disturbed by man) are those affected by disease or injury. In the sea, except in times of mass mortality caused by abnormal conditions, individuals weakened by disease or parasitism would almost inevitably be attacked and eaten by predators before their illness reached the point of death. Effects of parasites which would make the host more apt to be eaten by predators would include such things as blindness or partial blindness of fishes (caused by myxosporidia and by certain trematodes), interference with circulation caused by trematodes in the blood vascular system of fishes, interference with respiration by gill flukes and copepods of fishes, and partial paralysis of locomotor muscles in fishes and Crustacea infected by certain sporozoans, nematodes, cestodes, or trematodes. It is necessary for mollusks to be only a little slower in burrowing or in closing the shell, or for crustaceans or fish to be a little slower in swimming, to make them almost certain to fall prey to the predators which are constantly seeking and attacking them. Thus the combined action of parasites and predators is a steady drain upon the host population which results in a more or less static (as opposed to cyclic or fluctuating) biological control, maintaining the natural balance of the community.

This type of control is not conspicuous, and its importance becomes evident only when it fails and the host-prey population "escapes," as some crop-pest insects "escape" and cause enormous damage to crops when unusual weather prevents the controlling fungi from killing them, and as cotton mites "escape" and become more and more abundant in proportion to the completeness of the kill of insects by poisons. An example of a similar "escape" of a marine organism is the unusually large popula-

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tion of oysters which develops in some Louisiana waters, sometimes in places where no oysters grew before, following Mississippi River floods which kill off most of the controlling "pests;" several cases were reviewed by Gunter (1953). Oysters may also be said to have "escaped" when they became adapted to lower salinities than most of their parasites and predators can tolerate, for they have built up enormously larger populations in the low-salinity parts of their range than in the more nearly oceanic parts of the same estuaries; similarly, the densely populated intertidal reefs in high-salinity waters (in southern United States) represent populations which have "escaped" from the pests (less tolerant to exposure) which prevent such dense populations below the low-tide level. In this case (oysters of southern United States) one of the major controlling factors is known to be the tissue parasite *Dermocystidium* which does not flourish in salinities as low as those found on the oyster beds farthest up the estuaries.

The last examples also illustrate the role of parasites, or parasites and predators combined, in maintaining different types of communities in different environments. The presence of large oyster communities in low salinities and their absence in high salinities is not due to the direct effect of salinity on the dominant organisms but is due to the effect of salinity upon the "influent" organisms—namely, the parasites and predators. As a matter of fact, the oysters reproduce more prolifically, grow faster, and prosper better in general in waters of higher salinities than those in which they build up their largest populations; they would almost certainly form even larger communities in high salinities than in low if the controlling parasites and predators could be eliminated. Since low temperature does relieve parasite-predator pressure to some extent, large oyster populations are found in higher salinities as you go north along the Atlantic coast of North America, and are confined more and more to low salinities and to intertidal beds as you go south. The oyster is the classic example of a "dominant"; it makes the oyster community with its complex assemblage of organisms which live only on oyster beds, or at least do not form large populations in any other habitat. The organisms of the oyster community furnish a much larger supply of food for many fishes and Crustacea than can be found on bottoms not inhabited by oysters. Oyster beds in high-salinity waters have a much greater variety of associated plants and animals than do those in low salinities, for many of the organisms of the oyster community cannot tolerate salinities as low as those to which the oyster can adapt itself. Thus the fauna and flora of large areas is determined by the effect of salinity and temperature (and perhaps other factors) upon the parasites and predators of the oyster. The role of predators in such cases, because they are more conspicuous, is much better known, but that of parasites may be more important. Parasites make infected hosts available as prey to many predators which could not otherwise use them (for instance, direct observation of blue crabs on oyster beds has shown that their predation is confined almost entirely to oysters which cannot close their shells as quickly or as tightly as normal oysters). Some parasites, by parasitic castration or by more general effects on the health of the parent stock, decrease the rate of reproduction of the host population; this may have even more serious effects than an increase in rate of mortality.

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In the case of eelgrass disease, a change in the ecology of large areas is known to have been caused by parasites alone, without help from predators. Eelgrass (*Zostera marina*) formerly grew in many high-salinity areas along the Atlantic coast and was the dominant of the important eelgrass community, which had a characteristic assemblage of organisms found nowhere else in such numbers. In the early 1930's, eelgrass in all high-salinity waters became diseased and died out completely. Numerous organisms were found in and on diseased eelgrass, but the primary cause of the disease was apparently the protozoa *Labyrinthula*, which is usually classified in the Proteomyxa. The parasite evidently could not tolerate as low salinities as could the host, for eelgrass survived in many areas in the low-salinity fringe of its range and now spreads from these centers down the estuaries in wet years, only to be killed again when salinity rises. Some of the organisms of the eelgrass community are still found in these marginal areas, but others, less adaptable to low salinities, were wiped out. The bay scallop was (economically) the most important casualty; in Virginia, counties which formerly had a sizable scallop fishery now have none. Presumably, both eelgrass and scallop are still as well adapted to the physical conditions of their former habitat as they were before 1930; the nature of the community in the former eelgrass flats is determined by a parasite, not by the physical conditions acting directly on the eelgrass or on the scallop. Incidentally, some former eelgrass flats in Virginia are now occupied by oyster beds; in the marginal zone the reinvasion of eelgrass is welcomed by crabbers and deplored by oystermen; apparently the communities dominated by eelgrass and by oysters are incompatible, but the dynamics of this interrelationship is not known.

The important point is that the role of *Labyrinthula* in maintaining the present distribution of marine communities probably would not be known if the sensational die-off of eelgrass had occurred in ancient times instead of very recently. There must be many other cases in which the nature of a marine community is determined by parasites, but in which the role of the parasite has not been discovered.

Unfortunately for the paleoecologist, very few marine parasites leave any fossil remains. Shells of parasitic snails such as the Pyramidellidae, and the "galls" caused by Myzostomida on crinoids, are almost the only examples known to the author of fossil evidences of marine parasites. The parasitic Protozoa, fungi, and helminths, which are so important in the dynamics of modern marine communities, have left no evidence of their existence in ancient seas. Nevertheless, the paleoecologist must keep in mind that marine communities of the past were probably influenced by parasites as well as by predators and by physical factors. It is not possible to understand marine ecology without considering the role of parasites.

The ecologist who refers to a parasitology textbook in search of information is likely to get the impression that only trematodes, cestodes, acanthocephala, and some Protozoa, nematodes, and insects are parasites. This is due to the emphasis on medical parasitology in our colleges. Only Pearse (1942) gives a well-rounded picture of parasitology, and his book is too short to give a complete picture. Baer (1951) gives a good account of some of the parasitic groups which are ignored by the textbooks. Caullery (1952) is the classic reference on parasitism for the general biologist.

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SYNOPSIS OF PARASITISM IN THE SEA

In order to give some concept of the wide distribution of parasitic habits in the animal kingdom, the writer presents a brief survey of parasitism among animals arranged in taxonomic order. Special reference is made to marine parasites, some specific examples are given, and notes of interest to ecologists are offered.

Phylum Protozoa
- Subphylum Plasmodroma
  - Class Mastigophora
    - Subclass Phytomastigina. Six orders, mostly free living, but some symbiotic in animals
      - Order Cryptomonadina. Fresh water and marine, mostly free living. Several species of *Chrysidella* known as "Zooxanthellae" in Foraminifera and Radiolaria. Example: *Chrysidella schaudinni* in the foraminiferan *Peneroplis pertusus*
      - Order Dinoflagellata. A number of genera and species parasitic in marine copepods, annelids, Protozoa, etc. Examples: *Blastodinium spinulosum* in several copepods, *Haplozoon clymenellae* in the annelid *Clymenella torquata* at Woods Hole
    - Subclass Zoomastigina. Four orders, all including parasitic forms
      - Order Protomonadina. Includes a number of marine parasites. Examples: *Trypanosoma granulosum* in eel, *T. giganteum* and *T. rajae* in rays, *Cryptobia grobbeni* in Siphonophora.
      - Order Polymastigina. This order, mostly parasites of termites, also includes some parasites of marine hosts. Examples: *Protrichomonas legeri* in fish *Box boops*, *Hexamita salmonis* in salmon and trout, *Hexamita* sp. in oysters
  - Class Sarcodina. Two subclasses: Actinopoda are all free living, Rhizopoda are mostly free living but include many parasites.
    - Subclass Rhizopoda. Five orders, of which two include parasitic forms.
      - Order Proteomyxa. Saprophytic or parasitic on plants and protozoa, both fresh water and marine. Marine examples: *Labyrinthomyxa sauvageaui* in *Laminaria lejdisii*, *Labyrinthula macrocystis* in *Zostera marina* causing "eelgrass disease".
      - Order Amoebina. Includes many free living and many parasitic species. Many marine parasites. Examples: *Vahlkampfia patuxent* in oysters, *Schizamoeba salmonis* in salmonoid fishes, *Paramoeba pigmentifera* in Chaetognatha
  - Class Sporozoa. All parasitic.
    - Subclass Telosporidia.
      - Order Gregarinida. Parasites of invertebrates; marine, fresh water, and land.
        - Suborder Eugregarinina. Examples: *Urospora* spp. in nemerteans, sipunculids, holothurians. *Lithocystis brachycercus* and *Cystobia irregularis* in holothurians. *Gonospora minchini*, *Pterospora maldaneorum*, and many other genera and species in polychaete annelids. *Cephaloidophora olivia* and other species in crabs. *Pyxinoides balani* in balanoid barnacles. *Porospora gigantea*, sexual stages in lobster, asexual in mussels. *Nematopsis legeri*, *N. ostreum*, *N. prytherchi*, sexual stages in crabs, asexual in oysters and mussels
        - Suborder Schizogregarinina. *Merogregarina amaroucii* in ascidian *Amaroucium* sp., *Selenidium potamillae* in polychaete *Potamilla reniformis*
      - Order Coccidia. Parasites of vertebrates and invertebrates, especially on land
        - Suborder Eimeridia. Mostly intracellular parasites of gut epithelium. *Selenococcidium intermedium* in European lobster. *Aggregata eberthi*, schizogony in crab *Portunus depurator*, sporogony in cuttlefish *Sepia officinalis*. *Myriospora trophoniae* in polychaete *Trophonia*. *Merocystis kathae*, *Pseudoklossia pectinis*, *Hyaloklossia pelseneeri* in kidney of mollusks. *Eimeria sardinae*, *E. clupearum*, *E. gadi*, in fishes
    - Subclass Acnidosporidia
      - Order Haplosporidia. This is a "waste-basket" group; except for *Haplosporidium* the genera included here have uncertain status, and some have been proved to be fungi. *Haplosporidium nemertis* in nemertean *Lineus bilineatus*. *Haplosporidium chitonis* in amphineura.

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Anurosporidium pelseneeri in trematode parasitic in clam, *Donax*. *Ichthyosporidium giganteum*, *I. hertwigi*, *I. hoferi* in fishes.

Subclass Cnidosporidia

Order Myxosporidia. Myxosporidia are parasites of lower vertebrates. *Ceratomyxa mesospora*, *C. hopkinsi* in gall bladder of marine fishes. *Unicapsula muscularis* in muscle, cause of "wormy" halibut, Pacific

Order Actinomyxidia. Parasites of marine and freshwater annelids. *Tetractinomyxon intermedium* in coelom of sipunculid, *Petalostoma minutum*

Order Microsporidia. Microsporidia are parasites of lower vertebrates and invertebrates, especially arthropods. *Nosema notabilis* in myxosporidian *Sphaerospora polymorpha* in urinary bladder of *Opsanus* spp. *Nosema* spp., several in Crustacea including commercial shrimp. *Thelohania maenadis* in muscle of crab *Carcinus maenas*. *Thelohania* spp., several others in Crustacea including commercial shrimp.

Subphylum Ciliophora

Class Ciliata

Subclass Protociliata. Parasites of lower vertebrates, especially frogs and toads. *Protoopalina saturnalis* in marine fish *Box boops*

Subclass Euciliata. Mostly free living, but all four orders include parasitic forms

Order Holotricha

Suborder Astomata. All parasitic. *Rhizocaryum concavum* in gut of polychaetes, *Polydora* spp. *Orchitophrya stellarum* in gonad causes parasitic castration of starfish *Asteracanthion rubens*

Suborder Gymnostomata. *Parachaenia myae* in pericardial cavity and siphon of *Mya arenaria*

Suborder Trichostomata

Family Entorhipidiidae. All parasites of echinoderms

Examples: *Entorhipidium echini*, *Biggardia bermudense*, *Anophrys elongata*, and others in intestine of sea urchins

Suborder Hymenostomata. *Eurychilum actinae* in gastrovascular cavity of *Sagartia parasitica*. *Connilembus caeci* in gut of sea urchin, *Tripneustes esculentus*

Suborder Thigmotricha. *Conchophthirius mytili* on foot of *Mytilus edulis*. *Eupoterion pernix* in gut of limpet, *Acmaea persona*

Suborder Apostomea. *Ophiurespira weilli*, trophonts in intestine of ophiuroids. *Pericaryon cesticola* in gastrovascular cavity of ctenophore, *Cestus veneris*

Order Sphirotricha. *Metopus circumlabens* in gut of sea urchins. *Licnophora* spp. in holothurians, gastropods (*Crepidula*)

Order Peritricha. *Paravorticella clymenellae* in colon of polychaete *Clymenella torquata*. *Trichodina sphaeroides* parasitic on marine fish *Sphaeroides maculatus*

Class Suctoria. Fresh water and marine, mostly free living, epizoic, or commensal. A few true parasites. Example: *Endosphaera engelmanni* endoparasitic in parasitic ciliate *Trichodina spheroides* in marine fish *Sphaeroides maculatus*

Kudo (1947) is a good general reference on the parasitic protozoa.

Phyllum Mesozoa. All members of this phylum are endoparasites of marine invertebrates

Class Moruloidea

Order Dicyemida. Parasitic in nephridia of squids and octopuses. Examples: *Dicyema typus* in *Octopus*, *Pseudicyema truncatum* in *Sepia officinalis*

Order Orthonectida. Parasitic in internal spaces and tissues of flatworms, nemerteans ophiurans, annelids, and a clam. Examples: *Rhopalura granosa* in clam *Heteranomia*, *R. ophiocomae* in brittle star. Both of these cause parasitic castration of hosts.

For a general account of the Mesozoa see Stunkard (1954).

Phylum Porifera. All marine except Family Spongillidae. No true parasites.

The boring sponges, Family Clionidae, excavate deep branching tunnels in calcareous objects such as mollusk shells and the exoskeletal structures of corals. Examples: *Cliona celata* and *C. truitti* in shells of living and dead oysters. Species of *Cliona* can serve as indicators of environmental con-

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ditions. *C. celata* is confined to high (*i.e.*, nearly oceanic) salinity, while some of the other species are more tolerant of lowering of salinity. *C. truitti* extends up estuaries beyond all other sponges and almost (but not quite) to the extreme low-salinity limit of *Crassostrea virginica*. The species can be identified in old dried shells as well as in fresh specimens.

For further information on boring sponges, *see* Old (1941).

Phylum Coelenterata

Class Hydrozoa. Five orders

Order Hydroida. This order, nearly all free living, contains a few semiparasitic and parasitic genera (Chapter 15A, Table 1).

Order Trachylina. Nearly all free living, but several with parasitic stages in life cycles Examples: *Cunina proboscidea*, attach to hydroid *Geryonia* develop parasitically into stolons which bud off medusae. *Polypodium* has budding stolons inside eggs in ovary of sturgeon (in Black and Caspian seas); the polyp stage is free-living.

Class Scyphozoa. Five orders, all marine, all free living.

Class Anthozoa. Eleven orders, all marine, all free living

Most genera of Order Zoanthidea are epizoic on specific hosts, and some in other orders are also epizoic, but all catch their own food.

Reference: Hyman (1940)

Phylum Ctenophora. Nearly all free living. Of the five orders, only one includes parasites.

Order Platyctenea. Show various gradations between commensalism and parasitism. *Coeloplana* is ectocommensal on specific kinds of alcyonarians. *Gastrodes* has a parasitic stage embedded in mantle of *Salpa*; the adult is free living.

Reference: Hyman (1940)

Phylum Platyhelminthes

Class Turbellaria

Order Acoela. Exclusively marine, mostly free living. Also some inhabiting intestines of echinoderms: *Avagina incola* in a heart urchin *Otocelis chirodotae* and several others in sea cucumbers

Order Rhabdocoela. Marine, fresh water, and terrestrial, mostly free living, but many marine forms are parasitic: *Paravortex cardii* in ovary of *Cardium edule*, *Oekiocolax plagiostomorum* in mesenchyme of turbellarian *Plagiostomum*, and causing parasitic castration; *Graffilla* spp. in viscera of snails and shipworms; *Graffilla gamellipara* in liver and ovary of *Scrobicularia*; *Fecampia* spp. in haemocoel of Crustacea (Temnocephalids, in this order, are epizoic on fresh-water animals.)

Order Alloecoela. Predominantly marine, but some in fresh water; mostly free living, but some ectocommensal or ectoparasitic. Example: *Hypotrichina* spp. on the crustacean *Nebalia*, Mediterranean

Order Tricladida. Marine, fresh water, and terrestrial, mostly free living, but some ectocommensal or ectoparasitic: *Bdelloura* spp., *Syncoelidium pellucidum*, on horseshoe crab, *Limulus*. *Micropharynx* on skates

Order Polycladida. All marine, except one species. None are true parasites, but several are on the border line of parasitism: *Stylochus zebra* in shells inhabited by hermit crabs, *Stylochoplana parasitica* in mantle groove and gills of chitons, *Euplana takewakii* in genital bursae of ophiuroids, and *Hoploplana inquilina* in mantle chamber of snails. *Stylochus ellipticus* and *S. frontalis*, the "oyster leech", creep inside the shells of oysters to feed on the living flesh and are on the border line between predators and parasites. *S. frontalis* often causes malformations of the shell in oysters.

Reference: Hyman (1951a)

Class Trematoda. All parasitic

Order Monogenea. Marine species make up a large part of the group, and nearly all the suborder Polyopisthocotylea. They are ectoparasites, usually on the gills and skin, occasionally in the rectum or nasal fossae, of marine fishes. Many parasitize elasmobranchs, but the majority are on bony fishes. *Microcotyle*, with many species on a variety of marine fishes (and one on the fresh-water sciaenid *Aplodinotus grunniens*), will serve as an ex-

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ample. A few parasitize invertebrates: *Udonella* spp. on *Caligus*, a copepod parasite of teleosts, and *Isancistrum loliginis* on the squid *Loligo media*

Order Aspidobothria (Aspidocotylea, Aspidogastraea). Fairly evenly divided between marine and fresh-water forms. Some fresh-water forms become adult in mollusk hosts. The known marine forms have immature stages in invertebrates, mature stages in vertebrates. Examples: *Lobatostoma* spp., immature in marine bivalves, mature in teleosts. *Lophotaspis* spp. immature in snails and pearl oysters, adult in turtles. *Stichocotyle nephrops*, immature in lobsters, adult in skates

Order Digenea. Predominantly parasites of bony fishes, especially marine forms, but well represented in all large vertebrate groups except elasmobranchs, and include some families specialized for land life. Elasmobranchs, for some unknown reason, have only a very few species of Digenea. Of the approximately 70 families and 700 genera of Digenea, many are limited to marine teleosts. Digenea are well represented in marine mammals and in sea birds. Mollusks serve as first intermediate hosts: gastropods, pelecypods, and scaphopods, in descending order of importance. In most cases, either fishes or invertebrates serve as second intermediate hosts. Digenea are well represented in the deep-sea fauna as well as in the littoral. Examples: Family Bucephalidae all use bivalve mollusks as first intermediate hosts; the cercariae penetrate into certain fishes which serve as second intermediate hosts, and these are eaten by predaceous fishes in which the adults develop. *Zoogonus rubellus* and *Zoogonoides laevis* (Family Zoogonidae) use snails (*Nassa obsoleta* and *Columbella lunata*) as first intermediate hosts, *Nereis* as second host, and teleost fishes (toadfish, eel, tautog) as final host. *Parorchis avitus* (Family Echinostomatidae) uses snails (*Urosalpinx cinereus*, *Thais lapillus*, *Thais floridana*) as first intermediate hosts; the cercariae encyst on the shells of mollusks; when the mollusks are eaten by gulls, the metacercariae develop into adults in the cloaca of the final host. The rediae of *Parorchis avitus*, like the precercarial stages (sporocysts and rediae) of many other trematodes, cause parasitic castration of the mollusk hosts. *See* Miriam Rothschild (1936; 1938; 1941a; 1941b) for discussion of the effects of trematodes on growth and form of marine snails.

General references on trematodes: Hyman (1951a) Dawes (1946).

Class Cestoda. All parasitic

Subclass Cestodaria. Monozoic cestodes

Order Amphilinidea. Mostly fresh water. Adults in coelom of bony fishes. Larvae in amphipods. Example: *Amphilina foliacea* in sturgeon, *Acipenser*

Order Gyrocotylidea. All marine. Adults in intestine of chimaeroid fishes. Intermediate hosts not known. Example: *Gyrocotyle rugosa* in elephant fish, *Callorhynchus milii*

Subclass Eucestoda. Mostly polyzoic

Order Tetraphyllidea. (Phyllobothrioidea). Adults in gut of elasmobranchs. Larval stages in copepods, ctenophores, molluscs, and fishes. Example: *Phyllobothrium lactuca*, adult in dogfish, *Mustelus vulgaris*

Order Lecanicephaloidea. Adults in gut of elasmobranchs. Larval stages in mollusks. Example: *Tylocephalum pingue*, adult in *Rhinoptera bomasus*. Another species of *Tylocephalum* is believed to cause pearl formation in Ceylon pearl oysters.

Order Diphyllidea. Adults in gut of elasmobranchs. Larval stages in mollusks and crustaceans. Example: *Echinobothrium typus* in *Raja clavata*; larval stages in several Crustacea

Order Trypanorhyncha. (Tetrarhynchoidea). Adults in gut of elasmobranchs, except *Haplobothrium* in *Amia calva*. Larval stages in teleost fishes and in many invertebrates (medusae, echinoderms, snails, bivalves, cephalopods, crustaceans, etc.). Example: *Grillotia erinaceus*, adult in skates, rays, dogfish, sharks; immature forms in teleosts

Order Proteocephaloidea. Adults in fresh-water cold-blooded vertebrates, except *Lintoniella*. Larval stages in copepods. Example: *Lintoniella adhaerans* in hammerhead shark

Order Pseudophyllidea. Adults in intestines of all classes of vertebrates, including many marine forms; predominantly parasites of non-elasmobranch fishes. Copepods or other crustaceans serve as first intermediate hosts and fishes or other vetrebrates as second

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intermediate hosts. Example: *Bothriocephalus scorpii*, adult in *Cottus scorpio* and other marine fishes

Orders Nippotaeniidae, Taenioidea, and Aporidea include no marine forms.

General references on cestodes: Hyman (1951a), Wardle and McLeod (1952).

Phylum Nemertina. (Rhynchocoela). All marine except one fresh-water and one terrestrial genus

Subclass Anopla. Orders Palaeonemertini and Heteronemertini all free living

Subclass Enopla: Order Bdellomorpha or Bdellonemertini contains a single genus, *Malacobdella*, with three marine species inhabiting the mantle cavity of clams; these are supposedly commensal.

Order Hoplonemertini, mostly free living, includes a few parasitic species. Example: *Carcinonemertes carcinophila*, parasitic in the gills of crabs and on the egg masses of spawning female crabs. The worms in the gills are white in crabs which have not spawned and red in crabs which have spawned one or more times, thus serving as indicators of the reproductive history of the host (at least in the case of *Callinectes sapidus*).

Phylum Acanthocephala. Includes about 300 species, all parasitic throughout life. Adults live in gut of vertebrates of all classes, and larval stages occur in invertebrates. Of the three orders, one (Archiacanthocephala) is entirely terrestrial, and the other two (Paleacanthocephala and Eoacanthocephala) are mostly aquatic. Some genera are entirely marine, others have both fresh-water and marine species. Examples: *Corynosoma strumosum* and *C. semerme*, adults in seals and marine birds, first larval stages in amphipods, later immature stages in fishes

Phylum Aschelminthes

Class Rotifera

Order Seisonacea, smallest of the three orders, are all ectoparasites on gills of leptostracans.

Orders Bdelloidea and Monogononta are predominantly fresh water and free living but contain species which show various gradations between free-living and parasitic life. Most parasitic and semiparasitic rotifers are in fresh water. Only about 200 species of rotifers, nearly all free living, are marine. Example of marine parasite (Order Bdelloidea): *Zelinkiella synaptae*, in pits in skin of sea cucumbers

Class Gastrotricha. Free living, in fresh and salt water

Class Kinorhyncha. Free living, marine

Class Priapulida. Free living, marine

Class Nematoda. Marine, fresh water, and terrestrial. Predominantly free living, but include enough parasitic forms to parasitize all classes of metazoans, and probably all plants

Orders Enoploidea, Dorylaimoidea, Chromadoroidea, Araeolaimoidea, Monhysteroidea Desmoscolecoidea; all free living

Order Mermithoidea: Parasites of fresh-water and land invertebrates

Order Rhabditoidea: Free living, parasitic in plants, or parasitic in animals (invertebrates). Almost entirely terrestrial or fresh water. *Rhabditis ocypodis* on gills of crab *Ocypode*

Order Rhabdiasoidea: Parasites, fresh water and terrestrial

Order Oxyuroidea: Parasites, mainly of terrestrial vertebrates

Order Ascaroidea: Parasites, mainly of land vertebrates, but Family Anisakidae includes some marine forms (*Anisakis* in marine mammals, *Porrocaecum* in seals, *Contracaecum* in fishes, birds, and mammals). Examples: *Contracaecum spiculigerum* in pelicans and cormorants, *C. incurvum* in swordfish. Immature stages in fishes and invertebrates.

Order Strongyloidea: Parasites of land vertebrates almost entirely, but seals become infected on breeding grounds, and Family Pseudaliidae is confined to Cetacea. Example: *Pseudalius inflexus* in bronchi, blood vessels, heart of porpoises

Order Spiruroidea: Parasites of land and fresh-water vertebrates predominantly, but *Echinocephalus* juveniles occur in pearl oysters and sea urchins, and *Proleptus* juveniles in crabs. *Cucullanus* has a number of species in marine fishes. Example: *Cucullanus cirratus* in *Gadus morrhua* and other fishes

Order Dracunculoidea: Parasites of land and fresh-water hosts, except *Philometra globiceps* and other species of the genus in body cavity and tissues of marine fishes. Also *P. grayi* in sea urchin

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Order Filarioidea: Parasites of terrestrial and amphibious hosts exclusively

Order Trichiuroidea: Parasites of terrestrial and fresh-water vertebrates, except *Oncophora neglecta* in gall bladder of *Thynnus vulgaris*

Order Dioctophymoidea: Parasites of land and fresh-water vertebrates (larvae in invertebrates), except *Eustrongylides* spp. in aquatic birds, juveniles in *Fundulus*

Class Nematomorpha

Order Gordioidea (Gordiacea). Parasites of land and fresh-water invertebrates, chiefly insects

Order Nectonematoidea. One genus, *Nectonema*. Juveniles parasitic in crabs and hermit crabs, adults free swimming in the sea; widely distributed, equator to arctic

Example: *Nectonema agile*

General reference on Aschelminthes: (Hyman 1951b)

Phylum Annelida

Class Archiannelida. All marine, free living

Class Myzostoma. Myzostomids are often classed under Polychaeta. All live on or in echinoderms. They show various gradations of relationships, from commensals moving freely over outside surfaces of their hosts to internal parasites. Most are external parasites or commensals of crinoids, some of which harbor as many as nine species. Some myzostomids cause characteristic lesions, galls, or scars on the body of the host, and identical scars are shown on fossil crinoids all the way back to the Paleozoic. Example: *Protomyzostomum polynephris* in body cavity of ophiuroid, *Gorgonocephalus*, causes parasitic castration of host in some cases.

Class Oligochaeta. Fresh water and terrestrial, including a few species on ocean beaches; most free living, a few parasitic on other oligochaetes or Crustacea, one in ureter of frog, but no marine parasites

Class Hirudinea. Leeches show various gradations from predaceous to ectoparasitic, and some can become facultative endoparasites. Most leeches live in fresh water, a few live on land (especially in tropical rain forests), and several genera are marine.

Order Acanthobdellida. *Acanthobdella peledina*, parasitic on salmonid fishes

Order Rhynchobdellida. Members of the Family Ichthyobdellidae are external parasites of fishes and turtles, some in the sea and some in fresh water. Examples: *Piscicola rapax* on summer flounder, *Branchellion raveneli* on skates and rays

Order Gnathobdellida. The toothed leeches, the blood sucking leeches which attack man and other mammals. No marine parasites(?).

Order Herpobdellida. Freshwater and terrestrial leeches; no marine parasites

Class Polychaeta

Order Errantia. A number of Errantia have been found living in other annelids, mollusks, etc. The clearest case of parasitism seems to be *Ichthyotomus sanguineus*, attached by specialized piercing and grasping stylets on the fins of marine fishes, especially eels.

Order Sedentaria. None truly parasitic, but many epizoic or commensal on other animals. Several species of *Polydora* excavate burrows in the shells of living mollusks, and at least some of these extract food from the currents brought in by the mollusks. Example: *Polydora websteri* in shells of *Crassostrea virginica*. These worms are much more abundant on living oysters than on empty shells and are most abundant along the edges of the valves where the food-bearing currents pass.

Class Echiurida. All marine, none parasitic, except males parasitic on females in some genera (*e.g.*, *Bonellia*)

Class Sipunculida. All marine, none parasitic

Phylum Entoprocta. Bryozoa Entoprocta. All marine except *Urnatella*. None are true parasites, but some, especially Loxosomatidae, are epizoic on or commensal with other animals. *Loxosoma saltans* inhabits the tubes of polychaete annelids.

Phylum Bryozoa. Bryozoa Ectoprocta. All but a few genera are marine. None are true parasites, but many are epizoic. Some (*Terebripora*, *Spathipora*, Penetrantiidae, Immergentiidae) burrow in the shells of mollusks and barnacles, like the boring sponges.

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Phylum Phoronida. All marine, none parasitic. Some (*e.g.*, *Phoronis ovalis*) burrow in the shells of mollusks, and one occupies channels in the tube of a sea anemone.

Phylum Brachiopoda. All marine, none parasitic

Phylum Chaetognatha. All marine, none parasitic

Phylum Mollusca

Class Amphineura

Subclass Aplacophora (Solenogastres). All marine; no true parasites, but some commensal with colonial Coelenterates

Subclass Placophora. All marine, free living

Class Gastropoda. Marine, fresh water, and terrestrial. The predominantly marine order Prosobranchiata, though mostly free living, includes an interesting series of gradations between predation (by sucking blood and tissue fluids) and complete parasitism. *Odostomia* and other Pyramidellidae are typical snails in appearance, but many species live on other invertebrates (in some cases, within the mantle cavity of bivalve mollusks) and feed on their tissues. *Thyca*, *Melanella*, *Megadenus*, and *Stilifer* show various degrees of specialization for life as ectoparasites of echinoderms. *Gasterosiphon deimatis*, *Entocolax ludwigi*, *Entoconcha mirabilis*, and a number of other species are endoparasites in the body cavity of holothurians; some of them are so highly specialized that the adults have lost all resemblance to snails and would be considered worms except for the fact that they produce typical snail larvae. Starfishes have several species of parasitic snails which live embedded in the skin and produce distinctive swellings on the arms. Baer (1951) recognizes 17 living genera of parasitic snails. Fossil snails parasitic on echinoderms are also known.

Class Scaphopoda. All marine and free living

Class Pelecypoda. Marine and fresh water, nearly all free living. The Unionidae and some other fresh-water bivalves have larval stages (glochidia) which become true parasites in the gills and fins of fishes and salamanders. When these parasitic mollusks are found on marine fishes, they furnish conclusive proof that the fishes have spent some time in fresh water. Some marine bivalves are commensal, epizoic, or otherwise closely associated with certain animals; *e.g.*, *Martesia smithii*, on the Gulf of Mexico coast, is almost invariably found buried in pits which it excavates in the shells of living oysters. *Pholadidea parva* burrows in shells of the abalone, *Haliotis* spp., on the California coast.

Class Cephalopoda. All marine and free living

Phylum Arthropoda. Only the classes Tardigrada, Arachnida, Pycnogonida, and Crustacea include marine parasites. There are many parasitic insects, but none in marine hosts.

Class Tardigrada. Mostly terrestrial or in fresh water, and free living, but some marine forms are parasitic or semi-parasitic. Examples: *Tetrakentron synaptae*, parasitic on tentacles of holothurians; *Actiarctus doryphorus*, a facultative parasite on echinoid *Echinocyamus pusillus*; *Halechiniscus guiteli* in and on oysters, possibly parasitic. *See* Green (1950) and Marcus (1936) for literature.

Class Arachnida

Order Acarina. Predominantly terrestrial, but with many fresh-water and some marine species. Many free-living and many parasitic genera. Examples: *Halacarus verrilli* (Family Halacaridae) on hydroids, and other members of the same family on other animals, especially during immature stages of development. *Pontarachna punctulum* (Family Hygrobatidae) in or on oysters in Bay of Naples. For literature, *see* Andre and Lamy (1930), Piersig and Lohmann (1901), Pratt (1935), and Wolcott (1905). *Halarachne* spp. live in nasal passages of seals.

Order Pentastomida (Linguatulida). All endoparasitic, but none in marine hosts

Class Pycnogonida. Many adult pycnogonids are free living, preying upon various coelenterates or other soft-bodied animals; some are like ectoparasitic lice on sea anemones. Few larval or post-larval stages are known to occur independently of their parent or to be free living. The larvae of many species are parasitic in hydroids, and many form galls or cysts. Other species are parasitic in octocorals, anemones, clams, and nudibranchs. Immature forms are also associated with hydromedusae. An early report of a pycnogonid parasitic on fish has not

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been verified and is possibly a mistake. A summary of the hosts of pycnogonids is given by Helfer and Schlottke (1935, p. 198–201).

Class Crustacea

Subclass (or order) Branchiopoda. Includes Phyllopoda, represented by marine forms in past ages but confined to fresh water and salt lakes in recent times, and Cladocera, which are mostly fresh water but are represented in the sea. All are free living.

Subclass (or order) Ostracoda. Marine and fresh water; some fresh-water forms are parasitic or commensal, but no marine parasites are known.

Subclass (or order) Copepoda

Order (or suborder) Calanoida. Fresh water and marine, all free living

Order (or suborder) Harpacticoida. Mostly free living, many commensal. *Cancrincola* spp. live in the gills of Crustacea (land crab, hermit crab).

Order (or suborder) Cyclopoida. Marine and fresh water; free living, commensal, and parasitic. *Asterocheres* spp. and related genera are parasites of echinoderms. A number of Lichomolgidae are temporary parasites or semiparasites of mollusks and other marine invertebrates. Examples: *Myicola metissiensis* in gill tubes of *Mya arenaria*; *Tochocheres cylindracus* in mollusk *Lucina lactea*; *Modiolicola insignis* in *Mytilus galloprovincialis*. Some are injurious to their hosts and may be of commercial importance; *Mytilicola intestinalis* is apparently the cause of serious mortalities of commercially cultured mussels, *Mytilus edulis*, in Europe.

Order (or suborder) Notodelphoidea. All marine and either commensal or parasitic; some are highly specialized parasites. Examples: *Doropygus pulex* in *Molgula*; *Enterocola fulgens* in stomach of compound ascidians

Order (or suborder) Monstrilloida. All marine. Adults and nauplius larvae free-swimming, all intermediate stages parasitic in invertebrates. Highly specialized for parasitism; even the free-swimming stages lack a complete digestive system. Examples: *Haemocerca danae* in polychaete annelid; *Monstrilla helgolandica* in snail, *Odostomia rissoides*, or *O. scalaris*

Order (or suborder) Caligoida. Marine and fresh water. All parasitic, with free-swimming early larval stages; some must have two successive hosts to complete their development. Most are parasites of fish, but *Pennella* uses a cephalopod as first host, and some lernaeids parasitize whales. Examples: *Caligus rapax* on many marine teleosts and elasmobranchs; *Trebius tenuifurcatus* on sting ray; *Alebion glaber* on elasmobranchs; *Perissopus communis* on gills and fins of sharks; *Nesippus alatus* in throat of sharks; *Lernanthropus pomatomi* on gills of bluefish; *Lernaeenicus radiatus* and other species, very highly specialized and wormlike, partly buried in flesh of many marine teleosts; *Pennella filosa*, even more highly specialized, partly buried in flesh of swordfish and sunfish.

Order (or suborder) Lernaepodoida. Marine and fresh water. All very highly specialized parasites, mostly of fish. Examples: *Chondracanthus merluccii* in mouth and gill cavity of silver hake; *Thysanote pomacanthi* on gills of black angel fish; *Sphyrion lumpi* buried in tissues of rose fish of New England; *Xenocoeloma brumpti*, endoparasitic in annelids, including *Polycirrus arenivorus*

Order (or suborder) Arguloidea. The argulids are distinct from all other copepods and are sometimes put in a separate subclass or order, Branchiura. They are parasites of marine and fresh-water fishes, usually on the skin or in the gill cavity. Only the genus *Argulus*, with both marine and fresh-water species, is represented in North America. Examples: *Argulus megalops* on flounders and other bottom fishes; *Argulus funduli* on *Fundulus* spp.

Subclass Cirripedia

Order Thoracida. These are the typical barnacles, all marine, sessile, and free living. However, some live only in very close association with certain other animals and border on parasitism. Two of the four suborders include such semiparasitic forms as:

Suborders Lepadomorpha, the goose barnacles: *Octolasmis mulleri* on gills of blue crabs in the ocean or near-oceanic waters; presence of these little barnacles on bay crabs indicates a recent sojourn in the ocean. *Anelasma squalicola*, embedded in the muscles

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of sharks; filaments ramifying from the peduncle may serve to absorb nutrients from host tissues, in which case it is a true parasite.

Suborder Balanomorpha, the acorn barnacles: *Coronula diadema* and *Xenobalanus globiciptis* live embedded in the skin of whales. Others are regularly associated with specific hosts, but apparently all catch their own food from plankton; they are hitchhikers or epizoites rather than parasites.

Order Acrothoracida. These are boring barnacles. *Alcippe lampas* lives in holes which it excavates in shells occupied by hermit crabs, *Cryptophialus minutus* inhabits shells of *Concholepas*, and *Kochlorine hamata* bores shells of *Haliotis*. Dwarf males are attached to the females.

Order Ascothoracida. Atypical barnacles highly specialized for life in corals or echinoderms, and considered to be parasites. *Synagoga mira*, parasitic on zoantharian coral *Antipathes*. *Dendrogaster astericola*, parasitic on echinoderms. *Myriacladus* spp., endoparasitic in body cavity of starfishes.

Order Apodida. This order includes only the maggotlike crustacean *Proteolepas bivincta*, parasitic in the mantle cavity of the barnacle *Alepas*.

Order Rhizocephalida. All members of this order are obligate parasites, very highly specialized. Though typically a marine group, a few species are found on fresh-water crabs (at least two in mountain streams), and these have shortened life cycles. The marine forms have free-swimming nauplius and cypris larvae. The cypris larva attaches to a certain crustacean host, usually a crab, and undergoes a metamorphosis which ends in a highly specialized form with an external sacklike portion and internal rootlike outgrowths which absorb nutrients from host tissues. The form of the host is usually strikingly modified, especially in regard to secondary sexual characteristics, and the gonads fail to develop or become atrophied so that the host is sterile. This is the classic case of parasitic castration. *See* Baer (1951) for general account and entrance into literature. Examples: *Sacculina carcini* on *Carcinus moenas*, *Peltogaster paguri* on *Pagurus pubescens*, and *Loxothylacus texanus* on *Callinectes sapidus*.

Subclass Malacostraca. Of the dozen or so orders of Malacostraca, only the isopods, amphipods, and decapods have parasitic representatives.

Order Isopoda. Isopods include marine, fresh-water and terrestrial species. Most isopods are free living; entire subgroups of the order are obligate parasites, however.

Suborder Flabellifera. Marine, with few exceptions

Includes Cymothoidae and Aegidae which are fish parasites. Some, such as *Cymothoa*, generally occupy the gill chamber; others, such as *Ourozeutes*, penetrate the body cavity from the flesh on the side of the fish.

Suborder Gnathiidea. Marine. Includes forms parasitic on fish

Suborder Anthuridea. Marine. Some genera in this group are suspected to be parasitic as they have sucking mouth parts.

Suborder Valvifera. Marine, with few exceptions. Generally free living; genus *Colidotea* commensal or possibly parasitic on sea urchins

Suborder Asellota. Marine and fresh water. Composed largely of free living forms; some, such as *Iais* and *Caecijaera* are commensal on other isopods.

Suborder Bopyroidea (Epicaridea). Marine. Parasitic on other crustaceans, decapods, mysids, isopods, euphausids, etc.

Suborder Oniscoidea. Halophile and terrestrial; none known to be parasitic

Order Amphipoda. Members of the Family Hyperiidae are commensal in medusae, and *Phronima* lives in pelagic urochordates (*Salpa*, *Pyrosoma*), but only the Cyamidae or "whale lice" are specialized parasites. They parasitize fishes as well as cetaceans and cannot swim at any stage.

Example: *Paracyamus boopis* on the humpback whale

Order Decapoda. The decapods are typically free living, but many crabs and shrimps are commensal with other animals. Various shrimps and crabs form galls on corals or inhabit sponges or sea cucumbers, but apparently only the Pinnotheridae really border on

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parasitism. *Pinnotheres ostreum*, though usually called a commensal, should be considered a parasite. The females occupy a cavity which they "erode" in the tissues of the oyster and intercept the food as it is drawn into the mouth. Stauber (1945) reported an extensive mortality of oysters in New Jersey caused by an unusually heavy infestation of *Pinnotheres*.

Phylum Echinodermata. The echinoderms are the most free living of all the large phyla; none even borders on parasitism. Some boring or rock-burrowing species, such as the sea urchin *Psammechinus miliaris* of British oyster beds, occasionally kill mollusks by damaging the shell without any intent of feeding on the flesh. The starfishes which open oysters and clams to eat them are strictly predators.

Phylum Chordata. It is doubtful whether there are any true parasites among chordates. Those reported as parasites in the literature are border-line cases. The fishes which live inside various marine invertebrates, such as *Evermannichthys* in sponges, *Carapus* in sea cucumbers, *Fierasfer* in mollusks, and *Amphiprion* in sea anemones seem to be commensals or inquilines rather than parasites. The sucker fishes, *Remora* and *Echeneis*, do not obtain food from the host and might be called "hitchhikers". The lampreys and hagfishes, which attach themselves to larger fishes and obtain food from their tissues, are not so much parasites as predators, although some of these do border on parasitism. The small catfishes called *candiru*, which live on the gills of larger fishes and suck blood from them, may be true parasites, but they are not marine. Some of the deep-sea fishes—*e.g.*, *Ceratias*—have dwarf males which are parasites of the females; some of them become so degenerate that only the reproductive system remains functional.

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C. Symbiosis

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Symbiosis with unicellular algae, most usually with the so-called brown zooxanthellae or green zoochlorellae, is widespread among marine invertebrates. It is also common, and has been more extensively studied, in fresh-water invertebrates including Protozoa such as *Paramecium bursaria*, Porifera such as *Spongilla lacustris* or *Ephydatia fluviatilis*, and Turbellaria such as *Dalyellia viridis*. Buchner (1953) has summarized and discussed the literature, largely descriptive, up to 1953, while Yonge (1944) and Fritsch (1952) have reviewed more functional aspects of this type of symbiotic relationship. Reference should be made to these papers for literature dealing with fresh-water animals, many of which are associated with species of *Chlorella*.

ORIGIN OF THE ASSOCIATION

As noted (Yonge, 1934), the presence of symbiotic algae is almost always associated with the occurrence of intracellular digestion—*i.e.*, in Protozoa, Porifera Coelenterata, Turbellaria, and Mollusca (other than Cephalopoda). There are isolated cases of algae occurring in the tissues of animals which certainly digest extracellularly—*i.e.*, some Polyzoa, Annelida, Echinodermata, and Ascidia. But the only well-documented cases are those described by Berkeley (1930a) of infection in the Chaetopteridae (Annelida) and by Smith (1935) of association between compound ascidians and algae. In the former case, the algae are green, only from 1 to 3μ in diameter, and are without a cellulose wall, or indeed a cell wall of any kind, have no chromatophore or pyrenoid and apparently no algal pigment. Berkeley regarded them as flagellates belonging to the Chrysocapsinae but was unable to determine whether they were symbionts or parasites. Possibly they may invade the tissues at an early stage in development when digestion is intracellular. Berkeley (1930b) found similar, but red, flagellates in the subepithelial layers of the stomodaeum in the ctenophore, *Beroe abyssicola*.

In the compound ascidians, all from tropical waters, studied by Smith, zooxanthellae occurred in the cloacal cavity except in *Didemnum viridae* where they were embedded in the test. But these algae are present in many Protozoa and larvae which will be contained in the food of these ascidians. It is therefore possible that they are liberated in the gut when the animals they inhabit are digested and that they then accumulate in the cloacal cavities where the excrement from the ascidians would provide them with necessary inorganic salts.

Apart from the above cases and others in fresh-water animals, of undoubted parasitic infection, this type of symbiotic relationship is restricted to animals that digest intracellularly—*i.e.*, which are in the normal habit of ingesting particles certainly up to a diameter of 10μ which is that of the larger zooxanthellae. On the reasonable assumption that a permanent association was eventually established after initial

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ingestion of algal cells by the animal, then this must have taken a different course according to whether the animal was herbivorous (or omnivorous) or was exclusively carnivorous and so incapable of digesting plant material as, for instance, in Coelenterata and Turbellaria.

SYMBIOSIS IN HERBIVORES

The best examples (Yonge, 1944) are provided by fresh-water animals, but Radiolaria (Buchner, 1953) and Foraminifera, *e.g.*, *Orbitolites* (Doyle and Doyle, 1940), provide marine examples. In both of the latter a well-developed association with zooxanthellae exists. Broadly speaking in all such herbivores symbiosis must have been established as a result of specialization of the algal cells to resist digestive action within the cells of the animal.

SYMBIOSIS IN CARNIVORES

Symbiosis in carnivores occurs in many Coelenterata, Ctenophora, and Turbellaria. In these animals establishment of symbiosis demands initial specialization of the animal which does not normally swallow plant material and even when this is introduced into the gut does not ingest it. The extensive work of Goetsch (1924) on association between the fresh-water Hydrida and *Chlorella* indicates that the plants may infect the animals when they are enfeebled, apparently by a process of parasitic infection. Later a permanent association may become established. There is no such evidence as to the manner in which the association has come about in the marine Coelenterata. Although symbiosis is exceptional in temperate waters, almost every species of coelenterate in tropical waters contains zooxanthellae. For instance, on a coral reef, not only do the reef-building corals (Madreporaria) contain zooxanthellae but also the anemones (Actiniaria), soft corals (Alcyonacea), sea fans (Gorgonacea), hydroid corals (Hydrocorallinae), as well as Scyphozoa and members of other smaller groups.

Among the marine Turbellaria, the classic cases of mutualism, this time with green algae (possibly species of *Carteria* or *Chlamydomonas*), are provided by *Convoluta roscoffensis* and *C. paradoxa* (Gamble and Keeble, 1903; Keeble and Gamble, 1907; Keeble, 1910).

The initial, possibly parasitic, association does undoubtedly give rise in certain cases to a balanced relationship. This would seem to represent the condition in the fresh-water *Chlorohydra viridissima* and the turbellarian *Dalyellia viridis* (Yonge, 1944). But, as a possible further development from this balanced relationship, there are other cases in which it would appear that either (1) the animal becomes dependent on the plant which remains capable of free life, or (2) the plant becomes specialized for life possibly exclusively within the tissues of the animal, or again (3) animal and plant become dependent upon each other, and neither is capable of life apart from the other. Examples of these three conditions follow:

(*1*) *Animal dependent on plant.* According to the conclusions of Gamble and Keeble, this is the case in *Convoluta roscoffensis* although not in *C. paradoxa.* The animal is infected when it hatches; algae are present around the egg case. The animal will not develop in their absence, and indeed the algae are considered to be effectively organs of the animal. In early life nutrition is holozoic, but later the

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animals apparently become dependent on the contained algae. They are said to consume eventually all the plants and to die of starvation, but it may be that the animal in any case degenerates after reproduction and that this has nothing to do with the apparent consumption of the algal cells. The connection is not so intimate in the case of *C. paradoxa* although here also the animal apparently fails to develop if the zooxanthellae with which it is associated are absent.

(2) *Plant dependent on the animal.* The zooxanthellae present in so many marine Protozoa and Invertebrata appear to be dependent on life within the animal. The best description of such algae is given by Doyle and Doyle (1940) in an account of those associated with the foraminiferan, *Orbitolites* (Fig. 1). Zooxanthellae are never found free in the sea, even in coral-reef areas where millions of them occur within every coral colony and in most other coelenterates and in many other animals. This may not be a certain indication that they have no free-living stages, but it does seem probable because zooxanthellae are passed from generation to generation by way of the egg and certainly increase within the animal tissues by simple division without any evidence of the formation of spores or of sexual stages. Fritsch (1952) thinks it possible that zooxanthellae may be present in the sea as autotrophic flagellates, perhaps swarming only at certain times. Reinfection is necessary in every individual in the case of the Radiolaria, and Brandt (1883) found evidence that the algae persisted and that biflagellate swarmers were later freed. Gohar (1940) also considers that reinfection is necessary in every generation in the alcyonacean Xeniidae, while Kawaguti (1944) states that the zooxanthellae of madreporarian corals have a free-living stage as a *Gymnodinium*. He worked on *Acropora corymbosa* but he gives no convincing account of his technique, and his conclusions need confirmation. Attempts at the Millport Marine Station by Dr. S. M. Marshall to repeat this work,

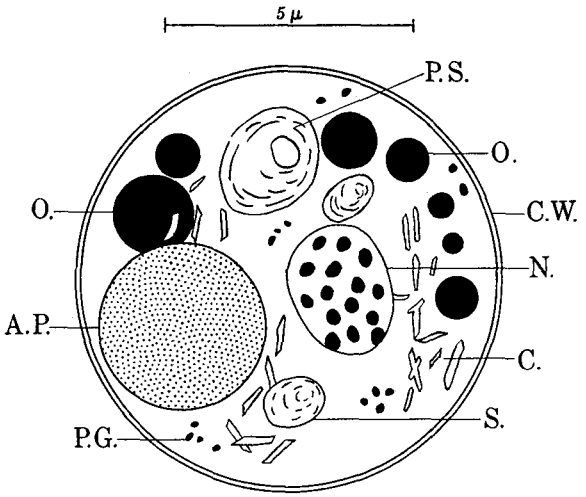

FIGURE 1.—*Structure of a typical zooxanthella*

Composite drawing. A.P., assimilation product; C., calcium oxalate crystals; C.W., cell wall; N., nucleus; O., oil; P.G., pigment granules; P.S., primary starch granules; S., secondary starch grain. From Doyle and Doyle (1940).

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using the zooxanthellae from sea anemones of temperate waters, proved unsuccessful (Personal communication). However, from a consideration of the structure of their nuclei both Brandt (1883) and more recently Hovasse (1937, quoted by Fritsch 1952) consider that zooxanthellae are related to the dinoflagellates. There is certainly further work to be done on this problem, but it remains true that, at any rate in their immotile form, the zooxanthellae are specialized for life with the cells of animals. They certainly never occur in the sea as free zooxanthellae.

(*3*) *Interdependence of plant and animal.* In alcyonaceans, especially the family Xeniidae, it was early shown by Ashworth (1899) and Pratt (1906) that the digestive organs are reduced. According to Gohar (1940) species of this family cannot capture animals and can live for any length of time in the light only when their contained zooxanthellae can increase and, he presumes, supply nutrition to the animal. But the algae also depend on the animal for inorganic nutrients so the two partners appear mutually interdependent. There must, of course, be some extraneous source of material in addition to the energy of sunlight.

INFECTION BY PREVIOUSLY INFECTED ALGAE

Herbivorous animals may thus acquire algal symbionts owing to specialization of these to resist digestion while carnivorous animals do so by specialization of the animal to ingest algae and to tolerate their presence. But there remain cases where it appears more reasonable to assume establishment of an association between an animal and some alga already specialized for life in another animal. This view is the more tenable because of the conditions in the nudibranch mollusk *Aeolidiella* (*Eolidina*) *alderi* (Naville, 1926; Graham, 1938). This feeds exclusively on the actiniarian, *Heliactis bellis*, with which zooxanthellae are always associated. Like allied nudibranchs, *A. alderi* accumulates nematocysts from its food in the dorsal cerata, and here zooxanthellae also collect. Naville believes that they increase in the body of this second "host," but Graham found no evidence of this. The possible origin of the association is evident, however.

Such may have been the origin of symbiosis between algae and opisthobranchs such as *Aeolis glauca*, *Doridoedes gardineri*, *Melibe rangii*, *Phyllirhoë* sp., *Spurilla neopolitana*, *Favorinus albus* (Buchner, 1953) also in *Tridachia crispata* (Yonge and Nicholas, 1940) where the animal is a highly specialized herbivore, and in *Placobranchus ocellatus* (Kawaguti, 1941). The remarkably intimate association between zooxanthellae and the species of the lamellibranch genera *Tridacna* and *Hippopus* (family Tridacnidae) may well have arisen in a similar manner; the algae bear a general resemblance to those living in the tissues of reef-building corals and other coelenterates with which the Tridacnidae are always associated. Kawaguti (1944) has also noted the presence of zooxanthellae in the mantle, gills, and other tissues of another tropical lamellibranch, *Corculum cardissa*, the heart-shaped shell of which is thin and translucent. There is also the case of the compound ascidians where the zooxanthellae must certainly have been acquired after prior specialization elsewhere.

MODIFICATIONS DUE TO THE ASSOCIATION

Although it is not always possible to be sure of the precise nature of the relationship between the animal and plant concerned, there are changes in structure and in

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function of both algae and animals which may reasonably be ascribed to the association. These may affect either the individual or the race.

(*1*) *Algae.* According to Keeble and Gamble (1907), the algae living in *Convoluta roscoffensis* never possess flagella, there are transient stigmata but no cell walls, and the nucleus degenerates and finally disappears. The mechanism of photosynthesis alone they consider to be unaffected. Free-living individuals, on the other hand, have four equal flagella, usually a stigma, a prominent nucleus and a pyrenoid, and a cell wall. They may be colorless and live saprophytically and when in this stage are apparently attracted chemotactically to the egg case of *C. roscoffensis*. In this instance, therefore, symbiosis affects the structure of those individuals which live within animals. In the case of the zooxanthellae generally it is the race which is affected, because, as noted above, certainly at that stage in the life history all individuals would seem to be affected.

(*2*) *Structure of Animals.* Pratt (1906) has shown that there is a reduction of the digestive regions of the mesenteries in a variety of tropical Alcyonacea in apparent correlation with the content of zooxanthellae. She indicates progressive reduction in the ventral and lateral mesenterial filaments in the series *Lobophytum–Sarcophytum–Alcyonium* (tropical species)–*Sclerophytum–Xenia*, and *Heteroxenia*. Gohar (1940) states that the tentacles of *Sclerophytum* and the Xeniidae, though large, do not react to animal food. This certainly renders them unique among those of the Coelenterata.

There is some effect on *Convoluta* but not to the extent stated in a previous review (Yonge, 1944). There reduction in the gut and loss of the excretory system was associated with the presence of zooxanthellae. But *Convoluta* belongs to the Acoela in which neither gut nor excretory system is present.

Undoubtedly the most spectacular effect of symbiosis with unicellular algae on the structure of an animal occurs in the Tridacnidae (Yonge, 1936; 1953b). Here the zooxanthellae are lodged in the greatly hypertrophied siphonal tissues (Yonge, 1953a; 1953b) which extend along the dorsal surface and so, in life, are directed upward toward the source of light (Fig. 2). The animals are attached by a byssus either throughout life or only in early life in which case they are later maintained solely by their great weight. As shown in Figure 3, the normal relationship between body and the mantle/shell is radically altered. It was originally suggested on purely morphological grounds (Lacaze-Duthiers, 1902) that the mantle and shell have rotated in relation to the body—*i.e.*, visceral mass and foot—with the result that the umbo and hinge come to lie on the ventral side, next to the foot (Fig. 3). In consequence of this rotation of the mantle and shell, the anterior adductor is lost, the Tridacnidae having attained the monomyarian condition in a manner peculiar to that family.

This change in the form of the animal can be associated directly with the presence of zooxanthellae which are literally "farmed" in vast numbers within blood sinuses in those regions of the mantle edge which are concerned with the formation of siphons. Selective value may reasonably be claimed for progressive movements that carried these originally posterior tissues farther and farther along the dorsal surface so that they were more fully exposed to light. The Tridacnidae are inhabitants of shallow

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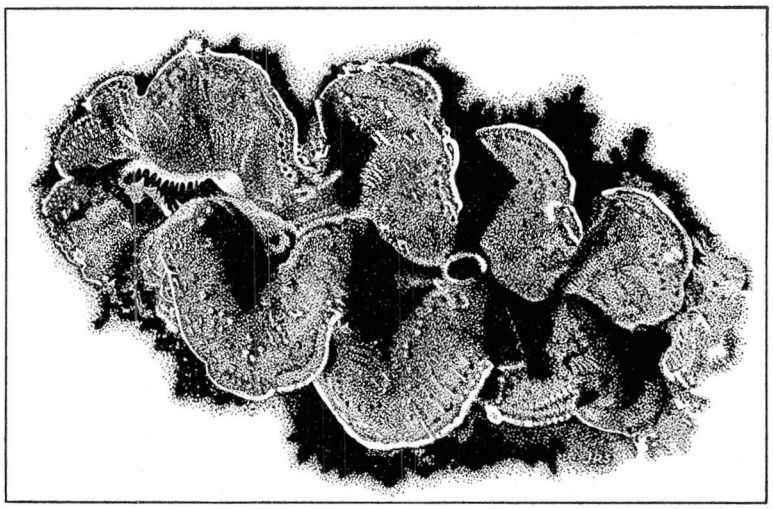

FIGURE 2.—*Tridacna crocea*
Appearance from above with siphonal tissues fully expanded

waters, in the tropical Indo-Pacific; they live on coral reefs and are usually expanded with the richly pigmented mantle edges widely exposed to the light even at low tide in the full blaze of the midday tropical sun. Moreover, light is focussed deep into the tissues by means of "hyaline organs" (Yonge, 1936) in the form of lenses which are always surrounded by great concentrations of zooxanthellae. Originally described as eyes (Brock, 1888) they have neither retina nor nerve and so cannot be sensory. It is however possible that ancestral species possessed pallial eyes in the siphonal tissues

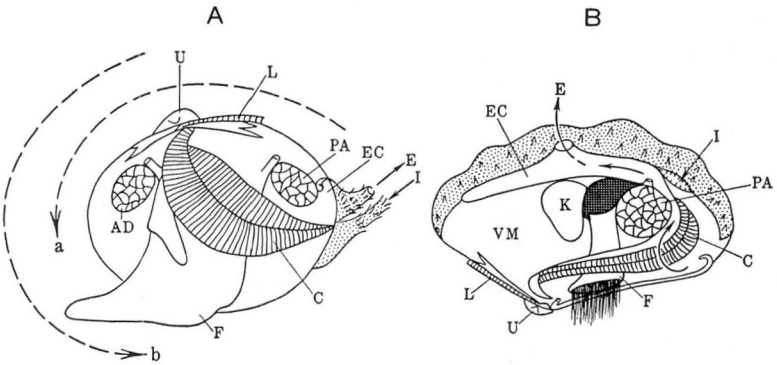

FIGURE 3.—*Evolution of the Tridacnidae* (*Cardiacea*)

Mantle cavity viewed from left side, A, Cardium; B, Tridacna. AD, anterior adductor; C, ctenidia; E, exhalant current emerging from exhalant aperture; EC, exhalant chamber, greatly extended anterodorsally in *Tridacna*; F, foot (with byssus in *Tridacna*); I, inhalant current entering inhalant aperture; K, kidney; L, ligament; PA, posterior adductor; U, umbo; VM, visceral mass. Siphonal tissues shown stippled. Broken arrows indicate rotation of mantle shell, in relation to body, which has taken place in the evolution of the Tridacnidae. a, movement of dorsal end of siphonal tissues; b, movement of umbo.

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(as does the allied *Cardium edule*) and that the hyaline organs of *Tridacna* represent the lenses of these former eyes. This is inherently more probable than that they represent new organs (Yonge, 1953a; 1953b).

The Tridacnidae possess normal ctenidia and labial palps (Fig. 3) with a well-developed alimentary system. They collect suspended food, largely phytoplankton, like other lamellibranchs. The zooxanthellae are contained within phagocytic blood cells in sinuses in the siphonal tissues. Here they increase by division, but many are also carried to the regions around—*but never in*—the digestive diverticula where they are digested within these blood cells. Ingestion and digestion within the blood cells of lamellibranchs are well known—*e.g.* in *Ostrea edulis* (Yonge, 1926; Takatsuki, 1934). As a result of digestion of zooxanthellae within the blood stream instead of within the gut, fecal matter must accumulate within the kidneys, and these are abnormally large (Fig. 3) with accumulated excrement in the form of spherical concretions.

In a series of papers, Mansour (1946a; 1946b; 1946c; 1946d) has made a number of statements about structure and physiology in the Tridacnidae. Although these are dealt with at greater length elsewhere (Yonge, 1953b), they may be briefly criticized here. He suggests that the Tridacnidae feed by pumping water from the ctenidia. But this would involve forcing water through the ciliated ctenidia (which differ only in size from those of other lamellibranchs). When the adductors contract water will be expelled, as in other lamellibranchs, through the inhalant as well as the exhalant aperture. The characteristically great extrusion of water through the exhalant aperture in *Tridacna* represents ejection of the contents of the enlarged dorsal exhalant chamber (Fig. 3, EC), which accompanies antero-dorsal extension of the siphons, and not water which has been forced through the ctenidia. A swelling on the posterior surface of the adductor, which Mansour claims to be a valve, is caused by the underlying visceral ganglia. Further postulates include the presence of a pair of tubes giving direct communication between the stomach and the mantle margins (enlarged siphonal tissues). These tubes around the ventral and posterior sides of the adductor and divide before running dorsally into the mantle edges. Series of transverse, longitudinal, and horizontal sections reveal no such tubes. Their distribution coincides precisely with that of the cerebro-visceral connectives, anterior to the adductor, and of the siphonal nerves posterior and dorsal to this as originally described by Vaillant (1865). Mansour also claims that there is a direct connection between the cavity of the kidneys and of the visceral mass. This would be of unique occurrence in the Mollusca, let alone the Lamellibranchia, but study of serial sections reveals that the openings (which Mansour illustrates by photographs) of the beginnings of the paired renal ducts which extend from the cavity of the kidney to open, as always, into the exhalant chamber above the ctenidia. There is no reason to modify previous views (Yonge, 1936) that the Tridacnidae are ciliary feeders like other Lamellibranchs and that zooxanthellae are carried about by phagocytes in the blood stream and digested by them, forming a very important, although not the sole source of food.

(*3*) *Habits of animals.* Where algae are housed in the tissues, the animals normally live in illuminated waters. In sedentary animals this is brought about by the habits

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of the larvae. Thus Kawaguti (1941; 1944) has associated the settlement of new colonies of reef-building corals with the positive phototropism of the planulae which contain zooxanthellae. The habits of the semisedentary scyphozoan, *Cassiopea*, which lies with the bell undermost in shallow tropical waters, are probably affected by the contained zooxanthellae (Bigelow, 1900; Smith, 1936). The habits of zooplankton containing algae are influenced, they do not make the usual migrations into deep water with increase in light (for references *see* Yonge, 1944). In *Tridacna*, the young animals crawl actively, very like young *Mytilus*, and always toward the source of light so that they finally settle in the zone of maximum illumination at the very edge of the water (Yonge, 1936).

Probably the two species of *Convoluta* show best the influence of contained algae on the habits of the animals in which they live. *C. roscoffensis* lives in sand at about the upper level of neap tides and always in an area of drainage. It comes to the surface when the tide is out and gets maximum illumination without risk of desiccation. This is due to positive phototaxis. With the return of the sea positive geotaxis is induced by vibration caused by the waves, and the animals retreat below the surface and are saved from being washed away. Fortnightly lunar variations also

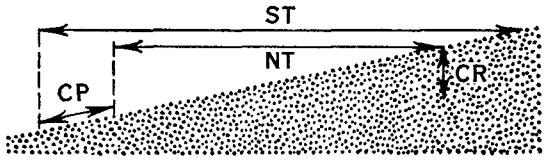

FIGURE 4.—*Diagram showing vertical and horizontal movements through and over sand by* Convoluta roscoffensis (*CR*) *and* C. paradoxa (*CP*) *respectively*
NT, ST, range of neap and spring tides. From Yonge (1944).

occur in connection with reproduction, when egg capsules are laid below the surface at the beginning of spring tides (Gamble and Keeble, 1903). In contrast to the vertical migration in this species, *C. paradoxa*, which lives on weed about low-water level, moves horizontally with the spring and neap tides, always keeping just covered and yet exposed to illumination (Keeble, 1908). Comparison between the movements of the two species in made in Figure 4.

Significance of the Association.[1] This is a matter of some dispute, but certainly conditions vary widely. A truly balanced relationship or mutualism is probably rare. The problem will be discussed first in terms of the algae, then of the animals.

In algae protection and food are gained within the animal. Food consists of carbon dioxide and inorganic salts, especially those containing nitrates or ammonia (for nitrogen) or phosphates (for phosphorus). Pütter (1911) showed that zooxanthellae in the actinian *Aiptasia* utilize excreted ammonia. Keeble and Gamble (1907) found that, for the algae in *C. roscoffensis*, uric acid and urea are better sources of nitrogen than are nitrates. More detailed experiments have been made on the utilization of phosphates by zooxanthellae within reef-building corals (Yonge and Nicholls, 1931a). The algae were shown to be capable of removing all phosphorus excreted by the corals

[1] Future work on this subject will have to consider the significance of external metabolites or ectorine substances, as suggested by Lucas (1947).

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and also of removing phosphate which had been added to the surrounding water in abnormally large amounts. The content of algae in such animals would seem to be limited by the amount of excreted phosphate (and presumably ammonia). Experiments with corals that had been kept in darkness for 152 days and so largely deprived of zooxanthellae showed great excretion of phosphate by the animals, with the content in the surrounding water increasing almost eight fold in 1 day. In *Tridacna crocea* also, excreted phosphate was intercepted by the zooxanthellae, and additional phosphate was removed from the surrounding water, whereas in *Spondylus* sp., a lamellibranch of similar size but without zooxanthellae and used as a control, there was great excretion of phosphates into the surrounding water (Yonge, 1936). Smith (1936) found similar interception of excreted phosphate and its removal from the surrounding water by the zooxanthellae in the scyphozoan, *Cassiopea*. He also reported that phosphate excretion in the actinian, *Anemonia sulcata*, which contains zooxanthellae, is about half that in *Actinia equina* (Smith, 1939). There is also some evidence, coming however mainly from fresh-water species (Yonge, 1944), that the algae may obtain food saprophytically from the animal, as in the case of *C. roscoffensis* when it utilizes uric acid or urea. There is little doubt that symbiotic algae are at an advantage by being able to intercept, at source, important supplies of available nitrogen and phosphorus. They may be said to represent, especially within tropical seas where this type of association is so common, "imprisoned plankton" (Yonge, 1944).

According to different workers the animal may, as a result of association with algae, gain in a variety of ways, namely, (1) from additional supplies of oxygen, (2) from additional supplies of food, (3) by removal from their bodies of excrement.

(1) Great quantities of oxygen are produced by zooxanthellae or other symbiotic algae when they are exposed to light. Details of the oxygen exchange between reef-building corals and the surrounding water over the 24 hours are given by Yonge, Yonge, and Nicholls (1932) and are shown graphically in Figure 5. Kawaguti (1937) gives further data for reef-building corals, Marshall (1932) for their planulae, Welsh (1936) for a marine turbellarian, *Amphiscolops langerhansii*, and Smith (1939) for *Anemonia sulcata*. In certain fresh-water species (Yonge, 1944) this additional source of oxygen may be of great value, but in the sea oxygen is seldom a limiting factor. Verwey (1931) has suggested that in coral-reef areas the production of oxygen by the zooxanthellae in daylight may be essential to meet the respiratory needs of the corals by night. He bases his statements on the estimates made by Mayor (1918; 1924) of the respiratory needs of corals, notably for species of the common stagshorn coral, *Acropora*. The figures for oxygen consumption are extremely high, equivalent, as Verwey admits, to those for a fish or squid and 18 times higher, per unit of tissue, than those obtained for another genus of corals, *Siderastrea*. The probable explanation of this wide variation is provided by the production of mucus, very great in *Acropora*, very small in *Siderastrea*, which is oxidized and so increases the *apparent* utilization of oxygen by the corals (Yonge, 1937). Certainly the acceptance by Verwey of the excessively high figures obtained by Mayor for *Acropora* invalidates his argument. Further evidence is necessary before it can be stated that marine invertebrates gain materially by the production of oxygen by their contained algae.

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(2) Animals may obtain food from the algae in one of three ways. (a) Organic matter may pass from the living algae; this has been postulated for various freshwater species (Buchner, 1953; Yonge, 1944). Gamble and Keeble (1904) believed that this occurred in *C. paradoxa* and in early life in *C. roscoffensis*. This involves excessive production of organic matter by the algae, and so not so great a concentration as occurs, for instance, in the reef-building corals. (b) Dead algae may be digested; this is suggested to occur in the foraminiferan, *Orbitolites*, which contains zooxanthellae (Doyle and Doyle, 1940). (c) Algae may be killed and digested; this may occur in later life in *C. roscoffensis* (Keeble and Gamble, 1907) and throughout life in the Xeniidae (Gohar, 1940) and in the Tridacnidae (Yonge, 1936).

There has been much controversy about the possible role of zooxanthellae as food for reef-building corals. Reviews have been made by Boschma and by Yonge and Nicholls. (*See* Yonge, 1944, for details and references.) Boschma maintained that zooxanthellae are consumed by the corals. His discovery that the algae appear in the absorptive zone of the mesenteries during starvation lost its significiance when it was shown by Mouchet (1930) and by Yonge (1931b) that this zone is also excretory, as are the gastric filaments in the scyphozoan, *Cassiopea* (Smith, 1936). Extensive experiments by Yonge and Nicholls (1931a; 1931b) showed that zooxanthellae are expelled from the tissues of corals whenever metabolism is lowered for any reason—*e.g.*, exposure to high temperature, to low oxygen tension or when starved. Under these conditions the zooxanthellae are starved, and they are than removed by way of the excretory (also absorptive) zone of the mesenteries. Moreover, when the corals are starved the tissues almost immediately retreat from the skeleton, while the zooxanthellae persist in vast numbers. This retreat is especially obvious in species of *Fungia*, as shown in Figure 6. In experiments on *Psammocora gonagra* over a period

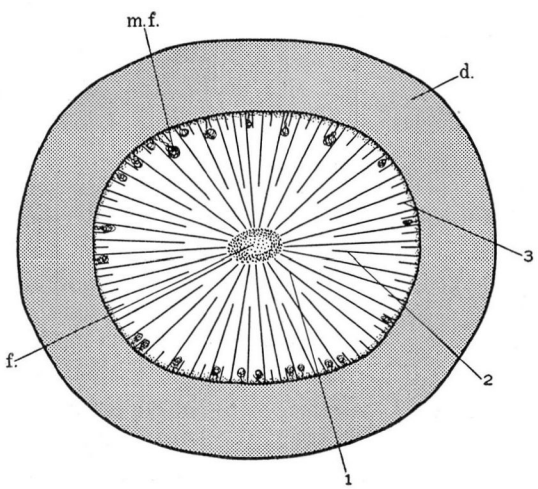

FIGURE 5.—Fungia danai

Diagram showing the reduction of the tissues of the disc in specimen A1 after it had been starved in the light for 73 days. Natural size. d., disc tissue; f., central fossa; m.f., mesenterial filaments; 1, 2, 3, first, second, and third cycle of septa. From Yonge and Nicholls (1931b).

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of 137 days, a specimen starved in light retained (on a basis of oxygen production) 64 per cent of the algae originally present, while specimens both fed and starved in darkness (affecting the algae in both cases) showed a further reduction to 40 per cent, owing to the effect on carbohydrate synthesis. In no instance was there any indication that reef-building corals can digest their contained zooxanthellae. There are many instances of individual coral colonies living for long periods or indefinitely in darkness and so without zooxanthellae.

(3) By removal of carbon dioxide and other waste material, most notably phosphates and ammonia or nitrates, the algae do act as automatic agents of excretion to the animals. The position is certainly peculiar in the Tridacnidae in which the digestion of zooxanthellae by the phagocytic blood cells leads to great hypertrophy of the kidneys. But this is for storage of what amounts to fecal material, and, as noted above, soluble waste products of value to the zooxanthellae, such as phosphates, are intercepted by these algae. The majority of other marine invertebrates that contain zooxanthellae, notably Protozoa, Coelenterata, Ctenophora, and (despite an erroneous statement to the contrary; Yonge, 1944), Turbellaria Acoela, do not possess organs of excretion so that the effect of the presence of algae is not easy to assess. It may well be significant owing to the increased efficiency which comes from the automatic removal of the end products of metabolism. Although it is a fact that individual coral colonies which normally contain zooxanthellae can live apparently indefinitely in darkness without them, this may not be true for coral reefs as a whole. Previous

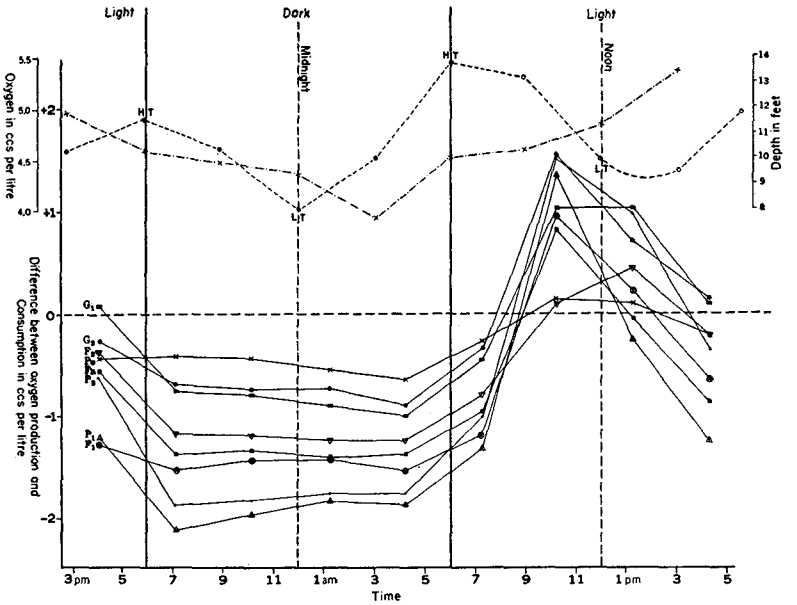

FIGURE 6.—*Graph showing difference between oxygen production and consumption in cc per liter, also oxygen content in the water and tidal changes over a period of 27 hours*

F_1, F_2, *Fungia*; Fa, *Favia*; G_1, G_2, *Galaxea*; P_1, P_2, *Psammocora*; Po, *Porites*. Vertical broken lines indicate midnight and noon, vertical unbroken lines indicate 6 p.m. and 6 a.m.—*i.e.* approximate times of dusk and dawn. H.T., high tide; L.T., low tide. From Yonge, Yonge, and Nicholls (1932).

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opinion may be repeated—namely, that the association between reef-building corals and zooxanthellae is probably essential to the plants, certainly not so to individual colonies, but, by assisting in the speed of metabolism, they may possibly be an indispensable factor in the necessarily exceptional powers of growth and repair possessed by the marine communities known as coral reefs (Yonge, 1931a).

GENERAL CONCLUSIONS

The significance of the association between marine invertebrates and unicellular algae clearly varies greatly. Rarely can it be described as a true symbiosis in the sense that the two partners are mutually interdependent; in most cases one partner in some measure exploits the other. The important fact remains that both in habits (*e.g.*, *Convoluta* spp.) and in structure (most notably in the Tridacnidae) the animals may be profoundly modified as a result of the association. The extreme prevalence of this type of association in tropical, as compared with temperate or polar, seas may well be due to the intense competition among the plants for the limited supplies of nutrient salts. Algae within the bodies of animals are at the source of such supplies. Moreover the animals themselves may gain by added nutriment (*e.g.*, Foraminifera, Radiolaria, Xeniidae, Tridacnidae) or by increased metabolic efficiency as postulated in the case of corals and allied coelenterates when considered in mass as marine communities and not as individual colonies.

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Chapter 16

Plankton*

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Marine organisms are divided into three major ecological groups: (1) the *benthos*, which includes the attached, burrowing, creeping, or skipping organisms; (2) the *nekton* or strongly swimming pelagic animals, such as fish, certain crustaceans, cephalopods, and whales, capable of stemming most water currents; and (3) the *plankton*, which includes all the floating or feebly swimming animals and plants that are swept about by the prevailing currents.

The plankton is divided into two natural groups: the *phytoplankton* and the *zooplankton*. Their members are either *oceanic*—*i.e.*, living upon the high seas—or *neritic*, living in coastal waters. Each group will be discussed separately in so far as possible, and it is fitting to begin with the phytoplankton since it is basic to all life in the sea because of its overwhelming importance in organic production.

By "organic production" is here meant the gross production or primary production. This may be defined as the amount of organic material synthesized by organisms from inorganic substances in unit time in a unit volume of water or in a column of water of unit-area cross section and extending from the surface to the bottom. The plant substance produced will be slightly less than gross production because of utilization by plants themselves in their living processes. (*See* Sverdrup, Johnson, and Fleming, 1946; Clarke, 1946, for additional definitions and units of production, and also Chapters 3, 17, 29).

PHYTOPLANKTON

The phytoplankton comprises all the freely floating photosynthetic forms. Individually they are microscopic in size and composed of only a single cell or chains of cells loosely bound together.

Among these tiny plants the diatoms rank first as producers of organic material especially in high latitudes. They are also usually the main contributors of siliceous material to the sediments. Their siliceous shells or frustules may differ greatly in weight and spination depending upon species, habitat, or season. Many of the planktonic species, especially the oceanic, produce light shells that are readily dissolved. Cold-water or winter forms with heavier shells may occur. The individual cells are commonly united into chains, and many are provided with long spines which aid in flotation. Reproduction is accomplished chiefly by binary fission in which each cell divides to produce two daughter cells. This population increase by geometric progression is of great ecological importance since it enables a rapid response to favorable growing conditions and in certain circumstances may result in a "bloom." The

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rate of cell division may be as much as 2.6 divisions per day in experimental cultures (Braarud, 1945).

The holophytic dinoflagellates are generally considered second in importance among the phytoplankton producers of organic material. However, in lower latitudes, where they have their greatest species development, they may also be the major element in the plankton for long periods of time. In higher latitudes, there sometimes occur sporadic outbursts of abundance during the summer. Numbers exceeding 100,000 cells per liter may occur in Oslofjord (Nordli, 1953). The common method of reproduction is binary fission.

The order Dinoflagellata is a complex one with respect to mode of nutrition. Dinoflagellates may be holozoic, saprophytic, or holophytic. The ecological significance of the saprophytic forms has not been studied, but the extent to which these heterotrophic organisms can reclaim decaying organic material must enhance their significance. Since the heterotrophs are consumers of organic material, they might best be included with the zooplankton.

Dinoflagellates are either naked or armed with cellulose plates that are destroyed through bacterial action. For this reason they contribute little or no skeletal material to sediments. They may nevertheless have profound effects on bottom deposits in connection with catastrophic mass mortalities (Chapter 29).

The dinoflagellates are capable of feeble swimming, and this may be of some ecological significance in enabling them to utilize dilute nutrients in the water by providing more adequate flushing of the surface of the cells and by better orientation to light. Some are shade-living species (Graham, 1941a).

Halosphaera of the order Heterococcales is a unicellular green plankton alga with only weakly silicified investing membranes. It is an abundant surface oceanic species in the Atlantic.

Other plankton organisms that are sometimes of appreciable importance as producers are the coccolithophores and silicoflagellates. The first are of special geological significance because there are great accumulations of their calcareous remains (coccoliths and rhabdoliths) in marine sediments. In certain habitats with high surface temperatures *Pontosphaera huxleyi* may give the water a milky appearance with populations up to 35 million cells per liter (Braarud, 1945). *Pontosphaera huxleyi* characterizes Atlantic water masses flowing into the northern part of the North Sea and southern part of the Norwegian Sea, and in the latter it forms large populations in the "older" Atlantic waters that have penetrated the area (Braarud, Gaarder, and Gröntved, 1953).

It is convenient to include the macroscopic brown alga *Sargassum* or "gulf weed" in its floating state with the phytoplankton. Originally the plants have been torn from their attachment at the coast and are kept afloat by air bladders and are transported by prevailing currents into large eddy areas (halastase). In the Sargasso Sea, *Sargassum* is concentrated through vegetative reproduction (fragmentation) and by the action of the great clockwise gyral of the west Atlantic north of the equator. Among the several species of *Sargassum* in the Atlantic *S. natans* and *S. fluitans* are considered pelagic, having established independence of recruitment from holobenthic

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species of coastal areas. These true pelagic "species" and their phenotypic varieties constitute about 99 per cent of the weed in the Sargasso Sea (Parr, 1939).

While large quantities of gulfweed are thus produced, they are still of relatively small importance in oceanic production. The gulfweed is nevertheless of great biological interest as it furnishes a unique offshore environment with a substrate capable of fostering certain littoral, sessile, or creeping animals that would normally be expected only at the coast either upon seaweed or upon the bottom (Timmermann, 1932). Among these semipelagic or epiphytic forms are encrusting bryozoans; *Spirorbis* (calcareous tube worms); various hydroids, including representatives of the genera *Obelia, Clytia,* and *Sertularia;* anemones; several mollusks, of which the most conspicuous is the nudibranch *Scyllaea pelagica; Planes minutus,* a small crab associated with drifting material; and many others. There are indications that the faunal assemblage is somewhat different on the sargassum of the Gulf of Mexico as compared with that of the Atlantic. Often the species are smaller than related littoral forms (Ekman, 1953); the community as a whole depends on the sargassum only for its substrate and obtains its food principally from the water.

ECOLOGICAL FACTORS IN ORGANIC PRODUCTION

There is abundant indirect evidence pointing to coastal regions as the areas of greatest organic production. Conspicuous among such evidence are (1) the yellow or brown color of coastal waters as contrasted to the blue of the open sea away from the immediate influence of coastal currents, and (2) the preponderance of benthic and pelagic animal life in coastal waters as compared with that of the open ocean or of abyssal depths.

This greater coastal production of phytoplankton and the resulting zooplankton is reflected in the richness of organic carbon in coastal marine sediments. Considerable variation occurs, depending upon bottom topography and currents, but average values of 2.5 per cent are found in coastal areas as contrasted with less than 1 per cent far from shore (Trask, 1939). Off the California coast, the average for 31 carbon values was 3.5 per cent; the highest was nearly 11 per cent (Emery and Rittenberg, 1952).

RADIATION

Of prime importance to organic production by phytoplankton is solar radiation (Chapter 6). Experiments and investigations by Steemann Nielsen (1937; 1951a) in Danish waters indicate that, for plankton algae, optimum photosynthesis occurs at 7000 lux, and half of optimum at about 2000 lux. At more than 20,000 lux the light is apparently too strong for plankton algae. It is further pointed out that in July the average light intensity at noon in Denmark is 45,000 lux, whereas in January it is 6,000 lux. Thus light must be a controlling factor in organic production during the winter months, and maximum photosynthesis during the summer must take place some distance below the surface. During such times a ceiling of clouds would enhance photosynthesis at the surface.

The light requirements for surface tropical plankton appear to be higher than for

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temperate plankton. On the GALATHEA expedition, the maximum photosynthesis for tropical surface plankton was obtained at 30,000 lux (Steemann Nielsen, 1951b).

Water is very transparent to light of wave lengths that fall within the visible range, between 0.45 and 0.6. Photosynthesis can be carried on within this portion of the spectrum. It has been estimated that only about 0.3 per cent of the solar energy applied at the sea surface is fixed by photosynthetic activity (Riley, 1941). Because of the gradual absorption of light by the water, the amount of energy available for photosynthesis diminishes with depth. The upper layer of the sea, which has sufficient light to support photosynthesis, is known as the photic layer. Obviously, all depths of the photic layer are not equally effective in supporting photosynthesis. Diatoms are essentially shadow plants and thrive best some distance below the surface, but photosynthesis is directly proportional to light only at low intensities. However, with increasing depth a threshold of light is reached within the photic layer where light intensity is so low that the oxygen produced by the plants through photosynthesis is just equal to that consumed by the plant in its metabolic processes. This is known as the compensation light intensity, and the water depth is known as the compensation depth. All daily crop increase must take place above this depth. Below this level, although photosynthesis may occur, it is too small to provide for needs of the plants which must, therefore, succumb when reserves have been used. The compensation depth varies with season, latitude, and turbidity of the water. In bays and coastal waters in about Lat. 40°–60° N. in summer, it appears to fall between depths of about 5 and 59 meters (Gaarder and Gran, 1927; Marshall and Orr, 1928; Gran and Thompson, 1930; Gran and Braarud, 1935; Jenkin, 1937; Steemann Nielsen, 1937; Clarke, 1946). In clear oceanic water of lower latitudes the photic layer may have a lower limit at 150 meters (Riley, Stommel, and Bumpus, 1949).

VERTICAL CIRCULATION AND FERTILITY OF WATERS

In order that waters be fertile, an adequate supply of dissolved plant nutrients must be present, especially compounds of nitrogen and phosphorus, and also of other elements such as silicon and iron that enter into the structure of the plant substance or construction of its shell.

Culture experiments with the diatom *Nitzschia closterium* indicate that there is a marked reduction in the rate of photosynthesis when the concentration of phosphate falls below 10 μg P per liter (Harvey, 1940). Ketchum (1951) has reviewed experiments relative to the nutrient requirements of phytoplankton and has summarized investigations, with estimates of tonnage of plankton produced in the sea. The figures range from 0.52 to 10.35 tons dry plankton per acre per year with an average of about 3.2 tons per acre per year. These values are roughly comparable with farm production.

In reporting more recent experiments using radioactive carbon (C 14) for measuring the rate of photosynthesis, Steemann Nielsen (1951b) concludes that some earlier estimates of total organic production in the sea are too high. In contrast to estimates of 15.5×10^{10} tons of carbon produced annually, his figures give a net production of 1.5×10^{10} tons of carbon per year.

During active multiplication and growth of phytoplankton in the lighted or photic layer of the sea the nutrients are heavily drawn upon in building up the cells of

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plants. In this process the phosphorus, nitrogen, and other essential elements that become bound in organic substance of the plants or animals that fed upon the plants are temporarily taken out of circulation. Much of this organic substance is eventually transformed to simple mineralized state by bacteria within the photic layer, but a part is slowly precipitated to the bottom or below the lighted layer in the rain of falling bodies. Thus a supply of plant nutrients is accumulated in the deeper waters out of reach of photosynthetic organisms.

The principal factor favoring coastal production appears to be the conveyance of these plant nutrients back to the lighted surface layers.

The nutrient-rich deep waters are brought back to the surface through action of the various types of ascending water currents. These currents are notably effective in the shallow coastal waters where the nutrient store is within range of the vertical components of circulation. In the Gulf of Maine, about 73 per cent of the phosphorus utilized by the phytoplankton during 6 summer months was provided by vertical transport (Ketchum, 1947). These ascending currents are typified especially by the following:

(1) *Coastal upwelling.*—This is usually a large-scale phenomenon occurring near coasts or banks. It is illustrated by conditions that prevail on the west coast of South America as a result of the Peru Coastal or Humboldt Current (Günther, 1936). Similar upwelling occurs on the west coast of Africa in connection with the Benguela Current (Defant, 1936) and at various points along the coast of California where it is associated with spring periods of northwest winds that result in outward transport of coastal surface waters with compensating waters flowing up from depths of about 200 meters (Sverdrup and Fleming, 1941). Recent investigations by the Marine Research Committee (1953) indicate that upwelling may occur in any month of the year between Pt. Conception and Punta Baja on the California coast. Each of these areas is notably rich in plankton concentrations (Günther, 1936; Hentschel, 1928; Sverdrup and Allen, 1939; Johnson, in press).

(2) *Divergences.*—These result in upwelling of subsurface water through the action of divergent currents that flow away from each other as in the equatorial-current system of the Pacific. This type of upwelling is important in bringing about organically rich areas far from shore (Sverdrup, Johnson, and Fleming, 1946; Arrhenius, 1952; King and Demond, 1953). Conversely, in areas of convergence, water that has been at the surface for a long time is relatively barren.

3. *Turbulence.*—This is another type of circulation contributing to the fertilization of surface layers. It is especially prevalent in such areas as Puget Sound and the Bay of Fundy where strong tidal action effects a turnover of water through narrow tortuous passages and channels. The beneficial effect of turbulence in conveying nutrient-rich water to the surface may be largely counteracted by the effect of the downward component of the currents conveying the phytoplankton to depths of low-light intensity (Gran and Braarud, 1935).

4. *Convection currents.*—These occur in areas where winter cooling produces a density of surface water sufficient to cause a sinking and replacing of deeper-water layers. This phenomenon is conspicuous in higher latitudes and may give rise to distinct spring and autumnal outbursts of phytoplankton when it follows a period of stabilization.

5. *"Wake Stream."*—Rossby (1936) has pointed out that deep water may be drawn nearer the surface along the continental slope at the edge of the Gulf Stream. The ecological importance of this has been considered by Redfield (1936), who shows that the products of decomposition, phosphate and nitrate, appear at a depth of 200–300 meters in the slope waters as contrasted to 800 meters in mid-ocean.

Among other inorganic factors in the analysis of the phytoplankton environment are temperature and salinity. Both of these factors operate largely as selective agents. It is well known that waters with either high or low values for these factors

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may be organically productive. This follows because certain phytoplankton species or groups of species are physiologically adjusted to given temperature or salinity ranges. A marked organic production may take place within the range when other conditions with respect to nutrients and light are favorable. In experimental cultures with dinoflagellates and coccolithophores in various salinity ranges, the optimum evidently falls nearest the lower end of the range (Braarud, 1951). In these experiments, *Syracosphaera carterae*, a coccolithophore, had a high rate of reproduction in salinities of 25–45‰ but with an optimum at 30‰. For the dinoflagellate, *Cryptomonas* sp., the optimum was at lower salinities, 15–20‰, and there was a relatively rapid fall in production in salinities above this value. Thus a succession of species may occur in response to salinity or temperature changes associated with the seasons or other conditions.

The influence of temperature and salinity in bringing about stability of a water mass through their action on density may be highly important to production. While turbulence has a significant bearing in the return of nutrients to the photic zone, it is nevertheless necessary to have a stability which limits the mixed layer to depths above the compensation depth for maximum phytoplankton bloom within water rich in nutrients.

Temperature may also have a pronounced bearing because of its effect on the viscosity of the water. Viscosity at 0°C is nearly double that at 25°C. Thus flotation, which is an all-important item to planktonic life, is increased by colder temperatures. Some planktonic species, especially among the dinoflagellates, have special structural adaptations to resist sinking in warm waters. Salinity is not so important in this respect. Further consideration of these factors will be given in the discussion of zooplankton.

Grazing by herbivorous zooplankton is obviously an outstanding factor in phytoplankton production. This will be touched upon later.

The synthesis of organic material and its subsequent consumption by animals in aerated waters can be considered the normal course of events in the economy of the sea, but outbursts of excessively heavy organic production in more or less limited areas may create anomalous situations.

EFFECTS OF OUTBURSTS OF PHYTOPLANKTON

Generally speaking, a great production of primary food would be reflected in an abundance of all kinds of animals, but this is not invariably the case since the response in animal reproduction and growth is too slow to take full advantage of a very rapid increase in pasturage, and in certain instances great production of dinoflagellates may lead to wholesale destruction.

Dinoflagellates.—Normally the dinoflagellates are an important source of food for animals, especially in the lower latitudes or during the summer in temperate seas. Many records, however, indicate that heavy growth flares of these organisms are associated with wholesale destruction of much of the animal life within the affected area of the sea. In fresh and brackish water mass mortality may also occur, but some species of blue-green algae is commonly involved.

"Mass mortality" is associated with the occurrence of "red water" or "red tide" and is primarily a coastal phenomenon, usually linked to spectacular outbursts of

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certain species of dinoflagellates. It must not be concluded, however, that the presence of large populations of these organisms invariably results in catastrophic destruction of associated animal life. It appears, for example, that of seven observed occurrences of pronounced "red water" on the coast of Southern California between 1901 and 1945 only one was seriously destructive, and two only moderately so (Allen, 1941). A review of planktonic organisms, inimical or otherwise, that cause discolored water is given by Hayes and Austin (1951).

The regularity with which the planktonic dinoflagellates are present in abundance in the water when and where mass mortality of littoral animals has occurred leaves little doubt that these organisms are somehow involved, but precisely how is not clear since there is much conflicting evidence. During the 1946–1947 period of mass mortality in the Gulf of Mexico, Gunter *et al.* (1948) found that the water contained up to 60,000,000 cells of *Gymnodinium* per liter. Not only are such holophytic genera as *Gonyaulax* and *Gymnodinium* incriminated, but also on rarer occasions the holozoic *Noctiluca* has been involved.

On the Madras coast of India great mortality occurred to both invertebrates and fish during a period of abundance of *Noctiluca miliaris* (Alyar, 1936). In the summer of 1947 in East Sound, a long narrow inlet in the Puget Sound area, much of the benthic life in the shallow head of the inlet was killed coincident with an excessively great production of Noctiluca (M. W. Johnson, unpublished).

A review of the many known cases and areas subject to either moderate or extreme mass mortality associated with dinoflagellate "red water" is given by Brongersma-Sanders (1948) and in Chapter 29.

Diatoms.—As early as 1908 Lohmann showed that during periods of high diatom production the excess of production over consumption by animals may be as high as 29 mm^3/100 l. of water. There is, however, no evidence that excessively large outbursts of diatoms are associated with mass mortality of animals, although Hardy (1936) and Hardy *et al.* (1936) are of the opinion that zooplankton and herring tend to avoid dense diatom patches.

Of interest to the sedimentologist is the seasonal occurrence of large crops of diatoms and their subsequent precipitation to the bottom where they may form annual layers in sediments under certain conditions, as in the Gulf of California (Revelle, 1950). The Gulf of California may serve in effect as a silica trap by extraction of silica from the incoming water by diatoms and its subsequent deposition on the bottom as frustules. Evidence of this is found in the fact that the silica content of water entering the Gulf from the sea is higher than that of compensating outward-flowing water.

The phenomenal outbursts of diatoms in high latitudes following winter accumulation of plant nutrients result in an excess of diatoms which then fall to the bottom contributing to diatomaceous ooze characteristic of certain areas as in the antarctic.

ZOOPLANKTON

The zooplankton is composed for the most part of a great array of micro- and macroscopic animals ranging in size from a fraction of a millimeter to 30–50 millimeters. A few are much larger, and certain jellyfish may be a meter in diameter. Myriads of plankters are completely adapted to a pelagic mode of existence and re-

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main floating or feebly swimming throughout their entire life cycle. These are known as permanent plankton or holoplankton. Included here are representatives of every major group of marine animals with the exception of sponges, bryozoans, brachiopods, ascidians, and mammals.

Contrasted with the permanent plankton are the transitory floating stages such as eggs, larvae, and juveniles of the benthos and nekton, and the medusoid stages of benthic coelenterates. These make up the temporary plankton. This category is often seasonal in occurrence and abundance and is principally neritic in distribution since most of the organisms are derived from the benthos and nekton of the shallow sea.

The vast majority of zooplankton has its greatest significance as an organic link in the biological economy of the sea. Many of these forms possess skeletal integuments composed of organic material such as chitin which is readily decomposed through bacterial action but contributes to material trapped in the bottom sediments under anaerobic conditions. There are, however, also a number of forms that in addition to contributing organic material to the sediments are uniquely important geologically because of their direct contribution of skeletal remains to sea-bottom deposits. Outstanding in importance in formation of calcareous and siliceous deposits respectively are the Foraminifera of the family Globigerinidae and the Radiolaria, all of which are planktonic. A few of the latter, such as *Acantharia*, possess skeletons of strontium sulfate. The plantonic pteropod mollusks are major contributors to bottom deposits; their aragonite shells are found in all latitudes.

All the above animals may be found in the plankton in varying concentrations in deep oceanic water. The limited thicknesses of their respective deposits is not an indication of unfavorable living conditions in surface waters over greater depth, but is evidently determined by the relative rate of dissolution of their shells under great hydrostatic pressure, low temperatures, and other conditions at great depths.

The horizontal distribution of abundant calcareous and siliceous oozes is nevertheless an indication of the environment of the planktonic organisms involved as well as their relative rates of production and conditions of dissolution (Arrhenius, 1952). The greater seasonal aspect of production of diatoms in cold nutrient-rich waters of high latitudes, such as the area of the antarctic convergence and the underlying diatomaceous ooze, also bears this out. The calcareous oozes characteristic of lower latitudes apparently owe their preponderance there to the greater ease with which organisms in warm surface waters can construct shells. A discussion of the organic oozes will be found in Chapter 22. We shall be concerned here mainly with the more salient features of the environment of the living forms.

ECOLOGY OF ZOOPLANKTON

Such fundamental environmental factors as temperature, light, currents, and food affecting zooplankton are similar to those that are important to the benthos. A very great difference is found, however, in the way in which the factors bear upon the organisms and in some instances in their mode of response to the factors. This difference arises because of the fluid nature and movement of the environment in which the plankton lives.

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Temperature and water currents.—Because of its direct bearing upon the metabolic activities of different species or groups of species, temperature has a far-reaching effect on the life of the individual organism and therefore upon the community as a whole. According to van't Hoff's law the rate of a chemical reaction is increased 2–3 times for each 10°C. rise in temperature within favorable limits. The optimum temperature is known for very few species, but the range of survival is fairly well known in many instances. This tolerance has led to establishment of biological groups or geographical ranges based on prevailing temperature ranges. We thus have arctic, subarctic, subtropical, and tropical animals. But the lines of demarcation are not always clear, and within each geographical area there may be further restrictions depending upon whether the species involved are stenothermic (tolerant to only small temperature range) to low or high temperatures or whether they are eurythermic (tolerant to a wide range of temperature).

In illustrating these effects it will be most expedient to include also the dependence of plankton on water currents and to consider the temporary and permanent plankton separately.

Since the temporary plankton is derived mainly from the benthos, its presence will be controlled initially by the temperature requirements for adult spawning. The temperature tolerance of the planktonic larvae through metamorphosis will in turn determine the geographical range of the adults as affected by dispersal of the larvae by water currents. Any discrepancy in the temperature requirements for development of the sex products and spawning and the tolerance of the larvae and adult will lead to an extension of the adult population into areas of sterile distribution (expatriation areas) where the stock is maintained only by recruitment by way of the temporary plankton from the reproductive areas. In such cases the reproductive range should be considered the true home of the animals (Ekman, 1953).

The influence of temperature on spawning has been studied in detail for certain pelecypod mollusks. Hopkins' review (1937) indicates that for four species of oysters the total range of temperature for spawning was 11°C. (14°–25°C.), but for any one of the species it was only 3°C. or less. The duration of the planktonic stage in oysters is only about 1–3 weeks depending on temperature. But this dispersal period is sufficiently long to carry many of the larvae into areas unfavorable to the adult for sexual maturation or spawning or even for vegetative existence.

In temperate coastal areas where there is a wide seasonal range in temperature, it is possible for subtropical species to find a suitable temperature for spawning and development of larvae during the summer. Similarly it may be possible for subarctic or arctic species to spawn during the colder seasons (Runnström, 1927). This results in a mixed benthonic fauna and tends to extend the geographic range of those species capable of adjusting their spawning season. The pelagic larval element must then give rise to a temporary plankton that may show characteristic variations depending upon the adults and the duration of their planktonic stages.

The duration of the planktonic larval stage is influenced by temperature. The larvae of *Mercenaria mercenaria*, the hard-shell clam, settled in 5–7 days at water temperature of 30°C., and in 16–24 days at 18°C. (Loosanoff, Miller, and Smith, 1951).

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Most of the benthic animals of temperate and tropical latitudes are represented as developmental stages in the temporary plankton, and concentrations of larvae may be very high—*i.e.*, 17,000 per cubic meter of water for certain pelecypods. The planktonic period involved depends upon the critical spawning temperatures for the species and upon the duration of the pelagic stages. Some, such as the intertidal sand crab *Emerita*, probably remain pelagic for 4 months. Many larvae are, therefore, widely dispersed into unfavorable areas, while others may settle on favorable beaches far from the point of their origin.

Thorson (1950) points out that, in order to survive in the high arctic areas, the pelagic larva has to complete its development from hatching to metamorphosis within 1–1½ months at temperatures below 2°–4°C. Only about 5 per cent of the arctic invertebrates are capable of doing this. Hence, the temporary plankton is poorly represented in the high arctic and antarctic areas. Nonpelagic development is apparently correlated with the short growing season for phytoplankton in these regions and is the rule for invertebrates in abyssal regions where organic production is inhibited by absence of radiant energy.

In the discussion of organic production, it was noted that abundant phytoplankton growth occurs in areas where ascending water currents bring plant nutrients to the photic layer. This increased production is usually reflected in the abundance of dependent zooplankton as evidenced in coastal areas, and also in oceanic areas such as the Pacific equatorial current system (Graham, 1941b; King and Demond, 1953; Johnson, in press). There are a number of striking instances in which the transport of organisms by currents is an ecological factor of great importance in both dispersal and maintenance of plankton populations.

Numerous surveys in many parts of the world provide evidence of the dependence of the permanent plankton on temperature. But, since the isotherms characterize specific water masses of currents, the correlation of plankton distribution with temperature may fit equally well for currents or portions of current systems. This is to be expected since the currents convey and disperse the solar heat. As currents advance from warm to cold areas, as in the Gulf Stream, the temperature characteristics and other factors of the environment change so that warmth-loving stenothermic species are eliminated from the waters while cold-tolerant ones are added coincident with admixture of cold water, or migrate upward from cold water at greater depths. Sömme (1933) has shown for the Norwegian coast that the adult copepods *Calanus finmarchicus* and *C. hyperboreus* winter in deep, relatively quiet cold water of the fjords. In spring they rise to the upper layers to spawn and are dispersed offshore by the fast surface currents; in some areas only about one-twentieth of the winter stock may be left. In summer and autumn the deep waters are again invaded. The general copepod stock is apparently maintained as a result of the great circular movement of water within the Norwegian sea (Dumas, 1905; Helland-Hansen and Nansen, 1909).

Large closed or semiclosed current systems such as the above or that existing in the Gulf of Maine are important factors in maintaining an endemic population (Bigelow, 1926; Redfield, 1941). This is true for the benthos as well as for the pelagic life since it leads to a conservation of temporary as well as permanent plankton. In more-restricted coastal areas, particularly in deeply indented bays, oscillating tidal currents

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conserve the temporary plankton in areas suitable for resumption of the bottom mode of life.

In more isolated regions as in lagoons of coral atolls within an area of strong oceanic currents such as the Pacific North Equatorial Current, a semiclosed circulation in a vertical as opposed to a horizontal plane operates to maintain the lagoonal population. In Bikini Lagoon this results in a concentration of oceanic holoplankton (representing the 11 most common animal groups) which is on an average at least 4 times greater than in the open-sea water outside the lagoon. The difference may be as great as 27 times in favor of the inside waters. Both the temporary plankton (derived from the atoll benthos) and the lagoonal endemic holoplankton are conserved through a combination of the action of these currents and the characteristic negative reaction of the plankton to light. This response to light keeps a large portion of the lagoonal population in the deeper water from being swept out of the lagoon by the upper-surface currents (Johnson, 1949). These currents flow westward through the lagoon over the reefs at a rate of 0.3 knots, as compared with a 0.1 knot eastward flow in the deeper water. A similar situation prevails at Bermuda (Boden, 1952).

Seasonal cooling of light neritic waters of lowered salinity probably results in local currents "cascading" over the edge of the continental slope, over banks or into deeper water of submarine canyons. Currents of this nature probably carry neritic plankton into adjacent oceanic waters (Cooper and Vaux, 1949). The extent of such transport has not been fully studied, but it may be operative in some instances and may thus explain the winter extension of the euphausiid *Nyctiphanes* over deep Atlantic water (Grover, 1952).

From what has been said about the passive transport of planktonic organisms, it is obvious that the plankters involved may serve as tiny drift bottles providing living information about the source and direction of flow of the water in which they occur.

In recent investigations along this line, Fraser (1952) demonstrates the use of chaetognaths and other zooplankton organisms in tracing the origin and flow of water off the Scottish coast. Braarud, Gaarder, and Gröntved (1953) point out the possibility of using nannoplankton (smallest of planktonic organisms) as indicators and find coccolithophores useful in characterizing the Atlantic water component of coastal water.

Light.—Reference has been made to the significance of reaction to light in the maintenance of plankton in a lagoon. Reaction to light is similarly prevalent in forms living in the open sea. There is a withdrawal of many forms from the upper water layers at daytime and a return toward the surface at night. This diurnal migration may involve depths to 800 meters (Waterman *et al.*, 1939). The complete ecological significance of these movements is not well understood, but a movement toward the surface from deep water at night will bring many animals into layers richer in phytoplankton at a time of darkness when predation is probably less. The differential in speed or direction of surface and deeper currents may also serve to segregate horizontally the excessively heavy patches of phytoplankton from the deeper zooplankton (Hardy, 1936).

Many planktonic forms—for example, certain copepods that frequent subsurface waters—migrate to the surface to spawn. Thus, the floating eggs and weakly swim-

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ming larvae can sink a certain depth during development before passing into depths unfavorable for feeding.

During the daytime much of the zooplankton known to perform diurnal migrations appears to be more or less concentrated in one or more horizontal layers at depths as great as 400 meters depending upon light conditions. The presence of these stratifications is detectable by means of fathometer sound signals sent out vertically from the surface. This was first noted in 1942 (Erying, Christensen, and Raitt, 1948). The return of the fathometer signal by the layer led to the term "deep scattering layer". In 1945 the layer was demonstrated to migrate diurnally in a manner characteristic of many planktonic animals (Johnson, 1948). Plankton hauls taken at the time supported the hypothesis that planktonic organisms or other pelagic life associated with them was the cause of sound scattering.

This has led to a use of sound signals in ecological study of the occurrence and behavior of pelagic animals that presumably reflect the sound signals. Investigations subsequent to discovery of the biological nature of the layer in 1945 support the early observations and implicate especially the Euphausiacea (Hersey and Moore, 1948; Boden, 1950; Moore, 1950), the lantern fish (myctophids) (Tucker, 1951), and other bathypelagic fishes (Marshall, 1951). While the wide distribution, abundance, and migratory behavior of these groups are in general keeping with the physical data on the layer, it is probable, depending upon locality and season, that other animals are involved. Improved techniques of sampling with controlable gear are needed to solve the riddle.

The vertical movements are apparently made in response to conditions of light.

The phenomenon of diurnal migrations of planktonic animals has been known for over a century, and many investigations have been carried out in attempting to explain the reactions involved by physical and biological conditions. A review of the literature has been made by Motoda (1953) and by Cushing (1951) who states:

> "It is concluded that the vertical migration of planktonic Crustacea is mediated by the change in light penetration throughout the day. Animals aggregate in an optimum band of light intensity. They have the capacity of moving phototactically, i.e. moving at constant speed towards or away from light; they also have the capacity of moving photokinetically, i.e. moving at speeds that vary with varying light intensity. In full darkness they move probably at minimal speeds. Migration between periods of full darkness may be operated by phototaxis, photokinesis or by a combination of these mechanisms."

While the above quotation refers only to the Crustacea, other groups such as chaetognaths, polychaetes, and fishes are involved, either in response to the inanimate conditions or perhaps to the migratory movements of the food upon which they prey.

Oxygen.—In most pelagic regions of the oceans there is sufficient oxygen to maintain planktonic life even in the oxygen-minimum layer where concentrations may drop to near depletion (Chapter 9). However, in restricted areas such as bays and deep fjords where the inner parts are only slowly or irregularly flushed, the plankton is confined to the upper layers. The Black Sea, with a depth of 2104 meters, provides the most striking instance of a large body of water in which there is an exclusion of plankton as well as other aerobic life from all but a relatively shallow surface layer

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(Chapter 25). The Bosporous Ridge forms a high sill preventing deep circulation with the Mediterranean, and the lighter surface water prevents effective deep overturn and replenishment of oxygen below depths of about 130 to 190 meters in the Black Sea itself. Hence, there is no living plankton below these levels (Nikitin, 1931).

Salinity.—The variation of salinity in the sea is usually within the ranges required by both neritic and oceanic plankton. Salinity acts principally upon the physiological balances of the organism (Chapter 7) and is thus effective primarily as a selective agent in distribution rather than as a factor governing production. Most invertebrates are isotonic with sea water, but the degree of this isotonicity is not very great. However, through selection, competitors for both food and space are eliminated in certain areas with rigorous conditions. This makes possible a large population of the species adapted to such conditions. Euryhaline forms can live in a wide range of salinity and therefore may enjoy a wide geographic or vertical distribution provided other factors are not inimical. On the other hand, stenohaline forms tolerate only a narrow salinity range, but different species are stenohaline within different salt concentrations. Other selective factors such as temperature operate similarly, and the more rigorous the environment becomes within a biotope the fewer are the species produced.

SIGNIFICANCE OF PLANKTON IN THE EVOLUTION OF MARINE ANIMALS

In order to understand how the interrelated organic and inorganic factors appear to have been operative in determining the development, distribution, and abundance of marine animals of all categories we must look first to the specific plant community which constitutes the principal source and type of basic food supply in the sea. We must consider the initial physical and chemical factors that have determined the nature of this primary food supply. Presumably the physical and chemical factors that controlled primary organic production in earlier seas are comparable to those existing today. First among these factors is the energy supplied by sunlight, followed by the dissolved plant nutrient supply in the water. In great depths of the ocean the plant-nutrient supply may be abundant due to gradual accumulation, but the absorption of light by the sea water is such that only in the upper 70 or so meters of the sea surface is there sufficient energy to provide for effective photosynthesis. The amount of sea bottom which is sufficiently shallow to receive the necessary light for abundant growth of attached plants is only about 2 per cent of the ocean floor. Many sessile species grow attached to the bottom in this small area, which is further reduced for favorable attachment of plants by the shifting of the sediments or by want of anchorage owing to sandy or muddy bottoms. But the plant crop that can be produced on the lighted bottom area is relatively very small. The major producers in the sea are, therefore, the free-floating microscopic diatoms, dinoflagellates, coccolithophores, etc., of the phytoplankton. The microscopic size of individual plants in the phytoplankton is an adaptation in response to the necessity of remaining afloat in the upper photic layer of the sea and at the same time to the utilization of dilute inorganic nutrients—phosphates, nitrates, etc.—in the water. In this way, the whole surface area of the sea to a depth of 70 meters or more is capable of organic production provided plant nutrients are available in sufficient con-

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centration to satisfy the plant's metabolic processes. This widespread crop of microscopic fodder has apparently had a profound effect on the type of animals that can exist in the sea for it is grazed upon mainly by microscopic herbivorous and omnivorous animals, especially by the copepods which usually constitute about 70 per cent or more of the plankton, but also by the euphausiids and many other small forms, including the temporary zooplankton.

In the Gulf of Maine the standing crop of calanoid copepods alone is estimated at about 4 million tons. The net gain between May and September is about 8 million tons (Redfield, 1941). These grazers are morphologically adapted for screening out the finely divided food from the water.

Thus, in nature there is built up a vast supply of microscopic particulate plant and animal substance. This widely dispersed food is the principal source of nourishment directly or indirectly for virtually all the other animals within the sea. The benthos and nekton are for this reason dependent ecological groups, many members of which must indeed have had a long evolutionary history of this dependence. The developmental response and mode of life which reflects this dependence on fine particulate food is abundantly illustrated by many of the animals in all habitats. Notable among these are the suspension or filter-feeding animals such as barnacles, bryozoans, brachiopods, tunicates, bivalve mollusks, and many, many others of the benthos. Only in an environment supplied with food wafted on water currents could attached or sessile forms such as these filter-feeding animals develop and survive. In the pelagic region the plankton-feeding fishes such as the herring, sardine, and menhaden constitute the bulk of fishes, and they are in turn fed upon by the more predaceous but fewer forms such as the tuna, salmon, etc.

The mud and detritus feeders of the bottom in the deeper waters are equally dependent directly or indirectly upon the rain of plankton or plankton-supported life from above and have developed along lines enabling them to use the detrital or colloidal food (Yonge, 1928; MacGinitie, 1939; McConnaughey and Fox, 1949). The heterotrophic bacteria that affect transformations in the bottom sediments or that replenish inorganic plant nutrients are nourished by this food buried or lying at the interface of water and bottom (ZoBell, 1946).

The far-reaching effect of this floating community of microscopic plants and animals is, therefore, fundamental to the study of present-day marine ecology and indirectly to an understanding of the fauna of ancient seas. From its study, we may see the dim outlines of the food chains that must have had links similar to those of the present day. A study of the factors that give rise to an abundant organic production and its eventual deposition on the bottom or its utilization by animals or transformations by bacteria must throw light on the physical conditions that prevailed in the past.

It seems reasonable to assume that, in earliest seas, benthic animals spread into deeper waters from coastal areas, and indeed most deep-sea animals are only modified members of shallow-water groups living upon the continental shelf (Chapter 22). Since the deep-sea animals, both the benthic and the bathypelagic, are dependent upon a rain of organic food from above, these deep-living groups were probably established later than the oceanic plankton.

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Chapter 17

Bottom Communities (Sublittoral or Shallow Shelf)

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INTRODUCTION

Two principal and ecologically different groups of benthic marine animals werfirst recognized by C. G. Joh. Petersen (1913, p. 15): (1) *The Epifauna* (Fig. 1), come prising all animals living upon or associated with rocks, stones, shells, piling, and vegetation—*i.e.*, sitting or crawling on a substratum (Examples: *Mytilus* beds, coral-reef fauna, animals inhabiting *Zostera* or kelp beds; and (2), *The Infauna* (Fig. 2), comprising all animals inhabiting the sandy or muddy surface layers of the sea bottom—*i.e.*, living buried or digging in a substratum (all animals associated with the level bottom). A third group, including bottom-dwelling fishes and motile invertebrates, is intimately related to the animals of the benthos.

The conditions under which these two types of bottom fauna live are, in many respects, quite different, and the factors governing their distribution, chances of survival, and even evolution are, therefore, not the same.

DIFFERENCE IN LIFE CONDITIONS FOR EPIFAUNA AND INFAUNA

The epifauna, occupying on an average less than 10 per cent of the total area of the sea bottom, seems to reach its absolute maximum in very shallow water, particularly in the intertidal zone. Here there are a great many micro-environments: reefs, rock pools, holes, and crevices exposed for a longer or shorter time to the air, in sunny or shady places, sheltered from or beaten by the waves, with bare surfaces or overgrown with different types of vegetation, and so on. This multitude of micro-environments with their different conditions for life supports a large number of species with a wide range of ecological requirements.

The epifaunas of the Arctic tidal zones are extremely poor. The thick crust of ice (3–4 m) covering the surface of the sea for 8–10 months each year, which changes into a stabilized brackish- or fresh-water layer when the thaw sets in, makes the tidal zone in high-arctic regions nearly impossible as a permanent habitat for animals (Madsen, 1936, p. 45; Thorson, 1933). Here cold is the "controlling factor" and outweighs all other factors.

Even in temperate seas the yearly temperature amplitudes will play an important part in reducing the number of species in the tidal zone epifaunas.[1]

Toward the tropics the annual temperature becomes more nearly constant. Accordingly, the selective effect of each single microlandscape in the intertidal zone acts

[1] Such temperature amplitudes will also affect the infauna of the tidal zones (see especially Hedgpeth, 1953, p. 186-187), although there will be less effect upon speciation than in the corresponding epifaunas since the environment is more uniform.

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FIGURE 1.—*Close-up of the North East Atlantic* Modiola modiolus *epifauna*

Taken from about 25 m depth in the Kattegat. On the valves of the left *Modiola* are: the hydroid, *Tubularia*, the octocoral *Alcyonium* with the ophiuran *Ophiothrix*, the polychaete *Pomatoceros*, the ophiuran *Ophiopholis* and a *Balanus*. On the valves of the right *Modiola* are: the holothurian *Psolus* and the hydroid *Hydrallmannia* with the cirriped *Scalpellum*. On the stones in front, starting from the left are: the hydroid *Abietinaria*, the crab *Eurynome*, the prosobranch *Calliostoma*, the red algae *Delesseria* and *Rhodymenia*, and the compound ascidian *Botryllus*. From Thorson (1950); drawn by Poul H. Winther.

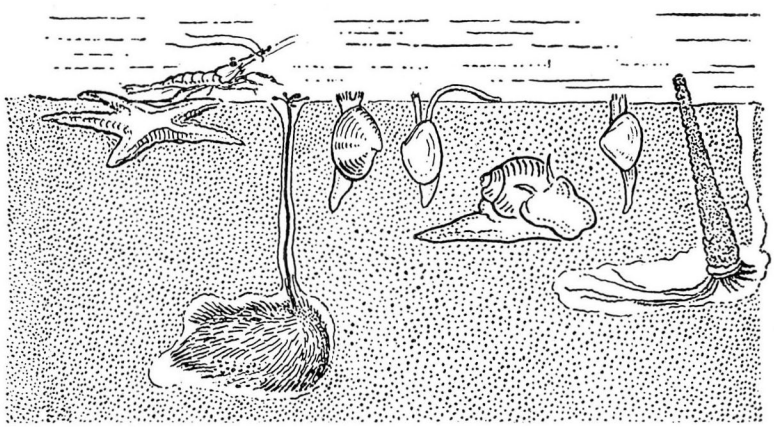

FIGURE 2.—*Close-up of a Northeast Atlantic infauna*

The *Venus gallina* infauna, taken on a sandy bottom at about 10 m depth in the Kattegat. The animals are (starting from the left): the starfish *Astropecten*, the shrimp *Leander*, the sea urchin *Echinocardium*, the lamellibranchs *Venus*, *Tellina*, and *Spisula*, the prosobranch *Natica* (= *Polynices*) (below), and the polychaete *Pectinaria*. From Thorson (1950); drawn by Poul H. Winther.

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upon those animals which find their optimal conditions there (Thorson, 1951; 1952). Furthermore, in many tropical coastal regions the number of microlandscapes is significantly increased by the varied surfaces of coral reefs and mangrove swamps. Here, where temperature is nearly constant and food is abundant "the rank growth with a high tendency to variations combined with the severe struggle for existence between different animals has produced the greatest amount of differentiation" (Hesse *et al.*, 1951, p. 30, 217). It is no wonder, therefore, that the coastal areas of warm seas are regarded by some as "the hypothetical original site of the development of life."

The infauna (which may occupy more than half the surface of our globe) is most fully developed below the intertidal zone. Such constantly submerged infaunas are associated with a level bottom (whether sandy or muddy) and are exposed to nearly the same types of environmental conditions in Arctic as in tropical seas, so that the only factor that is really different is the temperature. In contrast to the Arctic tidal zones, where the cold nearly wipes out all the epifauna, the submerged Arctic sand bottoms and mud bottoms are continuously inhabited by characteristic infaunas, able to thrive at these low temperatures. Even in Arctic seas level-bottom environments are occupied by characteristic infaunas, and in tropical seas no other types of level bottoms are available to infauna animals than those also present and inhabited in Arctic seas: shell gravel, sand, mixed-bottom, and mud. While among the epifauna animals several species are "grazers" or "browsers" and accordingly may specialize in different types of food in the tropical tidal zones, by far the majority of all infauna animals, whether Arctic or tropical, are dependent on approximately the same type of food: plankton, bacteria, and detritus, transported to them from the surface or, in the case of bacteria, growing near by. Thus, conditions are very similar for Arctic and tropical infauna animals. Temperature is the main factor influencing the mode of development in marine invertebrates (Thorson, 1950, p. 22–29), but it seems reasonable to assume that during the vegetative life the ecological effect of muddy (or sandy) bottom on its infauna will be about the same in Arctic and tropical seas, in spite of the difference in temperature, provided that the metabolic rate of these infaunas is adapted to the temperatures of their natural surroundings.

Thus, the epifauna of the tropical littoral zone has much better conditions for a varied and luxuriant development than does that of an Arctic tidal zone where the cold wipes out most animals, whereas the constantly submerged infauna has nearly the same chances to develop and thrive in Arctic, temperate, and tropical seas.

NUMBER OF EPIFAUNA AND INFAUNA SPECIES IN DIFFERENT LATITUDES

The number of species of aquatic invertebrates is rather small in Arctic areas and increases enormously as we approach the tropical regions. This increase in numbers of species toward the tropics is very pronounced in epifaunas, while the number of infauna species seems to be roughly the same in Arctic as in temperate or tropical seas. Figures 3 and 4, based on calculations from comprehensive faunistic papers (for literature *see* Thorson 1952, p. 304–306), show that the number of epifauna species increases toward the tropics, but that the number of infauna species from a similar

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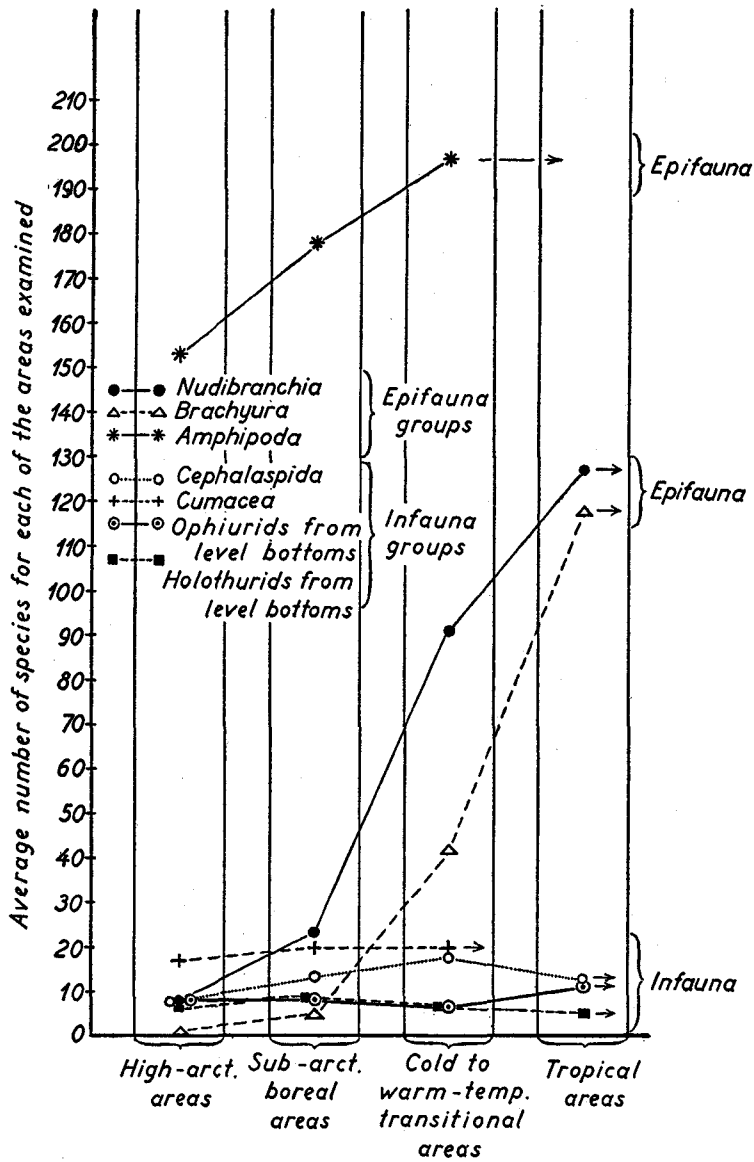

FIGURE 3.—*Average number of species of different groups of bottom invertebrates from equally large coastal areas, but in different latitudes*

The number of species belonging to typical epifauna groups (Nudibranchia, Brachyura, and Amphipoda) shows a heavy increase from the Arctic toward the tropics, while such groups which inhabit only the level-bottom areas (Cephalaspidae, *Cumacea*, and several genera of holothurians and ophiurans) show no increase in number of species toward the tropics. Only depths from the shore to 300 m have been regarded, and all pelagic and parasitic species have been neglected. From Thorson (1952, p. 305).

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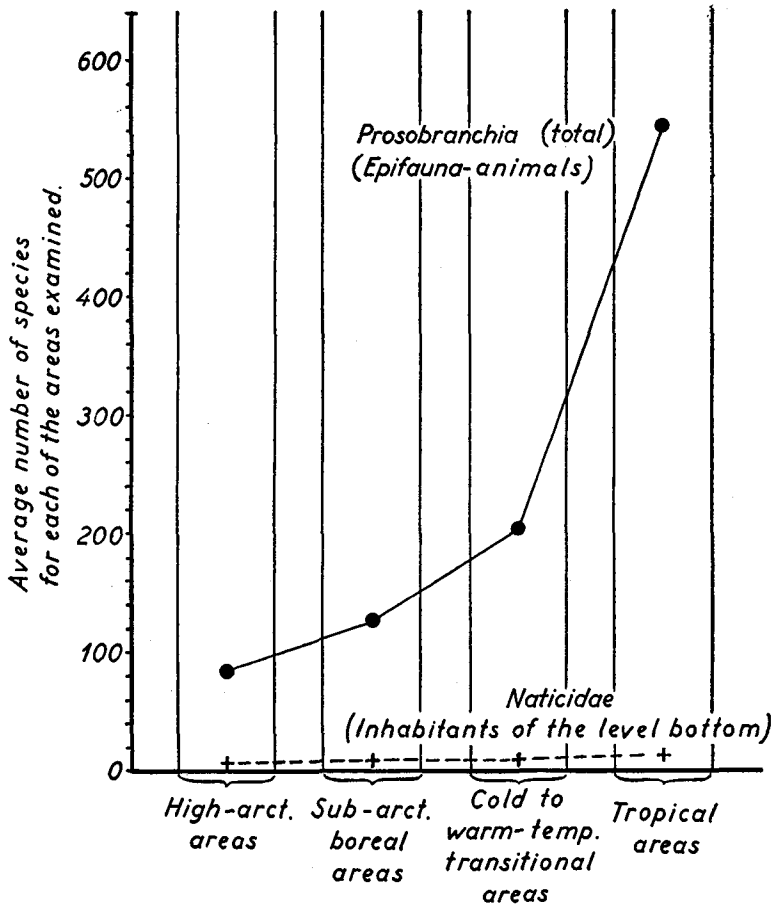

FIGURE 4.—*Average number of species of all prosobranchs from equally large coastal areas in different latitudes*

The heavy increase in the number from the Arctic toward the tropics is in good agreement with the epifaunistic habits of the prosobranchs. Below (spaced line with crosses) is given the corresponding curve for the Naticidae only—*i.e.*, for one of the few groups of prosobranchs which is constantly associated with the level bottom. Here the increase in the number of species toward the tropics is insignificant, although the pure tropical naticid genus *Sigalion* is included in the tropical counts. From Thorson (1952, p. 306).

series of latitudes is nearly the same. Several other figures might be added, such as those of the total number of ascidian species known from Arctic, subarctic, and tropical seas—*viz.*, 104, 432, and 635 species, respectively—showing an epifauna group increasing steeply toward the tropics (Hesse *et al.*, 1951, p. 31).

Of an estimated 1,000,000 species of Recent animals described, only something like one-fifth are aquatic and only about one-sixth live in the sea. The graphs also show that, although the number of epifauna and infauna species is practically of the same order of size in Arctic seas, the epifauna species greatly outnumber the infauna

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species in tropical waters. Exact figures are not available, but it is estimated that the total number of epifauna species in the sea is at least four times as large as that of infauna species. This relatively small number of species on the level bottom further simplifies the ecological patterns connected with a study of the infauna.

LEVEL-BOTTOM AREAS AS HABITATS FOR INVERTEBRATES

Ecological conditions are much more simple in the sea than on land, and their influence on benthic marine animals in general is mentioned elsewhere. The main conditions for life, especially for the *infauna* species, may be briefly summarized as follows:

(1) The fixed vegetation, an essential ecological part of the unity of the whole in terrestrial environments and several parts of the shallow sea (*cf.* Hesse *et al.*, 1951, p. 167), is absent from the level bottom. On land or on shallow marine hard bottoms, where plants are present, most of the animals are more closely associated with the plants than with the physical gradients which are the basis for distribution of the plants concerned (Elton, 1927, p. 10), a fact making an analysis of the ecological conditions of such faunas most complicated. On the level bottom the animals are associated only with other animals and directly with the physical-chemical conditions, which simplifies ecological analyses.

(2) The level bottom lacks the numerous "microlandscapes" (exposed or protected rocks, associations of different plants, holes, crevices, etc.), each with a special microclimate, so characteristic of epifauna environments. But for a local lack of oxygen just over the bottom and in the microclimate found in the burrows of certain animals, the infauna is roughly associated with macroclimatic (hydrographic) and not microclimatic conditions.

(3) While a hard bottom (stone, rock, shell) will always be a hard bottom whether exposed to weak or strong currents which may affect its community composition but not the consistency of the substratum, the composition of the uppermost layer of the level bottom, since it is the visible result of recent sedimentation, will vary in relation to the movement of the water and the character of sediments from near-by land masses. On land, for instance, sandy areas may be associated with quite different ecological conditions: on beaches, in deserts, or in front of glaciers in high mountains. In the sea, sandy areas are principally associated with an active movement of water which again normally occurs only in shallow areas and near the food-producing surface where fluctuations in salinity and temperature are relatively large. Muddy bottoms, however, are associated principally with calm water which normally occurs at somewhat greater depths which are more distant from the food-producing surface—*i.e.*, in strata with more stable salinity and temperature. This association of each particular type of infauna with its special type of bottom which serves as an indicator of food conditions, water movement, and range of salinity and temperature in that special habitat has hitherto been neglected by marine ecologists.

(4) Although an epifauna comprises several species that have specialized feeding habits (grazers, browsers, hydroid- and sponge eaters), by far the majority of infauna species are dependent on the same sources of food—phytoplankton and detritus; that is, they are "suspension feeders", and "deposit feeders." The composition of the food is much the same in both groups, though the proportions in which phytoplankton and detritus are eaten are different. This makes competition among infauna animals especially sharp.

(5) The relatively small number of animal species inhabiting the level bottom (as compared with the hard-bottom areas) reduces the number of possible combinations of animals and further simplifies ecological work with the infauna.

A good indication of the simplicity and uniformity of ecological conditions in huge areas of the level bottom of the sea is the occurrence of several animals dominant in shallow water in the Arctic (*e.g.*, *Arca glacialis*, *Pecten groenlandicus*, and *Natica groenlandica*) in depths of 1000–2000 meters on similar bottoms in warm temperate, or even subtropical areas. (*See* Thorson, 1936, p. 141.)

MacGinitie (1939, p. 32) has already pointed out that "it is from the marine animal communities that we should be able to get many of our fundamental concepts of animal communities." While conditions in marine epifauna communities may be very complicated, this statement is especially applicable to the constantly submerged evel-bottom areas of the sea. These areas are probably the most uniform large areas

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of our globe, and, as stated above, their stable and simple physical and biological conditions make them especially suitable as "pioneer areas" for ecological work. There is also the advantage that quantitative samples, so difficult to obtain in epifauna areas, are relatively easy to procure in these much softer and more uniform bottom flats.

PETERSEN CONCEPT OF ANIMAL COMMUNITIES

ANIMAL COMMUNITIES AS STATISTICAL UNITS

With a proper combination of quantitative samplers (Chapter 4), a fairly accurate idea of the quantity of larger animals living in each square unit of bottom may be obtained. Provided that the samples include all the larger animals present per square unit and that a sufficiently large number of samples is taken, the efficiency of this method for purely statistical purposes and in uniform bottom areas has been well demonstrated.

Petersen's primary intention to procure a series of quantitative samples of the more common larger animals of the sea bottom, and to use the figures obtained for a calculation of the quantity of fishfood available for bottom fish (especially flounders) living in the same areas, was followed up by himself with great success and was continued in Danish seas by Blegvad (1930, p. 17–19), in Arctic seas by Zenkevich (1930, p. 22), and in the Adriatic by Vatova (1949; *cf.* also Lindroth, 1935, p. 360).

Petersen had no intention of describing animal communities when he started his survey but wanted to obtain an idea of the statistical distribution of the animals. As he was unable to see the bottom or to know the exact place where his grab would land, Petersen avoided subjective sources of error and could work out his ideas on the basis of the animals procured.

Working up the thousands of bottom samples from Danish seas, Petersen observed that wide areas of the sea bottom were inhabited by a strikingly uniform combination of macrofauna species, a few of which were especially conspicuous owing to their large numbers. Other areas were inhabited by another combination in a similar uniform way, and here again a few species outnumbered all the others. Thus, for each large area only a few species of animals proved to be really common. When comparing fauna lists from such quantitative samples with those obtained from nonquantitative dredge hauls, the contrast was evident. Two areas examined only by dredgings might give nearly identical fauna lists, though the same areas examined by bottom grab might prove to be quite different as to the dominance of species (Petersen, 1913, p. 4; 1915, p. 13, 18; Spärck, 1935, p. 6).

After several years of observations on the constancy and uniformity of these large bottom flats and their characteristic sets of animals, Petersen was forced to accept the statistical community idea. (*Cf.* Shelford 1935, p. 326.) This was the background for his papers describing the bottom animal communities of Danish waters (1911; 1913; 1915; 1918), now regarded as the classical basis for marine level-bottom ecology. The most numerous, most conspicuous, and for the area most "characteristic" species of animals were used to designate the community.

The validity of the Petersen communities, even when regarded only as descriptive-statistical units, has been questioned by a few ecologists. MacGinitie (1939) stresses

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"that there are no two environments exactly alike, and . . . no two communities alike," and he also regards the muddy-bottom areas as extremely varying. Most of his work was, however, done on mud flats in the tidal zone, which are much more variable than the constantly submerged bottoms examined by Petersen. Furthermore, MacGinitie's experience beyond the tidal zone was based upon dredge hauls only, not on quantitative samples. Broch (1927, p. 29–32) and Lindroth (1935, p. 345), though they used the Petersen grab (small total number of samples only), were unable to find distinct animal communities in the fjords of southern Norway and western Sweden, respectively, where samples taken very near each other proved to be very different, and where the limits between the populations were "floating." Petersen himself had found, however, a similar "dissolution" of the communities in another narrow fjord (inner part of Oslo fjord). In the open sea, however, this may be of only minor significance. Ekman (1947) states that "the separation of two adjoining communities from each other is only justified if the continuity inside each is more definite than that between them," and this is actually the case in the open sea.

Most marine ecologists who have worked with quantitative bottom samples on a large scale have accepted Petersen's animal communities as statistical units. A good demonstration of the reality and value of Petersen's concept of communities is that his provisional map (Petersen, 1914) of the hypothetical distribution of the level-bottom communities throughout the North Atlantic has proved to be essentially true today after nearly 40 years of continued research. Still more convincing is the indication that communities parallel to those described from Danish waters, comprising characteristic animals of the same genera and associated with the same type of substratum, are now known from nearly all parts of our globe.

The fact that the communities described by Petersen cover large uniform areas of the level bottoms makes them especially useful to ecologists, because we may easily get an idea of their geographical distribution (*see* Spärck 1936, p. 132; Remane, 1940, p. 32; Einarsson, 1941, p. 29). When describing new level-bottom communities the ecologist must always realize that his concept as to where one community ends and the next one starts may be somewhat schematic and to some extent subjective. Accordingly he may divide the material procured into smaller or greater units, but it is up to him to see that his division will help to simplify conditions for work, and not to complicate them.

Elton states (1927, p. 17) that "the term 'animal community' is really a very elastic one, since we can use it to describe on the one hand the fauna of equatorial forest, and on the other hand the fauna of the mouse's caecum." This elasticity, however, may cause several difficulties. According to one point of view the transition found between adjoining populations may be so gradual that there is no basis for separating them into different communities (Tischler, 1950, p. 46), and the whole sea (bottom and plankton, since there is also a set of animals spending part of their life cycle swimming in the free water masses and part settled on the bottom) must be regarded as one unit only. Even such very large units ("major communities") as used by Shelford (1935), though actually divided into communities, seem to the author to be less fruitful to ecological work. At least, the idea of Clements and Shelford (1946, p. 340) to combine into one large "Echinocardium-Thyasira-community" the Syndosmya

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(= Abra)-, Venus-, Echinocardium-Amphiura-, and Brissopsis-Amphiura-communities of Petersen would mix together all that Petersen so convincingly separated without adding any new perspectives or wider views.

On the other hand there is the view that a "valid" community must be absolutely homogeneous. The logical consequence of this would be a splitting up into minimal units. As often as two different species are found closely together, such a homogeneous unit may be registered, and if such two species have met accidentally only, as will often be the case, such registrations seem to be of no value at all. (*Cf.* Remane, 1940, p. 3; Caspers, 1950a, p. 45.) If we repeatedly meet the same type of combination in such small units, it seems, however, worth while to undertake a closer examination (Remane, 1940, p. 33), but often our material will be too scarce to decide whether the combinations found are recurrent or accidental. In such cases we must realize again that our aim must be to simplify, not to complicate, ecological work.

The danger of splitting the populations into micro-units is, however, much less among level-bottom organisms than among epifaunas (and epifloras), because in the latter cases the presence of fixed marine plants will increase considerably the number of microlandscapes. Even highly qualified ecologists with much experience have been forced to describe a large number of communities. Thus Gislén, in his paper on the epibioses of the Gullmarfjord, western Sweden (1930), was forced to describe 45 communities ("associations"), and terrestrial ecologists have still more trouble for the same reasons. From northwest Germany no less than 170 plant communities have been described (Tischler, 1948, p. 236).

A similar splitting of level-bottom communities should be avoided. First, it must be realized that even in work with natural units there will always be a subjective element in ideas of how to divide the units. The systematist is often in the same dilemma; he obtains a truer idea of what is a "good species" and what is only a variety by using his intuition rather than by measurements and statistical calculations, but he obtains a still better basis when combining both methods. Several ecologists agree in this view; for example, MacGinitie (1939, p. 48) says: "I know of no way of making any hard or fast rule for determining the limits of a community other than the good judgment of the investigator," and Lindroth (1935, p. 346) notes: " . . . but these apparent errors" (in describing animal communities) "may be compensated for by the intuition of an experienced scientist" [transl.]. Similarly, Braun-Blanquet states that the limitation of "plant-association" is a question of "tact, sociological training and much experience" [transl.].

In the second place, animal communities may find no more uniform places on our globe to live upon than the level-bottom areas of the sea. As stated above, there is a close connection between the uniform substrata found over wide areas and the assemblage of animal species living there. It seems reasonable, therefore, to divide the animal communities in accordance with these large natural bottom units (*see also* Jones, 1950), the more so since recent investigations have proved that several pelagic larvae of bottom invertebrates, when ready to settle, will actively seek an appropriate substratum.

Third, the newly gained experience on "parallel" animal communities inhabiting similar types of bottom in widely different seas is of great help. We now have a basis

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of such "parallel" communities adequate enough for comparative use. We may compare series of samples from the same types of bottom in different regions of the sea to decide which is only a local phenomenon and which is of general significance. The future value of such comparisons, which may help us "read proofs" of new material, can hardly be overestimated in level-bottom ecology.

Remane (1940, p. 33) further stressed that with such a framework of Petersen communities as a sound starting point we may then, later on, unite the communities into "affinity groups" (thus obtain more exact larger units than those used by Shelford, 1935) or we may divide them up into smaller units (as did Petersen himself) including more and smaller species, thus approaching the very small, more nearly homogeneous units without losing the general view.

Thus, so far, as long as only statistical-descriptive units are concerned, the Petersen communities are realities and giving a general view of animal distribution on the sea bottom. Such a classification of animal communities would seem to be imperative for future work (Gislén, 1930, p. 43; Allee *et al.*, 1949, p. 436).

ANIMAL COMMUNITIES AS ECOLOGICAL UNITS

The next question is: Are the Petersen communities nothing more than descriptive statistical units or are they also to be regarded as ecological units—*i.e.*, biocoenoses?

There is no doubt that Petersen, when describing his communities, considered them statistical units only, as Petersen himself told the author. (*Cf.* also Spärck, 1935, p. 3, 1937, p. 2.) This agrees well, for example, with Molander's definition (1928b, p. 4): A Petersen community "is a regularly recurring combination of certain type animals, as a rule also strongly represented numerically." Those ecologists who have regarded his communities as biocoenoses (*e.g.*, Vatova, 1935) and also those who have criticized them on that basis (*e.g.*, Lindroth, 1935) have misunderstood Petersen's primary intentions.

Having described these statistical communities, a biologist then asks why these animals are found together (Caspers, 1950a, p. 45; Tischler, 1951, p. 137), and in trying to answer this question he already regards the animal communities from an ecological point of view. This states the thesis of Remane (1940, p. 32)—that studies of biocoenoses are to be regarded as a logical continuation of a study started on statistical units. Petersen himself speculated on the relations among these communities and the physical-chemical and biotic environment, and his discussions (Petersen, 1913, p. 32; 1915, p. 16) of the mutual competition and intimate relations among bottom invertebrates may be understood only as an attempt to find some ecological causality behind the animal communities which he had described. Nevertheless he approached these problems skeptically.

Lindroth (1935, p. 356–357), however, contends that the Petersen communities, when existing at all, are at best faunistic units, consisting of a number of more or less accidental species with overlapping distributions, but not linked by biotic factors. Ecological communities, however, do exist, but what are linked in them by biotic factors are not the faunistic units, the species, but the ecological units, the life forms. In striking contrast to Lindroth's criticism are the views of several other ecologists, who consider animal communities—including those described by Peter-

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sen—as ecological units: "Ecology is the science of animal communities" (Shelford, 1929, p. 2); "The community concept of modern ecology is one of the fruitful ideas contributed by biological science to modern civilization" (Allee *et al.*, 1949, p. 436), " . . . communities are composed, not of random assortments of species, but of ecologically compatible species populations whose collective ecological requirements of food, shelter and reproduction are satisfied . . . by a certain range of environment" (Allee *et al.*, 1949, p. 437).

MacGinitie (1939), while discussing and citing several other definitions, has given the most exhaustive but at the same time cautious definition of a biotic community—viz., " . . . an assemblage of animals or plants living in a common locality under similar conditions of environment and with some apparent association of activities and habits."

Having decided that our bottom communities are ecologically valid, we must next determine whether their composition is controlled mainly by physical or by biological factors. Schematically, there are three possibilities. A level bottom area may be recruited by:

(1) A set of animals voluntarily settling there, attracted by their favorite conditions. If so, all species that settle will have a fair chance to grow up. After they have settled, interspecific and intraspecific competition may reduce the number of some of the species to the benefit of other species, but no species settled voluntarily will totally perish, and, roughly speaking, the "adult" community will be composed of the same number of species as was found just after settling.

(2) Settling conditions as sketched in (1), but after settling the biotic competition may be so sharp (for instance between a dense population of brittle stars and slowly growing lamellibranchs) that some species, though well adapted to the physical-chemical environment, are eaten or forced out.

(3) Accidental young "rained down" at random from the plankton whether adapted to the physical-chemical environment or not. Hence a "survival-of-the-fittest-fight" will follow—*i.e.*, the newly settled set of species will be much different from the adult set of species, since only those best adapted to the milieu and for competition in that particular place will survive to the adult stage (this latter possibility seems to agree best with Petersen's ideas).

Several facts brought together during recent years seem to support the possibilities outlined in points (1) and (2), whereas Petersen's ideas as given above and in point (3) hardly seem to apply. Lindroth (1935, p. 395 [transl.]) states that "The animal species of marine level bottoms are, as to their distribution, in broad outline governed by the 'external milieu,' by the direct physical-chemical factors. The biotic factors are of subordinate significance . . . ," and Jones (1950) agrees, that " . . . there is little ground for believing that any large assemblage of animal species reacts as a unit or is bound together by purely biological factors." The significance of physical-chemical versus biological factors will be discussed in detail.

It has already been emphasized that studies of biocoeneses are to be regarded a logical continuation of a study on purely statistical units. The animal communities in the form described by Petersen himself cannot, however, be used for such ecological studies. A quantitative analysis, in order to be valid for biocoenetical studies, must include all species of all groups living in the samples procured, but Petersen neglected several of the smaller, and also the rarer species, to stress only the common forms in his samples (Remane, 1940, p. 32). Lastly, his samples do not include the motile fauna of the bottom, which is always there and affects the infauna in many ways. Nevertheless, his communities are of the greatest value as an ecological framework, and even Petersen himself regarded his communities as preliminary (Spärck, 1937, p. 2). We must improve the sieving methods and the technique of picking up the animals so that all macrofauna animals of each sample may be quantitatively registered. Several modern workers on quantitative level-bottom ecology (Vatova, 1949; Einarsson, 1941) have adopted such improved methods. The Petersen methods, therefore, in order to be of full value to modern level-bottom ecology, must be expanded and refined, but the basic procedure need not be changed. But even when more thorough methods are used and new and more compre-

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hensive facts are gained, the Petersen communities will continue to be a framework of world-wide and fundamental value. This framework of "parallel" level-bottom communities from the Arctic to the tropics will give us much-needed information on where to concentrate our future studies for the best results.

STABILITY OF THE LINKAGE BETWEEN ANIMAL COMMUNITY AND BOTTOM MILIEU

The most stable level-bottom community is one in which the whole set of animals is long-lived and without pelagic larval stages. The long average life of each individual will mean that several generations of each species overlap, thus reducing fluctuations in the population, and, as a result of the direct, nonpelagic development, the whole population is exposed to the same physical-chemical and biological conditions from birth to death. All young are born or hatched in the immediate vicinity and in the same milieu as were their parents, and invaders may "infect" the community only with difficulty, and usually by invasion along its frontiers.

Such stable communities will normally occur only in Arctic and Antarctic coastal waters and in the very deep sea, and for communities of that type the thesis given by Shelford holds good—*viz.*, that "The continued presence of an animal in an environment depends upon that developmental stage in which it has the least adaptability," and this stage, the weakest link of the chain, will normally be found during the breeding period and larval development. (*See* Thorson, 1950, p. 2.)

As the tropics are approached, the percentage of level-bottom species with a pelagic development will steadily increase and will reach its highest value on the tropical shelves (Thorson, 1950, p. 29). The average percentage of tropical bottom species with pelagic larvae probably ranges between 75 and 85 per cent, and, as the few species which even in these regions reproduce by direct development are mainly reef- and surf forms—*i.e.*, are epifauna—the percentage of tropical level-bottom species reproducing by pelagic larvae will probably be still higher, presumably about 85 to 90 per cent. This means that the closer a level-bottom community is situated to the tropics the less stable is the linkage between its inhabitants and the bottom milieu, because most of its species will spend the most sensitive period of their life cycle in another milieu.

Among the adult level-bottom invertebrates the linkage to the bottom may vary extremely from species to species. Sessile forms are the most stable, but usually such animals play an insignificant part on the level bottom. Next come such deeply burrowing, sedentary animals as the adults of *Mya, Balanoglossus, Lanice,* and *Chaetopterus,* which, together with less deeply digging but slowly moving animals like the adults of *Aporrhais, Turritella, Venus, Nucula, Echinocardium, Brissopsis* and *Amphiura,* make a very stable element of level-bottom communities. All these species are, in their adult stage, forced to endure all physical-chemical and biological fluctuations occurring in their bottom area—or to die. Other species, also intimately linked to the bottom, have nevertheless a fair chance of partially avoiding such unpleasant biological, and possibly microclimatic, changes as an invasion of predators or a lack of oxygen by a sudden change of their habitat: *Spisula, Lima,* and *Pecten* by swimming (flapping with their shells), *Nassa* by violent leaps, etc. Other species are so agile that they may avoid several enemies and local microclimatic changes (*see* also Verwey, 1949) although forced to endure the major fluctuations near the bottom. A species like *Arenicola marina* migrates from shallow to deeper water when growing up (Newell, 1949) and despite its burrowing habits is also able to swim.

Most of these examples are, however, only "narrow escapes," and the animals mentioned must as a rule endure the major fluctuations of bottom conditions throughout the year. Much more interesting in discussion of the stability problem are those species that leave the bottom to spawn. This is often the case among polychaetes, whether errantiate or sedentary. The animals will "load up" with eggs and sperm on the bottom and rise, mostly in an epitokous phase, to the surface, where after some swarming the sexual products are shed. In most seas there will be some change in temperature from bottom to surface, and, as such swarming takes place preferably in the warm season in temperate

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seas, the rise to the surface, both in temperate and tropical seas will mean a rise in temperature of the animal. It may be, therefore, that the eggs developed to their full size on the bottom demand an increase of temperature to become fully mature and fertilizable, and that the mature animals demand a temperature stimulation to start the act of spawning, a temperature which may occur only at the surface. The whole existence of such species in a level-bottom community may thus depend upon the physical-chemical conditions in quite another milieu, to which the animals migrate during their most sensitive periods. As such swarming of epitokous polychaetes is much more common in warm than in cold seas (though occurring also in a few Arctic species) the linkage between animals and bottom milieu is also in this respect less complete in tropical than in temperate waters. (For an account of the periodicity of spawning in warmer waters, *see* Chapter 27.)

Thus it might be expected that the Arctic-Antarctic and deep-sea communities, recruited by direct development—*i.e.*, by young born among their parents and exposed to the same constant milieu throughout their lives—would prove to be more homogeneous and stable in composition and better-defined than those from warmer seas. This does not seem to be the fact, however. All samples so far procured from temperate and tropical seas seem to indicate that the level-bottom communities are just as homogeneous and as well defined as are those in the Arctic seas.

PRINCIPAL RULES FOR THE DESCRIPTION OF LEVEL-BOTTOM COMMUNITIES

BIOTOPES VERSUS BIOCOENOSES AS FUNDAMENTAL DESCRIPTIVE UNITS

We may ask whether we should describe the animal communities on the basis of the substratum (the biotope) or on the basis of the animals. There is evidently a close connection between the composition of an animal population and the sediment in which it lives. This has led Davis (1925, p. 17) for example, who classified the bottom substrata according to grain-size groups, to state that "the simple number of the soil groups will show what species may be expected therein." Remane (1940, p. 40) also seems to agree with Davis that a description of and a division into animal communities has to start with the substratum.

In some ways it is an advantage to obtain a reliable and quantitative impression of a level-bottom population without knowing the biotope beforehand. It may be correct that a simple size grouping of the soil may show what species might be expected therein, but only approximately so. Recent investigations of Jägersten (1940) and of Wilson (1952; 1953) have clearly shown that the bottom invertebrates living constantly during long periods in close contact with the substratum will be influenced as to occurrence and distribution by much finer details in soil composition than can be registered by a simple series of grain-size tests. Even Davis (1925, p. 6) admits this: " . . . texture of soil *per se* may not be intrinsically a factor of great importance but merely the visible expression of something far more subtle." (*Cf.* also Tischler, 1950, p. 35; Caspers, 1950a.) This, in fact, means that the bottom animals are so sensitive that they may tell us much more about the substraum than the substratum, treated according to our recent coarse methods, may tell us about the animals. The bottom animals can give a much finer analysis of the bottom than we can and, therefore, are to be regarded as the best starting point for ecological studies.

Starting with the animals, the level-bottom ecologist must, however, compare his results constantly with the sediment samples obtained. These samples, many of them indicating the uniformity of large sea areas, may help him define the broad outlines of his animal communities, and the quantitative samples of animals may help him find out whether a more-detailed study of the sediment may lead to a better

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understanding of the relation between population and substratum. Such mutual corrections of animal communities by the aid of sediment studies and of sediments by the aid of the animals found will not necessarily be to proceed in a circle as suggested by Lindroth (1935, p. 354), but only to use one's common sense.

ADVANTAGE OF DESCRIBING ANIMAL COMMUNITIES ON A QUANTITATIVE BASIS

Several scientists look upon biocoenotic studies, with their profusion of terms, with much skepticism. This is not surprising, because many ecologists have worked with subjectively selected biotopes and have studied their animal populations without using quantitative methods.

Franz (1950) has had to consider this problem with terrestrial soil faunas and states that " . . . the limitation of biotic communities (*"Lebensgemeinschaften"*) must be based upon qualitative facts [transl.]", and even Remane (1940, p. 39), though especially familiar with marine microfauna, is of the opinion that "to the benefit of logical clarity" quantitative points of view have to be neglected when selecting "characteristic species." Tischler (1951, p. 137 [transl.]) agrees in this and states that "quantitative studies have proved to be of less value to sociological considerations, being, however, important for questions dealing with the dynamics and biology of productivity." Starting from this latter citation the writer argues that it seems both unreasonable and impractical to choose for sociological studies a method which will have to be completely changed, if we would proceed from purely sociological to all-round ecological studies. Such a continuation from sociology to all-round ecology is a logical development in which the dynamics of productivity also plays an essential part.

We know that most species in nature are distributed according to a sliding scale (*see* Remane, 1940, p. 32), and much more so on the level sea bottom than on land (Elton, 1927, p. 10). If an animal species finds its preferendum for several ecological factors in the same narrow locality, qualitative methods may be sufficient to indicate its distribution, but normally such optimal factors will not all fall in the same locality —*i.e.*, the individual species will be dispersed over a wider area and decrease slowly in number toward its frontiers. Such a gradual decline is registered much more exactly when using quantitative methods.

Furthermore, it will be nearly impossible, even for those ecologists who stress qualitative methods only, to avoid a quantitative point of view when describing a community. The term "abundance" (*"Abundanz"*), as used for example by Remane (1940, p. 36) to indicate that a species is bound to one definite biotope only, is a purely qualitative term, but as soon as "dominance" (referring to the number of individuals) "constancy"—*i.e.*, at least one specimen per square unit of known size; *see* Caspers (1950a, p. 50), "leading species" (*"Leitformen"*) and "steadiness" in distribution are included in the description, our thinking is already more or less quantitative.

Remane (1940, p. 36) distinguishes on a qualitative basis between species which are "biotopeigene"—*i.e.*, species which within a biotope are able to ripen their sexual products and to maintain their population generation after generation—and those which are "biotopverwandte" only—*i.e.*, species from related biotopes regularly invading the biotope concerned, where they may occasionally reproduce, though they

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are normally recruited from outside. Applying these definitions for the Sound between Denmark and Sweden, we find in the same biotope generations succeeding generations of the same species which are able to ripen and to spawn here, but all pelagic larvae are carried away, most of them to be killed by the brackish surface layer, and the new generations are regularly recruited by larval swarms produced in the Kattegat or the Skagerrack hundreds of kilometers away (Thorson, 1946a, p. 413–416). Using Remane's qualitative definitions, this would mean that the distinct and constant level-bottom communities of the Sound were inhabited by "biotopverwandte" species. The difficulties in applying qualitative definitions in cases like this again point to quantitative methods as the better approach.

Since it is a rather simple task to procure quantitative macrofauna samples on level-bottom flats which, furthermore, are so uniform that we are allowed to generalize the results, it seems a step backwards to abandon our quantitative methods. Having better chances for quantitative work than most other ecologists, who have to hunt directly for "some very simple association of animals in which the complications of species and time changes are reduced to a minimum" (Elton, 1927, p. 98), we should use this chance for pioneer work instead of adapting less-developed working methods for the reasons of coordination only.

Finally, qualitative samples taken with other gear and supplementing the quantitative samples are also of much value, in order to secure the more scattered and more motile species, and to give us a preliminary idea of the area we are going to examine in detail.

NECESSITY OF USING STANDARD UNITS OF BOTTOM AREAS

Before considering in more detail the quantitative requirements for a "characterizing," or "indicator" species we must consider the necessity of using standard units of level-bottom areas. Thus, it has been proposed that a "characterizing" species must be "constant" in the sense of the plant ecologists—*i.e.*, must occur "at least in 50 per cent of the samples from the community" (Spärck, 1937, p. 3)—but the proposer of this has in that same investigation used two sizes of samples—*viz.*, of $\frac{1}{10}$ and $\frac{1}{5}$ sq. m units. Obviously a species occurring in 50 per cent of the $\frac{1}{5}$ sq. m samples, thus being "constant" for these may, theoretically and on an average occur in only 25 per cent of the $\frac{1}{10}$ sq. m samples, thus being too scattered there to be considered "constant."

It might seem rather simple to remedy this by categorically stating that a certain unit must be regarded as a "standard unit" and should be used for all comparisons in the future. Since the number of species as well as specimens per square unit decrease significantly with increasing depths, a "standard unit" suitable for shallow-water studies is far too small for similar investigations in the deep sea. This is partially compensated for by the greater stability and uniformity of distribution in deep-sea communities, but the individuals in the deep sea are so scattered in occurrence that large standard units—*i.e.*, a great many samples—are needed to provide the basis for selecting the characterizing species.

The following "standard units" are suggested for future investigations of macrofauna animal communities: (1) $\frac{1}{10}$ sq. m units for depths between 0 and 200 m—

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i.e., for the whole sublittoral zone down to the "mud-line" or continental slope. This zone may include gravelly as well as sandy and muddy bottoms. (2) $\frac{1}{5}$ sq. m units for depths from 200 to 2000 m—*i.e.*, the bathyal or archibenthal zone—where the bottom conditions are much more uniform (soft bottom) and the animal populations are already somewhat scattered, although still fairly rich. (3) 1 sq. m for all depths from 2000 to 10,000 m or more—i.e., the abyssal zone—where the animal populations are scattered and poor.

These units will enable us to compare animal communities on a uniform basis and eventually to attain more strictly quantitative analyses. Nevertheless, we must realize that these proposed units are based partly on experience and, especially for the deep sea, still more on "intuition." The 1 sq. m unit may be too small for some deep-sea areas, and in the inner part of an East Greenland fjord, for instance, a level-bottom unit at a depth of only a few hundred meters will be as poor in animals as a level bottom of 2000 m depth or more in warm seas.

ANIMALS WHICH MUST BE AVOIDED AND STRESSED AS CHARACTERIZING SPECIES

The ideal distribution of a set of species confined to a single community and numerous enough to dominate there is exceptional in nature, and as a rule it is not easy to select the right set of species characterizing a level-bottom community. Common sense combined with experience and intuition play an essential part in selecting such species. Comparisons with communities of a similar structure are of basic value when describing new communities. Remembering this, we may use the following criteria when electing our animals:

(1) The characterization of a level-bottom community must be based upon more than one species—i.e., on a combination of species of different groups of animals (for instance lamellibranchs, echinoderms, polychaetes, crustaceans; an exception to this rule is found in the tropical crab communities where a single species is the dominant and only characterizing member of the community). The ideal case would be a set of characterizing animals of different groups representing the different feeding types (suspension feeders and deposit feeders, etc.) found in the community proper, but such bases for selection of characterizing species are only rarely practicable.

(2) If a community is composed of species with short life cycles (1 year or less), we must use more species to characterize it than in communities with long-lived animals. As breeding conditions may vary much from year to year, such short-lived species may disappear in some years without being recruited by new stocks that same year. If so, others of the common species will take over their role within the community for some time, and so on. This is often the case in, for instance, a Syndosmya- (= Abra-) community, but the long-lived species of a Macoma community, for example, makes its species composition very stable.

(3) We must avoid the following types of animals: predators, since they will normally not specialize on a single prey species and not even on prey from a special community; animals present during only short periods of the year; very mobile animals, since they are caught more or less accidentally; and ubiquitous animals, which, although numerous, also occur in large quantities in other communities and in other seas (Examples: the lamellibranch *Astarte borealis* in Arctic shallow water, the polychaete *Terebellides stroemi* in all seas, Arctic as well as tropical). Here again comparison with known animal communities will help indicate ubiquitous character of an animal.

(4) Characterizing species must be immediately conspicuous—*i.e.*, they must dominate by their mere appearance—but this criterion of a certain size at the same time means that their number on a standard unit will normally not be enormous, because "The smaller the animal the commoner it is on the whole" (Elton, 1927, p. 69). Furthermore, wherever possible, they must be easy to determine by a well-trained, all-round ecologist, without detailed treatment by a specialist.

(5) We must decide whether to stress the number of individuals (the quantity of specimens) or the total living weight (the quantity of grams) in selecting characterizing species. Again, what will give us the best information and the best basis for future work? The quantity of specimens alone is a reliable indicator only if the animals concerned are of average size for macrofauna invertebrates taken as a whole. If, however, the species to be selected is small (as for instance the amphipod *Haploops tubicola*, or *Hydrobia ulvae* in the *Macoma baltica* community), or if we are to select a species

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with a large number of tiny brood, a figure based only upon the quantity of specimens will give an impression of "dominance" which does not correspond with its food requirements, metabolic rate, and productivity. The total weight alone is, however, also an insufficient indicator, since a single large specimen of *Cardium groenlandicum*, *Cyprina*, *Brissopsis*, or *Spatangus*, living rather scattered and caught more or less accidentally may outweight all other animals combined. Furthermore, since the dry organic-weight/living-weight fraction varies enormously from group to group (Table 1) this will also confuse our ideas of the "true weight" per standard unit. On the other hand, the weight is essential for future calculations of productivity and must not be neglected. We must therefore so combine the data for number and weight that the quantitative structure of the community stands out distinctly.

The author prefers to retain the definitions of characterizing species given by Petersen (1924), but with some of the quantitative requirements proposed by Spärck (1937, p. 3), and with the standard bottom units described above as the natural base. If we do so, the following definitions may be made:

(1) Characterizing species of the 1st order: conspicuous animals, found only in one definite community, in some quantity (*i.e.*, occurring in at least 50 per cent of the standard unit samples and making at least 5 per cent of the total living weight per standard unit) and occurring practically everywhere in this community. Such animals correspond to the "Bionten" of Thienemann (1918; 1920) and to the "Characterarten: Treuegrad 5" of Braun-Blanquet, and they approximate the "exclusive animals" of Elton (1927, p. 11–12). Examples are the *Amphiura* species of the Scandinavian mud-bottom communities, the *Macoma* species in shallow-water mixed bottom communities, the *Venus* species in flat-sand communities, and the crabs *Xenophthalamus* and *Pinnixa* in certain tropical sand-bottom communities.

(2) Characterizing species of the 2nd order: conspicuous animals, found only in certain parts within one definite community in some quantity (*i.e.*, occurring in at least 50 per cent of the standard unit samples and making at least 5 per cent of the total living weight per standard unit). No parallels by Thienemann (1918; 1920) and Braun-Blanquet, but they are parallel to Davis "mosaics" (1925, p. 5). Examples are: *Cardium edule* in certain areas within the *Macoma baltica* community, *Spisula subtruncata* within the *Venus* community, *Turritella communis* within the Scandinavian *Amphiura* communities.

(3) Characterizing species of the 3rd order: animals found in such large quantities (*i.e.*, occurring in at least 70 per cent of the standard unit samples and making up at least 10 per cent of the total living weight per standard unit) that by their mere appearance they influence our notion of the community, but which may also be found in quantities in other communities. Such animals correspond to the "Philen" of Thienemann and approach the "*Charakterarten: Fest und Hold*" of Braun-Blanquet and the "characteristic animals" of Elton (1927, p. 11–12). Examples are: *Echinocardium cordatum* in Danish *Venus*, *Syndosmya*, and *Amphiura* communities and *Astarte elliptica*, *A. montagui*, and *A. borealis* in Arctic *Macoma* and *Venus* communities.

(4) Associated animals (= Influents): All other, more common animals of a community (*i.e.*, occurring in at least 25 per cent of the standard unit samples and making up at least 2 per cent of the total living weight of the standard unit) which are not of such great importance for the characterization of the community.

It should be stressed again that these definitions are to be regarded only as the "ideal rules" which we must approach as much as possible when selecting our characterizing species, and in practice we shall often be required to reduce our claims significantly. Above all, when treating samples procured during a few days in a remote sea area on an expedition, our treatment may suffer from lack of knowledge of habits and life histories, length of life cycle, annual fluctuations, and mode of reproduction in the individual species. Several observations seem to indicate tentatively that those level-bottom animals which occur frequently enough to be regarded as characterizing will also have a pronounced adaptation to the temperatures of the waters in which they live (*see* also the discussion in Thorson, 1951; 1952, p. 309–316; Bullock, 1955), and this adaptation allows each genus to be represented in a sea area by just that species which is able to carry out the normal functions of the genus concerned at the prevailing conditions (Fig. 5). Thus, for example, the genus *Macoma* within an area,

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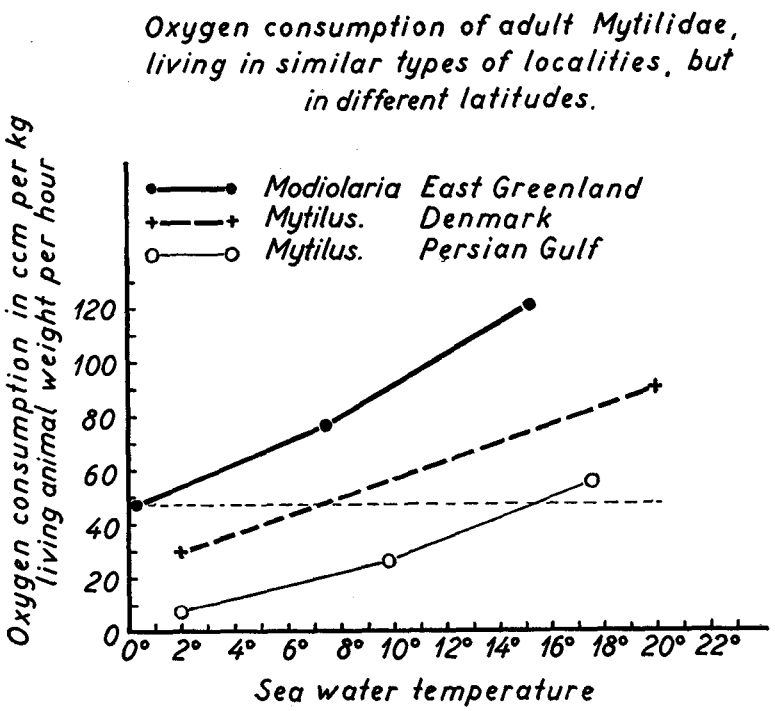

FIGURE 5.—*Graphs plotted against each other to demonstrate that the metabolic rate within the lamellibranch group* Mytilidae *is of about the same order of size*

In East Greenland at 0°C., in Danish seas at about 8°C., and in the Persian Gulf at about 16°C. This is a selected, especially clear example. Several other measurements of the metabolic rate in other lamellibranchs from the same three sea areas show, however, the same tendency, although less distinct than in the Mytilidae. From Thorson (1952, p. 312).

whether Arctic or tropical, will always be represented by a species which may carry out the normal functions of a *Macoma—i.e.*, rather low metabolic rate, slow growth, and a long life span, while representatives of the genus *Syndosmya* will always have a rather high metabolic rate, a rapid growth, and a rather short life span. This tendency may help us estimate the "biological type" of the animals found in samples from a remote, poorly studied area, and this estimate, together with a more general comparison with other animal communities of the same type, may significantly improve our chances to select the right characterizing species.

Petersen combined the generic name of one "characterizing species" with the specific name of another; thus, the name of his "*Echinocardium filiformis*" community consisted of the generic name of *Echinocardium cordatum* and the specific name of *Amphiura filiformis*. This idea has to be abandoned. We must give the full names of our characterizing species when describing a community.

Vatova (1947) proposed to add to the community name a "bio-index"—*i.e.*, the number of individuals per standard unit divided by the number of species. A unit with a few species occurring in large numbers would have a high bio-index, and a unit with many species with only a few individuals of each would have a low bio-index. Vatova's proposal may be of some help for a quick understanding of the outlines of the community pattern, but it is not exact, since two communities differing in their composition may have the same bio-index. For example, a community consisting of 100 individuals of four equally represented species (*i.e.*, 25 individuals each) and one with 97 representatives of one species and 1 each of the remaining three would both be represented as 100/4 = 25.

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HOW A LEVEL-BOTTOM ANIMAL COMMUNITY IS ESTABLISHED

COMMUNITIES RECRUITED BY PELAGIC OR BY NONPELAGIC LARVAL TYPES

As mentioned above, only the Arctic and Antarctic coastal waters and the very deep sea are inhabited by level-bottom communities of "ideal stability." As the delimitation of such stable communities, according to our experience from the Arctic seas (Thorson, 1933, p. 33; 1934), is very closely bound to the physical-chemical limits (especially to salinity and temperature) of the areas concerned, it follows that these communities will inhabit the same areas for long periods without being essentially disturbed by invaders.

In contrast to this are the tropical level-bottom communities where 85–90 per cent of all species have a long pelagic life. In the boreal—*i.e.*, cold-temperate—seas, two thirds (on an average) of the level-bottom animals have pelagic larvae, a fact which indicates that by far the majority of coastal communities belong to this less-stable type. The problems of recruiting the animal communities in such regions are quite different from those in the Arctic and the deep sea. The fight against invaders, which in Arctic and deep-sea communities takes place only along the frontiers, may be carried out in the very center of the community as well. If we accept Petersen's view that the community is recruited by an indiscriminate rain of larvae followed by a "survival of the fittest," such a mode of recruiting means a continuous revolution within a community, a continuous "embittered fight" for balance. Such a community is comparable to a country where invasions by "parachutists" take place constantly or at certain intervals, and where the "home guard" has to fight the invaders. If so it can be taken for granted that there will be some "weak points" in the defense of the home guard where the invaders may establish themselves for shorter or longer periods.

In level-bottom communities inhabited by species with a short life cycle and a pelagic larval development we actually know of such weak points. A characterizing animal, normally covering the bottom of such a community, may disappear from large areas during certain seasons. It may have died naturally or it may have been eaten by bottom fishes, etc., and unfavorable conditions during breeding and planktonic life may have prevented a new generation of that same species from immediately occupying the space after the old stock. (*Cf.* Davis, 1923, 1925.) Such abandoned spots may be attacked as "weak points" by invading swarms of foreign pelagic larvae. Here the invaders find no home guard to fight them; they may settle and establish their own population and grow up, totally or partially, thus infiltrating the original community.

Such infiltrations, repeated during thousands of years within a tropical or warm-water community, where they occur in every month of the year, must sooner or later influence the composition of the communities, making them more confluent, less distinct, and less sharply delimited than those of Arctic-Antiarctic waters and the deep sea. All this depends on the assumption that Petersen is right in his view that accidental larvae "rain down" at random to fight for their survival.

But the available information about level-bottom communities seems to indicate that the tropical communities consist of just as pure populations, are as uniform over wide areas, and are just as well delimited as those of the polar seas. We do not find

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the slightest indication of such infiltrations or dissolving communities as might be expected as the logical consequence of Petersen's suppositions. The reasons for this striking contrast must be sought for in the larval ecology; we must be familiar with the problems during pelagic development, metamorphosis, and settling of the larvae. It must be remembered that when Petersen wrote his papers 30 to 35 years ago, our knowledge of larval ecology was nearly negligible. It has, however, increased significantly during the last 20 years.

SELECTIVE EFFECT OF PELAGIC LARVAL LIFE

Pelagic larvae of polychaetes, echinoderms, and Mollusca live on an average about 3 weeks in the free water masses before settling on the bottom. This period of 3 weeks seems to be valid for cold-water species as well as for warm-water species at their normal temperatures. Newly hatched larvae within all groups are photopositive—*i.e.*, they rise to the surface of the water. Older larvae ready to metamorphose and settle are in most cases photonegative—*i.e.*, they swim near the bottom. We know, however, of a series of remarkable exceptions from this latter rule. In waters with a high salinity it has been proved that larvae of *Pygospio elegans*, *Spirobis borealis*, *Pomatoceros triqueter*, *Asterias rubens*, *Balanus balanoides*, and *Mytilus edulis* are also photopositive when ready to metamorphose, an ability which enables them to crowd near the surface and to settle in quite shallow water or in the intertidal zone. Where the surface layer is brackish, however, some of these larvae (*e.g.*, *Pomatoceros* and *Asterias*) will react in another way. Although experiments have shown that the larvae ready to metamorphose are also photopositive, the newly settled young will never be found in quite shallow water, but they often occur in great numbers at depths of 15–20 m (*Pomatoceros*) and 20–25 m (*Asterias*) respectively. The settling larvae here have had to balance between their photopositive attraction to the surface and their negative reaction to brackish water, and have had to find a depth for settling which acts as a "common denominator" for the most optimal milieu to be obtained under the prevailing conditions. (For details *see* Thorson, 1946a, and Banse, 1955.)

In some groups of larvae the balance between attractive and repellent factors may be still more complicated. Thus it has been shown by Hardy and Bainbridge (1951) that pelagic larvae of decapod crustaceans are very sensitive to changes of pressure; for instance they rise immediately toward the surface if pressure increases. There may also be several other factors still unknown to us, which together with those already mentioned may act upon the larvae and influence their position and distribution in the water during the most critical period of settling.

This stratification is, of course, of the greatest significance for the choice of substratum when the larvae are going to settle, since many of these "stratified" species of larvae will not have a chance to get in contact with all the types of bottom in the sea area in which they live. A larva of *Pygospio elegans*, for example, has no chance to get in contact with a muddy bottom in deep, salt water, because its resistance to brackish water together with its photopositivity will keep it close to the surface during its whole larval life, including the settling period. Similarly, a larva of *Pectinaria auricoma* in the Sound will never get in contact with the mixed or sandy bottoms in very shallow water, since it is unable to migrate from its habitat in the saline bottom layer through the spring layer to the brackish surface.

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This concentration of the different larval species in horizontal strata may help several larvae to survive, because by crowding in a certain stratum they may find a rather constant milieu, following the same water mass up and down or in and out. (*Cf.* Boden, 1952; Boden and Kampa, 1953.) Though surrounded by water masses less favorable for their demands, they may thus develop under conditions as optimal as possible. This ability of larvae to select favorable water layers may, on the other hand, deeply influence the composition of such level-bottom communities which the larvae are going to supply. Each type of bottom will be exposed to a particular set of larval species—*i.e.*, even at the moment of settling the number of competitor species for each single bottom type is significantly reduced as compared with the total number of larval species in water.

The pelagic larval life will also influence this composition in other ways, since competition among plankton is very keen and since each day, not to say each hour and each minute, spent there is extremely hazardous. The author has elsewhere (1950) reviewed the factors causing wastage among planktonic larvae.

The changing composition of the swarms of larval species in different years and seasons may deeply influence the bottom fauna, since its recruitment may take place only in accordance with "the principle of existing possibilities" (Fig. 6). These possibilities may vary enormously in different localities, years, and seasons (*see, e.g.* Spärck, 1926, p. 279), and therefore we find large fluctuations in bottom populations recruited from such changing larval swarms. Varying speeds of larval transport by currents may, of course, further contribute to these fluctuations. The influence of such fluctuations is most conspicuous in communities composed of annual species since the recruiting from the plankton in such cases is directly decisive for the community pattern during the next year.

Thus, even if we accept the Petersen idea for the recruitment of level-bottom com-

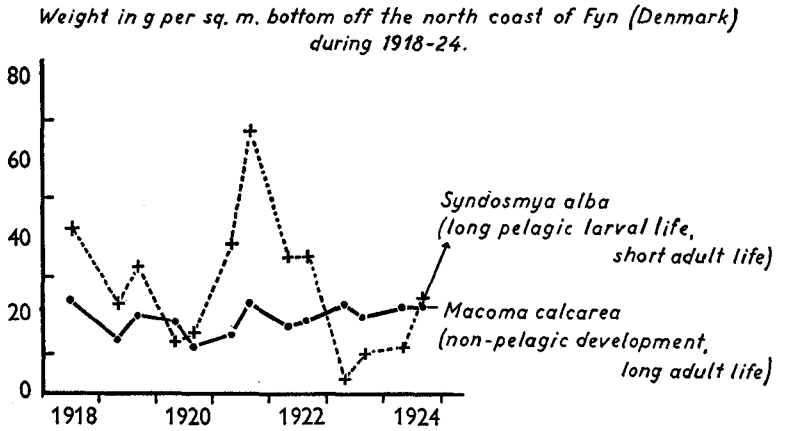

FIGURE 6.—*Graphs showing the fluctuations from year to year in a population of bottom invertebrates from Danish seas*

Syndosmya (= *Abra*) *alba* with its heavy fluctuations, is recruited from larvae with a long planctotrophic pelagic life, while *Macoma calcaria*, with its small fluctuations only, is recruited from embryos with a nonpelagic development. From Thorson (1946).

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munities, we must realize that the conditions for development of pelagic larvae, and more or less narrow stratification of the larvae when ready to settle directly, influence the species composition of the set of larvae which might "rain down" on a given level-bottom area. These circumstances help to reduce greatly the competition on a given bottom area.

LARVAL SETTLING AND CHOICE OF SUBSTRATUM

It has already been pointed out that modern ecologists familiar with marine level-bottom problems agree in recognizing the close association between the animal communities and the bottom type they inhabit. This, however, does not solve the question of whether this association is the result of a deliberate choice of the larvae or whether it is a "fait accompli" after a bitter "survival-of-the-fittest fight."

In a fine paper Wilson (1952) reviews the influence of the substratum on the metamorphoses of the larvae of marine animals. It has been proved experimentally that the larvae of a number of polychaetes and echinoderms are able to test the bottom substrata, some of which are repellent and others attractive, and that larvae ready to metamorphose may postpone metamorphosis until they find a substratum suitable for adult life, meanwhile continuing to swim or grow for a shorter or longer period, sometimes several days to several weeks. The conjecture that larvae of other bottom invertebrates are able to respond positively or negatively to their substratum receives support from the "swimming-crawling stage" which seems to be a normal feature in the development of lamellibranchs and marine gastropods, allowing them to crawl and carefully examine the substratum they have settled in and then to swim up again.

The only large-scale experiment in nature so far, carried out in the Danish Waddensea by Smidt (1951), showed that only those invertebrates that also inhabited the waddens as adults were present as newly settled young in spite of the large number of "foreign larvae" brought into the area at each flood tide. Much work remains to be done, but we have evidence enough to abandon the "raining down at random" theory hitherto accepted by most marine ecologists. (It must, however, be borne in mind that this ability of the larvae to postpone settling until they find an attractive substratum also has a serious drawback; every day of prolonged larval life means that the larvae must pay a further high tax to their predators. Another drawback is that in certain cases the substratum may deceive the larvae and tempt them to settle on a bottom which will prove unfavorable to the adults—for instance, if larvae of *Mya*, *Bonellia*, and *Urechis*, which in adult stages live about 25–30 cm below the bottom surface, are stimulated to settle in a layer of substratum only a few cm thick and covering a hard rocky bottom.)

These considerations clearly support the close association between the type of bottom and the animal species inhabiting it. It has been supposed (Smidt, 1951, p. 93) that a bottom flooded by a water mass containing a set of larval species ready to metamorphose will act directly as a magnet pulling the "right larvae" out of the plankton. Wilson (1953, p. 423) in a paper on settlement of the polychaete *Ophelia* states, however, that "Larvae find the sand by chance contact, they are not attracted to it from a distance by olfactory or other sense. This should be remembered when a sand is described as being attractive," and "Nothing dissolves out of the sand to induce the metamorphosis of larvae not in actual contact with it." (This is parallel to what is known for instance for wood-boring species like *Teredo*. Here the larvae are not attracted by the wood, but the wood induces them to metamorphose when they get in contact with it. [Yonge 1948, p. 593]). If these observations are valid also for other larvae, Smidt's view, which has been shared also by the author, must be revised.

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Although it must now be regarded extremely probable that the larvae respond positively to appropriate substrata, how they do it is still an outstanding question. "All the explanations so far advanced, effects of light, texture of surface, grade of bottom soil, metamorphosis-inducing substances, olfactory attraction, etc. . . . , are at best partial answers to that problem" (Wilson, 1952, p. 57). Several problems are still to be solved: Is the final species composition of a level-bottom community determined from the very moment of settling, and is it the soil composition alone which decides what set of species may settle and grow up in each single locality?

INFLUENCE OF ADULT LEVEL-BOTTOM POPULATIONS ON THE SUBSTRATUM AND THE NEWLY SETTLED YOUNG

When the larvae find and respond to their favorite substratum and settle there, this very substratum will already be inhabited by populations of adult animals. Will the secretions or excretions of such more or less dense populations influence the sediment in which they live, and may such an influence, if present at all, help to attract or to drive away the testing larvae?

The larvae of several sessile animals will not settle on clean surfaces, but will do so in large numbers on the same surfaces as soon as these have been covered by a film of bacteria or other organic matter (Wilson, 1952; 1953, p. 428; Thorson, 1946a, p. 22). It seems reasonable to assume that the level-bottom substratum must also be associated with such organic substances, which may play their part in making the soil attractive or repellent to the different species of larvae (Wilson, 1952, p. 117).

If we assume that such organic secretions or excretions of the adult animal population are actually mixed up with the bottom substratum and influence the settling larvae (except for a few ubiquitous species which are especially tenacious and more or less indifferent to the type of substraum they inhabit), this influence may be: (1) attractive to larvae of species already inhabiting the area (*cf.* Wilson, 1952, p. 54–55), or (2) attractive to larvae of foreign species, and at the same time probably neutral or repellent to larvae of "native" species, or (3) repugnant to larvae of foreign species and, perhaps, sometimes to those of "native" species also.

(1) Recent investigations have supported the view that larvae of such sessile epifauna organisms as *Ostrea*, *Spirorbis*, and balanids are directly attracted and induced to settle by the presence of established populations of their own species (for this "gregariousness problem" *see* Spärck, 1951b; Knight-Jones, 1951a; 1951b; Knight-Jones and Stephenson, 1950; Knight-Jones and Crisp, 1953; and Thorson, 1952, p. 291). However, for level-bottom lamellibranchs of the genera *Tellina*, *Spisula*, and *Cardium* observations seem to indicate that an attraction of larvae to areas where the adults of their own species occur in large quantities is far from being desirable and may often be catastrophic. Old individuals have a relatively lower metabolic rate and a greater resistance to changing physical conditions than do the newly settled young. In dense populations of different ages of the same species the adults will always compete better—*i.e.*, will be more economical—than the newly settled young. If food conditions are inadequate to nourish the whole population, the young stages will simply be forced out and will die, as was the case for the lamellibranchs mentioned above. Blegvad (1928, p. 46) points out that the most unsuccessful recruitings of the individual species in the level-bottom communities of the Limfjord will take place in those years when the adult populations of the species concerned are especially dense, and MacGinitie and MacGinitie (1949, p. 40) also stress the difficulty of the settling young of lamellibranchs in competing with adults of their own species. This unequal fight between young and adults is emphasized by the fact that pelagic larvae will normally settle in large swarms during a very limited time, which is again the direct consequence of the "epidemic spawning" (*see* Thorson, 1946, p. 443–446), which started their development. This drawback is avoided by those forms with a nonpelagic development, since such forms will normally produce their young in a more-developed state, and during a much longer period of the year, which again makes their mutual competition less keen. (*See* Thorson, 1952, p. 291–300). The value of such attractive

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substances, whether acting directly from an adult species upon its larvae or indirectly as part of the soil seems, therefore, to be highly questionable for level-bottom invertebrates, and theoretically it seems most logical that such intraspecific attractive substances are absent among level-bottom invertebrates. Turner's (1949, p. 21) discussion of gregariousness, in which he confirms it for the epifaunic oyster but questions it for the level-bottom *Cyprina ilandica*, is in full agreement with this point of view.

(2) If, however, such influence of dense populations on the characteristics of the sediment in which they live is carried through to the bitter end, the result may be quite contrary to that discussed above. For a population of the lamellibranch *Spisula subtruncata* in the southern North Sea, which will normally prefer a pure, loose sandy bottom, Hagmeier (1930b, p. 134, transl.) mentions the possibility ". . . that the content of silt may be increased through the excrements of the increasing number of lamellibranchs, which will in turn prepare the bottom for the deposit-feeders, *i.e.*, for a new set of animal species." It seems very likely that such conditions may actually occur in certain areas. If so, an adult, well-established population of *Spisula* may very well stand such silty conditions caused by their own excretions, while the next generation, the very sensitive *Spisula* larvae, will not settle on such a bottom. This must be considered when we try to explain the patchiness of *Spisula subtruncata* on the Dogger Bank, for example (Davis, 1923, p. 18), where each patch consists exclusively of a single year group. Such patchiness may be caused by fluctuations in the larval swarms from year to year, by varying directions and distance of the larval transports by changing currents, or by competition between adult and young individuals, in which the young are quickly knocked out, but it may also happen that the bottom has been made repugnant to new *Spisula* swarms by the excretions of adults of their own species. The great part played by such excrements, "faecal pellets,' of planktonic as well as bottom animals for the composition of the upper stratum of level bottoms has clearly been shown by Moore (1931a; 1931b). If excrements of *Spisula* may so change the consistency of a sandy bottom as to prevent *Spisula* larvae from settling there, this bottom may at the same time have changed so as to be attractive to other larval species. If so, this may be similar to what occurs in terrestrial plant communities; one community may prepare the way for a new community by producing vegetable mould. Thus ". . . plants react on their surroundings and in many cases drive themselves out" (Elton, 1927, p. 21, but *see* (3) below; for the general problem of repellent or even poisonous metabolites, *see* Lucas, 1947)

(3) The possibility that a population of a level-bottom area may make the soil more or less repugnant to foreign species by excretions or secretions seems to contradict the situation sketched in (2) above. It does not seem logical that a small amount of excretory products may help to exclude foreign larvae, while a large amount of the same products may attract them. Hence, returning to the patchy *Spisula* populations of the Dogger Bank, it is possible that large amounts of excretory products will be repellent to the "native" as well as the foreign larvae. It is well known that large areas of the Dogger Bank outside the patches may be desertlike, nearly or totally deprived of animal life. They may be areas lying fallow, and for some time uninhabitable by young of all species.

These considerations have mainly been theoretical, since we still have very few facts to substantiate them. For the experimental biologist who intends to continue work along these lines, it is, however, necessary to realize the ecological background for his experiments. This may help him to concentrate on the key points and to solve some of these essential, but intricate problems.

BOTTOM SUBSTRATUM AS AN INDICATOR FOR THE PHYSICAL-CHEMICAL CONDITIONS OF THE ENVIRONMENT

The association between settling larvae and bottom type may thus be based upon (1) the physical composition of the soil (grain size, shape, mineral composition), (2) the content of organic substances adhering to or lying between the mineral grains, or (3) a combination of both. The organic substance may originate from microfauna or microflora, from bacterial activity, from settling plankton, from excretions or secretions of the animals living in the bottom, or from different combinations of these sources.

The main factor determining the broad pattern of animal-community distribution on the level bottom, however, may be the physical-chemical composition of the sediment. Wilson (1953, p. 425) found for *Ophelia* larvae that "some sands which are relatively unattractive under free-choice conditions will, in conical or flat-bottomed

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vessels where the bottom is completely covered, induce good and sometimes heavy settlements and good metamorphosis rates, although likely to be delayed when compared with a strongly attractive sand under the same conditions."

Metamorphosing larvae will very rarely be exposed in nature to such optimal conditions as they find in Wilson's "free-choice vessels" where they may contact up to five different more or less attractive substrata mutually separated by a distance of only a few centimeters. Larvae exposed for a relatively long time to only one uniform type of substratum (and this may often happen in nature) may thus be forced to settle on a substratum that has relatively few attractive qualities since they have in reality no chance for "free choice." The choice of a substratum by larvae in nature will rarely be so precise as in the "free-choice vessels," since in most cases they will have no chance to find a more attractive bottom within a reasonable period of time. These factors, reducing to a certain extent the full effect of "free choice" by larvae in nature, must be remembered when we consider the relatively coarse pattern of community:sediment relations actually found. An *Amphiura* community is always associated with "muddy bottoms" though the character of this mud may be varying; a *Venus* community is always associated with a sandy bottom, though the sand may be fine and hard, or coarse or loose. (*See* Davis, 1925, p. 16; Jones, 1952.)

Only a few scientists (Molander, 1928b, p. 5; Shelford *et al.*, 1935; Clements and Shelford, 1946, p. 313) regard the hydrographic conditions as more essential to the bottom fauna than the soil composition, but these authors have carried out their investigations in narrow fjords and sounds (Gullmar at W. Sweden, and Puget Sound near San Juan Island respectively), where conditions may deviate considerably from those found in the open sea. (*See* Chapter 23.) It is, of course, imperative for future work to know precisely the most decisive physical-chemical factor, and we must admit that we are often reluctant "to record any condition with which a particular species appears to be constantly associated, even if it is a condition which is only correlated with the real limiting factor or factors and has no significance in the life of the animal" (Elton, 1927, p. 43). Nevertheless we now have evidence that the "naked" level-bottom soil (deprived of all plants complicating conditions on land) is among the limiting factors. Swan (1952) has shown that different kinds of bottom placed side by side in the same hydrographic milieu seem to give quite different rates of growth to young stages of *Mya arenaria* exposed to them.

In open-sea areas there is a close connection between the type of bottom sediment and a series of physical-chemical conditions of the environment just above the bottom, a fact hitherto neglected by most marine ecologists. This has already been emphasized by Davis (1925, p. 6): " . . . the texture of soil is probably a direct function of depth, current and the distance from the shore and river basins. The size and specific gravity of the particles settling bear a relationship to the pace and nature of the water movements in the area, the finer particles settling in undisturbed and slowly moving water." Thus, muddy sediments will settle at greater depth than sandy sediments, since the water movements are, on an average, most turbulent near the surface.* Further, a muddy bottom is farther from the phytoplankton-producing surface layer and

* Exceptions to this are noted for the Chinese coast (Shepard, 1948, Fig. 52) and the coast of Sierra Leone, West Africa (A. R. Longhurst, personal communication).

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is exposed to smaller amplitudes of temperature and salinity than is a sandy bottom (all taken relatively and in broad outlines). In this way the types of bottom in the open sea will serve as rough indicators for water movement, food conditions, and amplitudes of salinity and temperature in the surrounding milieu.

Since the larvae tend to concentrate in the most favorable water mass which will also be characteristic of the most suitable depth and bottom for the species concerned, it seems reasonable to assume that, having once settled voluntarily in a level bottom, and being more resistant to varying physical-chemical conditions when growing up, the young will only rarely be exposed to such physical-chemical conditions, which they cannot withstand during the remainder of their lives.

Exceptions may of course occur. Animals that have settled in very shallow water under optimal conditions may be exposed to low temperature in cold and temperate seas, and those in tropical seas may be exposed to brackish water during the rainy seasons—*i.e.*, in both cases to conditions which they may be unable to resist. Bottom populations near river mouths may be killed by brackish water during heavy rains or during a thaw. In narrow fjords with quiet water movements muddy substrata may even occur at such shallow depths that their animals may suffer from high temperatures and low salinities which they are unable to endure. Even large sea areas may normally be invaded by foreign water masses at intervals of several years—for instance, salt Skagerrack-water invading the Baltic; warm, salt, Lusitanian water invading the southern North Sea through the Channel. Such invasions may be devastating for the whole bottom fauna and may deeply influence its composition for a shorter or longer time.

Normally, however, conditions in the open sea will be so stable that animals which have settled voluntarily in a level-bottom soil will seldom be exposed to lethal physical-chemical changes. If so, this is of importance to future studies. If, for instance in the North Sea during a normal year (*i.e.*, a year without heavy invasions of foreign water masses), a population of *Spisula* has settled successfully and is growing up at a normal rate—and then disappears before having reached the adult stage—there will be a strong probability that this sudden loss is caused by biological factors (such as shortage of food or competition, or both, or even predation) and not by physical-chemical ones. In this way such a mortality, which has hitherto been regarded and has been treated as an "all-round ecological" problem, may now be treated exclusively as a biological problem, which means that we may focus our efforts on only a few factors of the problem.

BALANCE BETWEEN PREDATORS AND NEWLY SETTLED YOUNG

The next problem to be considered is the influence of established bottom populations on a newly settled larval swarm. Such predators as fishes, gastropods, sea stars, brittle stars, and crabs take a heavy toll. Brittle stars, for example, occur in such dense swarms that every centimeter of surface must be swept by their arms, as indicated by photographs taken by Vevers (1951, 1952) and by the abundance of ophiurans in some bottom samples from many boreal seas. In such places it does not seem possible that settling larvae could avoid their potential predators.

On the other hand, observations suggest that larvae of predator species are attracted primarily by suitable sediment rather than by populations of potential prey

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on a given bottom. Larvae of such predator animals as *Nassa*, *Asterias*, *Ophiura*, and *Amphiura* may defer metamorphosis and continue to live on phytoplankton for several days in the absence of favorable substrata on which to settle. Some predator species will not begin feeding upon their prey immediately; Coe (1912) found that *Asterias forbesi* did not start eating lamellibranchs until 3 days after settling, and Mead (1899) observed that this species (*see* also Thorson, 1956, pp. 391–392) would often settle a few days in advance of the larvae of its prey species.

This ability to prolong vegetarian diet seems to contradict any urgent need of animal food at the moment of settling. Further indications of the lack of attraction of predators to prey at the time of metamorphosis are the observations of simultaneous settling of predator and prey (Orton and Fraser, 1930; Davis, 1923) and the facultative or "potential" nature of such predators as certain ophiurans which are also detritus feeders. The gradual physiological changes of *Asterias* and *Nassa* during metamorphosis and the period of change from vegetable to animal diet (Zeuthen, 1947) also indicate that such predators do not have an immediate need for animal prey.

Furthermore, most predators do not seem to be highly specialized as to their prey in a particular community. It seems reasonable to assume from this that larvae of such predators are attracted by the substratum and after settling will hunt the prey associated with that bottom type. The mutual relationships among the animals (even predators and prey) of a given substratum may thus be of secondary importance in determining the species composition of a community. This may be determined at the outset, and all species that settle in reasonable numbers will have a fair chance of persisting as adults. The comparative percentages of the community shortly after settling may be changed materially by predators and competition before the adult stages, but in the long run a certain stock of all species will survive.

Of course there may be circumstances in which predators are so numerous that they may nearly wipe out a certain species. For several invertebrate predators, however, there seems to be a balance between the numbers of predator and prey. The mutual dependence of predator and prey larvae upon the same type of food—phytoplankton for example—means that, when the food is poor or scarce, both classes of larvae will suffer about equally, especially in those groups where both predator and prey have about the same period of larval life. Conversely, good feeding conditions will mean a large survival of both predator and prey.

This fine balance is, however, not valid for all predator-prey relations among level-bottom invertebrates. Pelagic larvae of decapod crustaceans are carnivorous and prey especially on larval Mollusca. A prolonged pelagic phase of molluscan larvae because of poor supplies of vegetable food may be advantageous to the larval decapods feeding upon them, since in such cases the molluscan larvae will occur in the plankton during an unusually long period. If so, poor conditions for molluscan larvae may lead to large loss among their larval swarms and settling young, while decapod larvae may thrive especially well, getting an exceptionally heavy survival. As soon as they have settled, decapod young will, however, change to much more omnivorous habits than found for young of *Asterias* and *Natica* and are therefore not so dependent on the presence of prey.

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The balance mechanism between predator and prey populations described above is, however, of value only if the predators and their prey have about the same duration of life. A phytoplankton production controlling at the same time the herds of larval lamellibranchs and of larval ophiurans or amphiurans settling together with them will have no balancing effect if the bottom is already covered by a dense layer of ophiurans or amphiurans 1 or 2 years old and ready to prey upon the settling lamellibranchs. This is actually the case in several soft-bottom communities.

A priori, it hardly seems possible that any larvae could settle and grow up successfully among the dense networks of *Ophiura* arms and *Amphiura* arms, of which *Ophiura texturata* is certainly known to be a voracious predator (Petersen, 1911, p. 39; 1913, p. 25, 34). Examination of the stomach contents of *Amphiura* seems to indicate that detritus, however, is the chief food. Nevertheless, it has been observed that any small living prey brought in contact with an *Amphiura* arm will be seized and carried to the mouth. This means that all organisms settling on a dense *Ophiura*- or *Amphiura* community run an enormous danger, since the arms of these predators control each square centimeter of bottom surface. An exclusive predator like *Natica* is doomed to death as soon as the prey population is wiped out. Such predators will normally be related to only one generation of prey and will thrive and perish together with this generation. Furthermore, they will always be less numerous than the prey animals on which they feed, as they are closer to the top of the "pyramid of numbers" (Elton, 1927, p. 50). A potential predator like *Amphiura*, able to feed on animal food when it is available and on detritus when no prey is found, in the long run seems to be much more dangerous to the settling young than is a "pure" predator, since the potential predators are a constant menace. Furthermore, such potential predators, since they may feed on "detritus" also, are farther from the top of the "food chain" and may accordingly occur in much larger quantities than do "pure" predators, whose numbers are restricted by the available prey.

It is most surprising to realize, therefore, that the *Amphiura* bottoms of boreal seas swarm with young of several species of prey during late summer and autumn and that several of these young are able to grow up to the adult stage. Ford (1923, p. 176) found off Plymouth, June 1922, 220 *Amphiura filiformis* and 1800 *Syndosmya alba* per sq m; 1091 of these Syndosmyas and 180 adult Amphiuras per sq m were still alive 1 year later, to which may be added 295 Syndosmyas per sq m of the next generation. How is that possible?

Predator activity, as all other activity of poikilotherms, is basically a function of temperature; the activity is relatively slight in cold seasons of the year but rises to a maximum when the water temperature over the bottom is highest. In Danish waters this maximum temperature will occur in late summer and autumn, at the same time that most young settle from the plankton. It might therefore be expected that the brittle stars would be especially voracious just during this critical period for the settling swarms of young. But during this warm season a most fundamental thing is happening to the brittle stars: they are going to breed, which will for some time nearly or totally inactivate them as predators. Early in the summer they start "loading up" for spawning, which will take place normally "epidemically" in August–September for the Danish amphiurans and for *Ophiura albida* (Thorson, 1946a, p.

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350–353, 444). One month or more before the spawning sets in, the ripe, swollen gonads will fill out nearly the whole lumen of their disc, reducing the lumen of the stomach to a small fraction of its normal capacity, which must necessarily reduce voraciousness to a minimum.

As soon as spawning is over, it might be expected that conditions would totally change. The water temperature is still high enough to support a maximum activity of the brittle stars, the stomach has regained its normal lumen, and the brittle stars, having spent a large percentage of their surplus as sperm and eggs, and having been unable to feed effectively for at most a month, might be expected to attack the young prey animals with great voracity.

This, however, does not seem to be the case, although our information is as yet preliminary. Experiments by Glaser (1907) indicate that the New England brittle star *Ophiura brevispina* undergoes a lethargic stage for some time after spawning. A similar lethargic period for the Scandanavian *Ophiura albida* and *Ophiothrix fragilis* is indicated by the studies of Wintzell (1918). The stomach wall of the latter species was observed to be reduced and thin—*i.e.*, histolyzed—and evidently the stomach wall must be rebuilt by the ophiuran before it can resume feeding.

If these observations prove to be generally applicable to ophiurians, we have not only a period of at least a month before breeding when the feeding ability of ophiurians is significantly reduced if not suspended, but a post-breeding period when the brittle stars cannot eat at all. Such a "passive period" of an important soft-bottom predator during the most critical periods for settling and growth of the potential prey species may strongly influence the species composition of mixed and muddy-bottom communities. This aspect of bottom ecology must be studied in detail.

CALCULATIONS OF LEVEL-BOTTOM PRODUCTION

DEFINITIONS OF "STANDING CROP," "BIOMASS," "PRODUCTION," "PRODUCTIVITY" AND "TURNOVER"

Several level-bottom ecologists have regarded their problem as solved when they have procured a sufficiently large number of samples (often from one single year or season only), arranged them into animal communities, and calculated the momentary number and living weight per square meter of each individual species. Such investigators, however, have exploited their quantitative samples much less than they should and furthermore run the danger of regarding their "proof samples" as identical with production. If so, and if they use the figures for "living weight" found in their samples for comparison with "living weight" in other communities and even in other seas, and from this draw any conclusions on poor or rich communities, they have actually finished a well-planned and thorough investigation in a most uncritical way. Petersen (1915, p. 20) warned against this, and Jensen (1919, p. 8–18) gave a thorough review of all the details which must be considered in order to get an exact idea of the animal production of a level-bottom community.

"Standing crop" or "biomass."—By "standing crop" or "biomass" we understand ". . . the quantity of substance in live organisms per unit of surface or volume expressed in weight units" (Brotskaya and Zenkevich, 1939).

Calculations of "standing crop" or "biomass," from a series of level-bottom samples treated as to number of species, specimens, and living weight, is often based on samples procured within a few

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hours to a few days. This will normally be the case during an expedition, and by far the majority of determinations of level-bottom "biomass" procured so far have been obtained in this way. A much better basis for calculations of this type is gained by determining the "average biomass" for a total cycle of seasons in a series of successive years. A rather reliable picture of the "average biomass" may, however, be obtained with less effort by comparing the minimum and maximum "biomass" within the total cycle of seasons and in successive years, as Jensen (1919) did in the Danish Limfjord.

The "standing crop" or "biomass" may be determined for the whole stock of living organisms within a limited area of the sea. This concept is close to that of Demoll's (1927) original "biomass."

We may, however, also take the term "biomass" in a narrower sense, for instance focusing on the bottom-dwelling animals only, on the population within a single level-bottom community, or—finally—on the population of each individual species, thus approaching Demoll's starting point (1927, p. 461), when he studied the "biomass" of a pure population of *Gammarus* kept in a "closed system" in a covered soup dish.

In recent literature many use the term "biomass" without any definition and in such a way that new students might get the impression that "biomass" has something to do with production though in reality "biomass" is only "the expression of the momentary equilibrium of nitrogen," and though "the biomass has no constant relation to the production" (Demoll, 1927, p. 462 transl.). The present author therefore proposes that the term "biomass" be abandoned in favor of "standing crop" as used in British literature since the very word "standing" stresses that we are dealing with a momentary phenomenon, and not with the idea of production, which must always be associated with a time factor.

Demoll (1927, p. 461) stresses that "only the consideration of the whole living mass" will be of any value rather than a calculation of "biomass" for each individual species within an inhabited area. Such a consideration of all species of an animal community as a whole, as a unity, however, prevents the full ecological and practical exploitation of valuable material and will "even at best be unusable for ecological purposes" (Remane, 1940, p. 38).

The only fact which the "standing crop" or "biomass" may give us, apart from data about the quantitative- and species composition of the community concerned is that the level-bottom area examined is able to support as a minimum the number of animals (calculated in living weight) actually found upon it.

When, however, we start calculating the "standing crop," our final aim must be to find out what this "standing crop" means in terms of production. If we compare two or more determinations of the standing crop taken at different seasons or successive years on the same bottom area, we may find the following situations: (1) the standing crop has increased from the first to the last determination. This indicates that production has taken place, though it tells us nothing about the size of this production. (2) The standing crop is of the same order of size in the first and the last determination. This gives us no information on production which has, however, undoubtedly taken place. (3) The standing crop has decreased from the first to the last determination. While this tells us nothing about the production, it must be remembered that, even if the standing crop has decreased, production has probably taken place.

We must therefore find out what has happened between our calculations. In a "closed system," such as Demoll's pure *Gammarus* population in a covered soup dish (1927, p. 461), where the same limited quantity of nitrogen is used again and again by a successive series of generations, the weight of the standing crop will always be of about the same order of size, irrespective of the rate of turnover. In such an "open system" as a level-bottom community, such conditions will never occur, and a standing crop of the same order of size after a certain time will normally indicate that production has taken place, since the population has been able to maintain its living weight by growth and recruitment ("upgrowth") despite the losses caused by consumption and natural death.

To follow growth increment and recruitment means to follow each generation. Jensen (1919) determined the standing crop every time a new generation had settled, but an estimate in broad outline may also be obtained if we know, roughly, the rate of settling, growth, and average life span for each of the characterizing species.

Whether we deal with the production of "the whole living mass" or only with that of each individual species, then adding the results for each species to obtain a gross figure, the picture is still obscured by the puzzling problem that the compounds are inevitably repeated at the expense of some

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groups being eaten by others. When calculating the production of the individual species, we include in the final expression for production the consumption by predators, and, when calculating the production for such a predator species, we include the growth increment it has gained from consuming the lower link of the chain. Thus these compounds expressed as living weight are repeated, but they are not doubled! It is a well-known physiological fact that only about 10 per cent of the weight of the animals devoured will be retained as "growth increase" by the predators which have fed upon them, a fact which will again be repeated when these predators are eaten by the still higher predators. Since we express production in weight per unit, this means that, by repeating what we regard as consumption in one species as growth increment in its predator, our final estimate on production calculating on this basis will be only 10 per cent too high. If we had calculated in calories instead of in weight, and one day perhaps we shall have to do so, this error by repeating the compounds from link to link in the food chain would have been much more serious.

Although the standing crop will give us no information on production, such calculations have been confused with production. Spärck (1935, p. 5–6) recommends the bottom-sampling technique as an easy method to find "the production of fish food in a certain area" during a short cruise, and Zenkevich (1927, p. 61; 1930, p. 23) and Zenkevich *et al.* (1928, p. 311) repeatedly mention the figures immediately appearing from their bottom samples as "productivity," though later on, when penetrating deeper into the problem (Brotskaya and Zenkevich, 1939), they have done much to clear up this confusion.

Furthermore, on the basis of such calculation of the standing crop, an attempt has been made to arrange the bottom areas according to "isobenths," which are defined as "the lines uniting the points of equal bottom productivity" (Zenkevich, 1930, p. 23; *see also* Zenkevich *et al.*, 1928; 1930; Idelson, 1933). What is called "bottom productivity" here seems to be only the standing crop. In Zenkevich's paper (1930, p. 17, Fig. 5) is given a map with "isobenths" for "bottom productivities" of 10, 50, 100, and 200 g respectively, and the same "isobenths" are indicated as crossing over two or more level-bottom communities. This again means that the "productivity" of *two* level-bottom communities comprising different species of animals—*i.e.*, with different contents of dry organic matter, with a different length of life, etc.—are regarded as identical simply because the momentary weight of a few bottom samples is found to be at about the same order of size. This, of course, will not give us a true picture of the "richness" of the bottom areas considered.

"Productivity" and "production".—The biological productivity is defined as the power or capacity to produce organic matter in live organisms. It is no exact term, since it is qualitative only, indicating the fertility of any ocean region irrespective of time (Thienemann, 1931, p. 616; Brotskaya and Zenkevich, 1939; Sverdrup *et al.*, 1946, p. 924). For our quantitative purposes this term is of no practical value, and, since it has furthermore given rise to much confusion (*cf.* for example Stroem, 1932), it would be better to abandon it and use the more exact term "production."

By "production" we understand the sum of organic matter produced by living organisms in a given area or volume and a given time, inclusive of such organisms, which in the given time might have developed and disappeared. Or, production is the total quantity of organisms formed in a given area or volume during a definite period of time, with no relation to their further destiny. (*Cf.* Thienemann, 1931, p. 619; Brotskaya and Zenkevich, 1939; Sverdrup *et al.*, 1946 p. 924.) This is the "annual production" in the sense of Jensen (1919, p. 13), the "gross production" in the sense of Stroem (1932), and the "actual production" in the sense of Brotskaya and Zenkevich (1939).

This "actual production" per year and unit of space (whether expressed in living weight, dry organic matter, organic carbon, protein [*i.e.*, nitrogen], or even in calories) is based upon two figures which must be added—the recruitment of new generations and the growth increments of the old stock. This growth increment also comprises two figures—the actual growth of all surviving specimens of the old stock, and the organic substance of all specimens which have disappeared from the area during the year, whether by "endogeneous senescence" or by predation (predation is very pronounced in most bottom communities) or even by migration. Jensen (1919, p. 8–17) has given the classic calculation of the annual production of each individual species inhabiting the level-bottom areas of the Danish Limfjord based on large series of quantitative samples.

"Turnover."—By "turnover" we understand the number of animal generations which replace each other within a given time.

An increase in temperature will normally increase the rate of development and maturity and

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shorten the life cycle of the individual specimens, thus also increasing the "turnover." Theoretically, Demoll's pure *Gammarus* cultures will show no "net production," since the weight of the standing crop will always be of about the same order of size. In the open sea, however, where predation—*i.e.*, consumption—plays an enormous part, an increase in the "turnover" will normally mean an increase in the production at the same time, and a high "actual production" will be impossible without a high degree of turnover.

In order to compare the production of one level-bottom community with another, each series of quantitative bottom samples, however reliable, must be thoroughly revised. Ideal would be a revision of the "actual production" as indicated by Jensen, but even if the samples available do not permit such exact calculations we may try to obtain as much information as possible for each individual species of a certain frequency concerning (1) the content of dry organic matter, (2) the average of growth per year, and (3) the average life span under natural conditions (including premature mortality by predators as well as "endogenous senescence," cfr. Deevey, 1947, p. 310).

WET VERSUS DRY WEIGHT

Although it should be standard practice to obtain the living or wet weight of the organisms in the community being studied, the dry weight will actually give us more information about the food value and ecological significance of the species involved. The dry weight may be estimated, as a first approximation, from the wet weight after the ratio has been established, and such dry:wet ratios have been determined for a number of bottom invertebrates (Table 1). Table 1 has been compiled from various sources (in some cases the ratio has been computed from the data presented). As can be seen, these ratios are surprisingly consistent. Some alcohol:dry weight ratios are indicated in Table 2.

The following technique is recommended for obtaining wet weights: Lamellibranchs and gastropods must be weighed with their shells, since they are organically connected. Tubiculous polychaetes, hermit crabs, and other nestling species are weighed without tubes or shells. Before weighing excess moisture is removed by rolling the animal on blotting paper. Clams may be drained of excess water by pouring hot water on them, which will cause them to open their shells. Such organisms as echinoids and *Arenicola*, which have large amounts of sand or mud in their intestines, pose a special problem. The procedure of holding them in clean containers for several days until their guts are emptied of sediment is not satisfactory when we require the weight of living substance, including the food in the alimentary tract, at the time of capture. For the final analyses for dry weight the intestines must be slit open and washed out before drying. A still better method is to subtract the ash content after drying (von Brand, 1927, p. 654–655).

Dry weights are obtained after desiccation, or treatment in a drying oven, first at about 60°C, later at 100–110°C until the weight is constant. Mollusks must be removed from their shells, and echinoderms and most Crustacea must be decalcified. If the specimens have been preserved, the fixative must be evaporated, and the residue included in the dry weight.

Circumstances such as intensive field work or a rolling ship may make it impossible to obtain living weight at the time of collection, and it will be necessary to preserve the material for weighing in the laboratory. The animals should be washed in sea water and preserved immediately. Each species must be kept in a separate container since the preservative will extract a certain amount of organic matter which must be included in the final calculation of the dry weight. All the animals should be preserved in the same type and strength of preservative (alcohol will extract more than formalin), which must be fresh. Comparisons between the fresh living weight-dry weight and alcohol weight-dry weight ratios indicate that, although the alcohol weight gives a somewhat smaller percentage of dry organic matter, the proportion is reasonably correct.

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The percentage of dry organic matter (Table 1) is very high in crustaceans (19.6%) and polychaetes (19.0%), which supports Blegvad's statement (1928, p. 29) that polychaetes and crustaceans are the most valuable fish food in Danish seas. The percentage is also rather high in tectibranchs (13.7%). Prosobranchs (7.8%) and lamellibranchs (6.6%) and echinoderms (6.7%), have much less dry organic matter. For the echinoderms this is deceptive, since the starfishes have a relatively high average (9.3%), and the genera *Ophiura*, *Echinus*, and *Spatangus* a remarkably low average (3.7%) of dry organic matter. (The brittle stars *Ophiothrix* and *Ophiocomina*, which are epifauna animals, differ morphologically from the level-bottom ophiurans and seem to be much richer in organic matter.) This impression is further supported by Table 2; the dry organic matter as compared with the rough alcohol weight is 5.5% for *Asterias*, but on an average only 3.25% for the level-bottom brittle stars and 1.5% for the sea urchins. In these latter groups where the content of dry organic matter on the whole is very low, the ratio may vary extremely in accordance with the sexual cycle of the animals. It is well known that, when ripe, gonads in echinoids and ophiurans will fill a large part of the body cavity, while in a spent condition their volume is insignificant. The writer ascribes the considerable fluctuations found in *Ophiura albida* (3.9–7.0%) and in *Echinus esculentus* (0.7–3.9%) to such physiological changes. They are also significant, though less marked, in the other groups of bottom invertebrates. (*Cf.* Gislén, 1930, p. 129.) There seems to be a close relation between the thickness of shells in lamellibranchs and the percentage of dry organic matter. Those with thin shells (*e.g.*, *Cutellus* and *Syndosmya*, Table 1) show much higher ratios (about 8.5%) than those with the very thick shells (*Astarte*, about 2%, alcohol weight, Table 2). Also, the thicker-shelled epifauna prosobranchs (*Littorina*, *Trochus*, average 6%) have less dry organic matter than the thinner-shelled level-bottom species (*Nassa* and *Buccinum*, average 9.5%; the extremely thin-shelled tectibranchs, 13.7%). For crustaceans, especially the smaller forms, the "living-weight" methods seem to be much more reliable than the "rough alcohol-weight" methods in Table 2.

Holme (1953, p. 22–25) gives somewhat higher figures for different bottom animals on the basis of alcohol weights. He estimates the dry weight of *Chaetopterus* at 25%, of *Callianassa* at 20%, of *Gonoplax* and other crabs at 24%. His figures for *Echinocardium* (2.29%) and for *Amphiura* (5.54%) seem to show dry weights comparable with those of Table 2. Holme's figures for Mollusca do not seem to be comparable, since the rough alcohol weight was calculated without the shells.

Figure 7 has been constructed to illustrate the approximate living volumes and weights required to produce one gram of dry organic matter in each of a set of level-bottom species. The large weight and volume of the echinoderms clearly contrasts with the small volumes and weights of the polychaetes; the Mollusca maintain an intermediate position.

The figures for dry organic matter require a revision of our view of the "productivity" of different seas. Most Arctic communities at relatively shallow depths are dominated by lamellibranchs and polychaetes, while the corresponding boreal communities are to a much greater extent dominated by ophiurans and irregular echinoids (Zenkevich *et al.*, 1928, p. 378; Spärck, 1937, p. 20). This means that a rather small "living weight" per square meter in an Arctic polychaete-molluscan community may have the same "dry weight" as a significantly larger "living weight" in a boreal ophiurid-spatangoid community at about the same depth. Similar differences may occur inside a rather narrow area of boreal seas, if for instance we advance from a community dominated by the thin-shelled lamellibranchs *Syndosmya* and *Cultellus* (dry organic matter about 8.5%) and the polychaete *Pectinaria* (dry organic matter about 17.25%) to a neighboring community dominated by the brittle star *Amphiura* (about 4%) and the spatangoid *Echinocardium* (less than 2%). It is obvious that it would be quite deceptive to combine by "isobenths" areas of these two communities on the basis of living weights.

Such calculations of dry organic matter will give valuable hints about production,

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TABLE 1.—*Percentage of dry organic matter of living or wet weight of some marine-bottom invertebrates*

Compiled from various sources: J.—Jensen (*in* Petersen, 1911); v. Br.—von Brand (1927); S. & K.—Struve and Kairies (1930); G.—Gislén (1930); D. & L.—Durchon and Lafon, 1951. Also Delff (1912) and Meyer (1914) have been used.

Species	% of dry org. mat.	*Authors*
Free living polychaetes	about	
Perinereis cultrifera	21.5–22.5	v.Br., D. & L.
Nereis diversicolor	22.0–27.5	Delff, D. & L.
Nereis pelagica	20.5	v.Br.
Nereis virens	5.5	v.Br.
Nephthys hombergi	20.0	D.&L.
Nephthys scolopendroides	18.25	v.Br.
Aphrodite aculeata	16.0	J., D. & L. (v.Br.)
Hermione hystrix	13.5	v.Br.
Sigalion squamatum	16.5	v.Br.
Lumbrinereis impatiens	24.5	v.Br.
Eunice gigantea	24.0	v.Br.
Eunice siciliensis	28.25	v.Br.
Halla parthenopeia	26.0	v.Br.
Diopatra neapolitana	17.25	v.Br.
Marphysa sanguinea	23.75	v.Br.
Staurocephalus rudolphi	19.0	v.Br.
Glycera siphonostoma	18.75	v.Br.
Average % of dry org. mat.	19.7%	
Sedentary polychaetes	about	
Aricia foetida	13.75	v.Br.
Scolecolepis fuliginosa	13.75–14.5	v.Br. S.&K.
Nerine cirratulus	23.75	v.Br.
Chaetopterus norvegicus	19.0	G.
Chaetopterus variopedatus	10.75–12.0	v.Br., D. & L.
Audouinia tentaculata	12.5–22.0	v.Br., D. & L.
Dasybranchus caducus	11.0	v.Br.
Arenicola marina	21.0	Delff, D. & L.
Owenia fusiformis	21.5	v.Br.
Pectinaria koreni	16.0–18.5	J., D. & L.
Amphitrite rubra	17.0	v.Br.
Terebella lapidaria	22.5	D. & L.
Terebella nebulosa	14.75	v.Br.
Lanica conchilega	29.0	v.Br.
Thelepus cincinnatus	18.5	G.
Sabella penicillus	14.0	G.
Spirographis spallanzani	29.0	v.Br.
Branchiomma vesiculosum	20.5	v.Br.
Myxicola infundibulum	23.5	v.Br.
Protula protula	15.5	v.Br.
Average % of dry org. mat.	18.4%	
Average % for all polych.	19.0%	

Species	% of dry org. mat.	*Authors*
Prosobranchs	about	
Gibbula cineraria	6–5	J.
Littorina littorea	5.0–6.0	J., G., Delff
Nassa reticulata	9.5	J.
Buccinum undatum	7.5–11.25	J., G.
Average % of dry org. mat.	7.8%	
Tectibranchs		
Philine aperta	14.0	J.
Acera bullata	13.5	J.
Average % of dry org. mat.	13.7%	
Lamellibranchs		
Nucula nitida	5.5	J.
Nucula nucleus	7.0	S. & K.
Venus ovata	7.0	S. & K.
Cardium fasciatum	7.5	J.
Mytilus edulis	4.25–6.5	G., Delff
Modiola modiolus	3.0	G.
Cultellus pellucidus	8.25	J.
Macoma baltica	5.0	S. & K.
Syndosmya alba	8.5	J.
Mya arenaria	6.0–10.5	J., Delff
Average % of dry org. mat.	6.6%	
Echinoderms		
Hippasteria phrygiana	12.5	Meyer
Asterias glacialis	8.25	G.
Asterias rubens	7.25	J., G.
Ophiura texturata	3.75	J.
Ophiura albida	4.0–7.0	G., S. & K.
Ophiopholis aculeata	7.5	G.
Ophiothrix fragilis	8.5	G.
Echinus esculentus	0.75–4.0	G., Meyer
Echinocyamus pusillus	6.75	S. & K.
Spatangus purpureus	3.5	Meyer
Average % of dry org. mat.	6.7%	
Crustaceans		
Gammarus locusta	16.5	Delff
Podocerus falcatus	13.5	S. & K.
Orchestia littorea	24.75	S. & K.
Crangon vulgaris	24.25	Delff
Leander adspersus	19.75	G.
Carcinus maenas	12.0–28.25	G., Delff
Nephrops norvegicus	17.75	Meyer
Eupagurus bernhardus	20.5	G.
Average % of dry org. mat.	19.6%	

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TABLE 2.—*Percentage of dry organic matter as compared with the rough alcohol weight in some marine bottom invertebrates*

From Jensen, *in* Petersen (1911) and Molander (1928a)

Species	% of dry org. mat.	*Authors*
Polychaetes	about	
Nereis sp.	14.5	Mol.
Nephthys sp.	14.0	Mol.
Lumbrinereis sp.	11.5	Mol.
Aphrodite aculeata	16.5	J.
Pectinaria koreni	13.75–15.0	Mol.
Eumenia crassa	16.5	Mol.
Maldanidae	12.0	Mol.
Melinna cristata	13.0	Mol.
Average % of dry org. mat.	14.0%	
Prosobranchs		
Littorina littorea	5.0	J.
Aporrhais pespelecani pespelecani	6.0	J.
Turritella communis	4.0	Mol.
Buccinum undatum	11.0	J.
Average % of dry org. mat.	6.6%	
Tectibranchs		
Philine aperta	13.5–14.0	J., Mol.
Acera bullata	13.5	J.
Average % of dry org. mat.	13.7%	
Lamellibranchs		
Nucula nitida	3.0	J.
Leda pernula	5.0	J.
Pecten septemradiatus	4.75–5.25	J., Mol.
Lima loscombi	12.5	J.
Venus gallina	5.0–6.0	J., Mol.
Cardium fasciatum	7.75	J.
Cardium edule	2.5	J.
Mytilus edulis	3.0	J.
Modiolaria nigra	7.0	J.
Cultellus pellucidus	6.25	J.
Cyprina islandica	3.0	J.
Macoma calcarea	7.5	J.
Macoma baltica	5.75	J.
Scrobicularia plana	5.5	J.
Syndosmya alba	7.0	J.
Lucina spinifera	5.5	Mol.
Astarte borealis	2.25	J.
Astarte montagui	2.25	J.
Astarte sulcata	1.75	J.
Spisula subtruncata	4.0–5.5	J., Davis
Corbula gibba	2.0–2.5	J., Mol.
Thracia papyracea	10.0	J.
Neaera abbreviata	7.0	Mol.
Mya truncata	8.25	J.
Mya arenaria	5.0	J.
Average % of dry org. mat.	5.4%	
Echinoderms		
Asterias rubens	5.5	J.
Ophiura texturata	2.0	Mol.
Ophiura albida	3.75	J.
Amphiura sp.	4.0	Mol.
Echinus esculentus	2.0	J.
Echinocardium cordatum	1–1.25	J., Mol.
Brissopsis lyrifera	1.25	Mol.
Average % of dry org. mat.	2.8%	
Crustaceans		
Diastylis rathkei	1.5	J.
Eudorella sp.	2.0	Mol.
Ampelisca and *Pontoporeia*	2.5	Mol.
Calocaris mc'andreae	8.25	Mol.
Average % of dry org. mat.	4.06%	

but this is not necessarily an expression for the available fish food, since some invertebrates with a high organic content may burrow too deeply to be caught, while others may be unpalatable to predators (Lindroth, 1935, p. 350–52; Einarsson, 1941). On the other hand, the eggs of some animals which seem to be nearly useless as food in the adult stage (in Danish seas the prosobranchs *Turritella* and *Aporrhais*) are eaten in large numbers by starfishes.

AVERAGE LIFE TIME AND RATE OF GROWTH PER YEAR

The next question to be solved, if we intend to approach the problems of true productivity, is that of the average life span and growth rate of level-bottom animals under natural conditions.

It is imperative to know whether an area comprising a certain amount of dry

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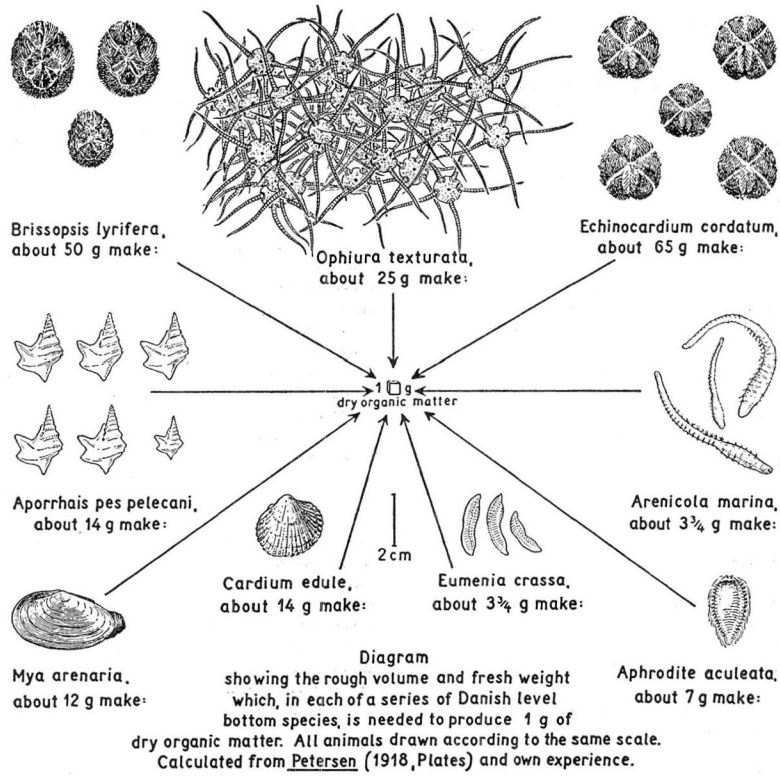

FIGURE 7.—*Volume and weight of each of a series of Danish level-bottom invertebrates needed to produce 1 g of dry organic matter*

Drawn by Poul H. Winther; G. Thorson dir. Orig.

organic matter is composed of several year classes of animals or of one year class only—or perhaps of animals occurring in such short seasons that they need only a few months to grow up and disappear. As examples of different life cycles we may mention the following: The high-arctic East Greenland fjords seem to be inhabited on an average by roughly 6 to 8 (for some species even 12 to 14) year classes of invertebrates at the same time (Thorson, 1936, p. 95–106), which means that the organic matter present has required 7 years to accumulate. In the W. Limfjord (northwest Denmark) the animal stock found per square unit seems to be based on a single 1-year class (Petersen, 1911, p. 66). Finally, in the brackish Åland-sea and Bottensea between Sweden and Finland, large areas of level bottom are dominated by numerous individuals of the small amphipod *Pontoporeia affinis* (Hessle, 1924, Table 5A). The females live in shallow water for 1 year only, while all males die off immediately after mating half a year earlier (Segerstråle, 1937, p. 171), so that quantitative samples from the summer or autumn seasons will include a whole generation, females as well as males, while samples from the winter or spring seasons will include only half a generation, the females. Autumn samples will therefore give too high an impression of the "productivity," while winter samples will be too low.

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Existing information about the life expectancies of various species under natural conditions is fragmentary, and that which is available must be used with caution. Some species have a faster growth and mature earlier and have a shorter total life expectancy in warmer waters, while others have physiological races which are of about the same life expectancy in different parts of their range. In general, with the exception of lamellibranchs, the females have a faster growth rate, later maturation, and longer life expectancy than the males. Then we must remember that theoretical life expectancies, which may be terminated by "endogenous senescence" (Deevey, 1947), are rarely encountered in nature. *Syndosmya alba*, for example, which may live as long as 3 or 4 years, is preyed upon to such a scale in the Limfjord that it is effectively an annual, and some polychaetes that may live at least 2 years will seldom survive a year of life. In such cases, however, spawning takes place in the first year so the species is able to maintain itself in the community. Other species may for the most part survive; such echinoderms as *Echinocardium cordatum* and ophiurans, which are eaten by few animals, belong to this group. There are also some lamellibranchs which after the first critical year may live out their lives in virtual immunity from all but the largest predators. MacGinitie (1939) is of the opinion that the more deeply burrowing clams have on an average a longer life span than the shallow burrowers.

The following list is compiled from the literature (and is based principally on lamellibranchs) to give an idea of the life expectancies of various bottom invertebrates. It must, of course, be used with the reservations discussed above:

One-year life cycles: most nudibranchiate gastropods (Løyning, 1922); the tectibranch *Aplysia punctata* (Eales, 1921); several small prosobranchs such as *Lacuna divaricata* (Havinga, 1922), *Rissoa membranacea*, and *R. inconspicua* (Petersen, 1913); the polychaetes *Nereis diversicolor* (18 months at Essex, Dales, 1951) and probably *Pygospio elegans* (Smidt, 1951, p. 93); and several of the smaller crustaceans: *Pontoporeia affinis* and *P. femorata* in shallow water (Segerstråle, 1937; 1938); *Corophium volutator* (Segerstråle, 1940); *Idothea neglecta* (Kjennerud, 1950); and *Sphaeroma hookeri* (18–20 months).

Two-year life cycles: the nudibranch *Dendronotus frondosus* (Larsen, 1925); the tectibranch *Acera bullata* (Blegvad, 1928, p. 37); the prosobranch *Hydrobia ulvae* (1–5 years, Quick, 1924, 1–1½ year in the Danish Waddensea, Smidt, 1951, p. 93); the lamellibranchs *Cardium fasciatum* (Blegvad, 1928, p. 37); *Spisula subtruncata* (possibly also 3 or 4 years, Davis, 1923, p. 21, p. 44); *Mactra stultorum* (Ford, 1923); *Cultellus pellucidus* (Mortensen, 1897; Jensen 1919); *Macoma baltica* at Scotland (Stephen, 1931); and *Paphia* (= *Tapes*) *undulata* (Winckworth, 1931); the polychaetes *Pectinaria koreni*, *Nephthys hombergi*, and *Scalibregma inflatum* (Blegvad, 1928, p. 37); and *Eunice fucata* (Mayer, 1902); and the echinoderms *Ophiura texturata* (2 years at least, Mortensen, 1897, p. 321) and *Stichopus japonicus* (at least, Mitsukuri, 1903).

Three-year life cycles: the tectibranch gastropods *Philine aperta* (2–4 years, Blegvad, 1928, p. 37; Brown, 1934) and *Bulla hydatis* (3–4 years, Berrill, 1931); the prosobranch *Nassa obsoleta* (3 years at least, Dimon, 1902); the lamellibranchs *Modiolaria discors* (3 years at least in East Greenland, Thorson, 1936), *Macoma baltica* (in the Limfjord, Jensen, 1919, p. 24), *Tellina fabula* (Scotland, Stephen, 1932), *Syndosmya alba* (Ford, 1923; Stephen, 1932), *Pecten* (*Chlamys*) *septemradiatus* (3–4 years, Allen, 1953, p. 259), and the echinoderms *Echinocardium cordatum* (Jensen, 1919, p. 28), *Luidia ciliaris* (3–4 years, Renouf, 1937) and *Ophiura albida* (2 years and 8 months at least, Möbius, 1873), and the crab *Carcinus maenas*.

Four-year life cycles: the lamellibranchs *Cardium edule* (Orton, 1926, p. 267; Stephen, 1932; up to 6 years at Holland, Kreger, 1940), *Tellina tenuis* (Stephen, 1931; 1932), *Cummingia tellinoides* (Grave

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1933), and *Corbula gibba* (Jensen, 1919); and the sea urchin *Echinus esculentus* (4 years at least, Elmhirst, 1922).

Longer life cycles: Asterias rubens lives 5–6 years (Bull, 1934), *Arenicola marina* 6 years (Thamdrup, 1935), and *Buccinum undatum* 10 years (Dakin, 1912), and among the lamellibranchs many species are known to have a long life. This for instance is the case for most of the Arctic species included in such genera as *Mya, Saxicava, Astarte,* and *Arca* (6–10 years, Thorson, 1936), and other individual examples are *Paphia* (= *Tapes*) *staminea* (7–10 years, Fraser and Smith, 1928a), *Tapes pullastra* (up to 8 years, Quayle, 1952), *Pecten yessoensis* (7 years at least, Bazikalova, 1934), *Cyprina islandica* (10–11 years, Lovén, 1929), *Cardium corbis* (7–15 years, Weymouth and Thompson, 1931), *Cardium* (= *Serripes*) *groenlandicum* (12–14 years, writer's observations in East Greenland), *Mya truncata* (8 years at least, Jensen, 1919), *Mya arenaria* (7–17 years, Newcombe, 1935), *Saxidomus giganteus* (9–16 years, Fraser and Smith, 1928b), *Siliqua patula* (13 years, Weymouth and others, 1931), and *Tivela stultorum* (up to 20 years, Weymouth, 1923).

For several of the species with a short life cycle (1 or 2 years), we know that they die off shortly after spawning, and even for a 4-year-species like *Tellina tenuis* Stephen (1932) has shown that there is a heavy mortality after breeding.

If we compare these figures with those for the animal communities in different sea areas, we find that the majority of quickly growing species with a short life cycle are absent from the Arctic seas and the deep sea. This tells us immediately that growth is on an average slow in Arctic animal communities and that several generations of the individual species are present at the same time on the same bottom area.

Vibe (1939, p. 17–22, Figs. 2–3) described from northwest Greenland a special *Cardium groenlandicum* zone of the *Macoma calcarea* community which, owing to the presence of this giant *Cardium*, looks extremely "rich" and may contain up to 3.5 to 4 kg (rough alcohol weight) per sq. m. In the stomach of a walrus which had foraged at 35 m depth on the *Cardium* of this zone, Vibe (1950, p. 32–33, p. 44) found 795 *Cardium*. Vibe calculated that the walrus had to take *Cardium* from about 200 sq m of bottom to obtain this quantity of food. These stripped areas, which a few hours earlier looked so rich, will be deserts to the walruses for several years afterward since a new population of *Cardium* requires 12–14 years to grow to full size. This may be at least part of the explanation of the extensive food migrations in walrus (Vibe, 1950, p. 23–29).

It does not follow from this that slowly growing forms with a long life are absent from temperate and warm seas. We have *Macoma* communities in the Arctic, in boreal seas, and off the east and even west coast of tropical Africa. In all cases these communities seem to have a slow growth and to consist of rather long-lived species. Temperate and tropical seas do have, however, communities with a rapid growth, an early maturity, and a short life (example: the *Syndosmya* communities). This short natural life is normally shortened by predation, and the problem for such animals is to mature early enough that each generation may reproduce before it is eaten. This latter mode of balance is very near the optimum for total productivity of a community. A rich population will grow up quickly, will breed when only about 10–11 months old, and then disappear before its young are settling from the plankton. Since the young stages have a quicker rate of growth than do the old ones (the very old ones nearly stop growing) which have now disappeared, they will contribute much more to a high productivity than will the adults. For most populations of bottom invertebrates which must maintain their stock in spite of the attacks of predators, the urgent problem is not how long they may live under optimal condi-

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tions, but how early they are able to spawn to recruit their next generation on the bottom with a surplus large enough to maintain their populations.

To the ecologist studying productivity the problem is intricate and many-sided. (1) He must know how many generations of the same species he is dealing with in his samples—*i.e.*, how many years' production he has before his eyes; (2) he must try to find out how many years the individual species requires to attain a reproductive rate large enough to secure the next generation; and (3) in most cases he must find out how large a percentage of each generation present in his samples has already disappeared during the period from settling to its present age.

If the animal community comprises several overlapping generations of the same species, this means that the community will have a very constant appearance with ionly small fluctuations from season to season and from year to year. A few samples n whatever season they have been taken, will always give a good impression of this type of community, for instance a *Macoma* community. If only one short-lived generation of each species is present in a community, and if at the same time the community is recruited by pelagic larvae, large fluctuations from season to season and from year to year may occur, and for this type of community, for instance a *Syndosmya* community, series of samples taken at different seasons and in successive years are needed to get a true impression of the community.

We have already seen that for most species endogenous senescense plays a much smaller part as a reducing factor than does predation. Blegvad (1928, p. 37) gives a most striking example: square units of level bottom, which in the W. Limfjord were protected by wire netting from the predation of bottom fishes, contained after one summer up to 60 times as many specimens of *Syndosmya*, *Tapes*, *Cardium*, and *Pectinaria* as the neighboring, unprotected square units where the fishes had been allowed to forage. The findings in our samples will thus normally be only a smaller or larger fraction of the number of specimens present at the moment of settling. As we approach the next spawning season the number of surviving individuals decreases; this, however, does not necessarily mean that the animal weight is also correspondingly reduced, since the surviving specimens, now less restrained by competition, may compensate for the loss by a quicker rate of growth.

Jensen (1919, p. 8–15) gives a detailed review of these problems and of the whole technique of calculating the true annual production of a level-bottom area examined twice a year—*i.e.*, in spring before a new spatfall sets in, and in autumn. A special calculation is needed for each species, and in the papers cited only the dominating fish-food animals have been considered. The annual animal production which is to be determined must be found by comparing the stock, the consumption, the growth increment, and the upgrowth. These terms are defined as follows:

Stock: the quantity of the individual species, expressed in living (or rough) weight per square meter. The rest stock is the amount which is left of the stock in the following spring.

Consumption: the quantity of the individual species eaten during a year (living or rough weight per sq m), calculated from one series of spring samples to the next.

Growth increment: the increment of the stock (in living or rough weight) during 1 year, to the death of the individual specimens.

Upgrowth: the weight of the new brood (*i.e.*, the "O group"), per sq m (*i.e.*, "recruitment").

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Animal production: the sum of growth increment plus upgrowth.

On the basis of the figures found for the lamellibranch *Cultellus pellucidus* in the Limfjord 1912–1913, Jensen gives a diagram for the productivity as living or rough weight in g per sq m (Fig. 8).

For this calculation, which of course is possible only if the different year classes can be distinguished, the stock, the rest stock, and the upgrowth (recruitment) are determined directly. The consumption = $(a \div a_1)x$ and the growth increment = consumption + rest stock ÷ stock. For details and further examples, *see* Jensen (1919, p. 13).

For communities like those treated by Jensen the animal consumption is so large that a series of bottom samples taken at random in any one season will give us no true idea of the maximum population the bottom area might support. Estimates based on samples from any season may, however, be made for high arctic and deep-sea communities.

Another possible way to estimate the productivity of a community may be from the predators. In the fjords of northeast Greenland, for example, there are no preda-

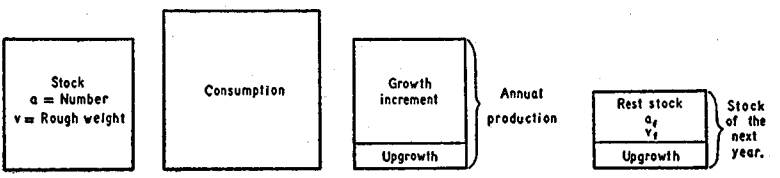

FIGURE 8.—*Diagram for calculations of the animal production of the individual species of level-bottom invertebrates in the Danish Limfjord*

For explanation *see* the text (from Boysen Jensen 1919).

tory bottom fish, and there are few enemies of bottom invertebrates other than a few carnivorous prosobranchs. There are also a few scavenging prosobranchs and omnivorous ophiurans. In such a community there is a very high survival of the new brood (the "O group"). In such regions as the Limfjord, the Doggerbank, and the Wadden-sea, however, up to 90 per cent or more of the O group disappears during the first year. It would appear that the part played by predators in arctic communities is negligible, or that conversely the productivity of prey species is so low that only a few predators can be supported. Since fishes are the highest link in the food chain, they are the most expensive in terms of the community and may be expected to be absent from areas where productivity is poor or slow. A less expensive link in the food chain is composed of the invertebrate predators. There may, however, be a situation in which the bottom area is too unproductive to maintain even invertebrate macropredators. The presence or absence of certain groups of invertebrate macropredators may give us an indication of the rate of production in Arctic and deep-sea communities, which cannot be obtained from a random series of samples of the forage animals, since we do not know their age and rate of growth.

MAIN FEATURES OF PRODUCTIVITY ON THE LEVEL BOTTOM

In Arctic (and Antarctic) coastal areas productivity is low, several generations overlap, growth is slow, maturity sets in rather late, and the life cycles are long. In

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temperate and tropical coastal areas we may find bottoms with a low productivity (*e.g.*, *Macoma* and *Tellina* communities) and others with a very high productivity (*e.g.*, *Syndosmya* communities, tropical crab communities). In large fjord areas and in gulfs with narrow mouths the productivity as well as the weight of the standing crop will gradually decline with increase in distance from the open sea (except the Sea of Azov; *see* Chapter 25). This decline seems to be especially pronounced in areas where the mouth is provided with a sill or "threshold" (The Mediterranean, the White Sea, etc., *cf.* Spärck, 1931, p. 3–4; 1935, p. 3–5). This may be demonstrated (Fig. 9) on the basis of personal observations from the East Greenland fjords and the Persian Gulf—a high—arctic sea area and the warmest sea area of our globe. The tendency of both waters is the same, and the smaller weights per square unit in the Persian Gulf as compared with those from Scoresby Sound are most probably compensated for by a quicker growth rate and much heavier predation in the tropical area.

The graphs from Scoresby Sound clearly demonstrate another main feature—the decrease in the standing crop from the surface toward deeper water. The Foraminifera community in the Scoresby Sound area at 200–350 m depth had an average weight of 10–15 g/m^2 (Thorson, 1934, p. 53), and in several localities between 300 and 600 m in the still more narrow Franz Joseph Fjord the weight dropped to 1–2 g/m^2 (Spärck, 1933, Table 4; *see* also Zenkevich, 1927; Idelson, 1933, p. 67).

But what about the very deep sea? The Danish Deep Sea Expedition, 1950–1952, obtained 7 good hauls with the $\frac{1}{5}$ sq m Petersen grab from tropical deep-sea bottoms between 6000 and 10,000 m, and 59 hauls from 1000 to 6000 m (Spärck, 1951b; 1952). From these samples Spärck estimated " . . . that the density of animal life at the bottom of the oceans is in the order of 1 g per sq. m. This is an astonishingly high figure considering that in productive coastal waters it is generally a few hundred grammes." But what does this figure tell us about the productivity? First of all, the estimate of about 1 g/m^2 seems to be somewhat high, since the smallest animals were not weighed but were estimated to weigh about 10 milligrams, which for many was much more than their actual weight (information courtesy the staff who sorted out the samples). Secondly, the content of dry organic matter (though no direct analyses are at hand) seems to be very small in most bottom invertebrates from the deep sea. On the basis of work in the Gullmarfjord (120 m deep) Gislén (1930, p. 133) stated that "Within a systematic group the shallow water forms generally show higher dry-weights than the deep-water ones." The principal animals found at 9765 to 10,189 m in the Philippine Trench were small actinians, and synaptid holothurians belonging to the genus *Myriotrochus* (Bruun, 1951; depths later corrected). The content of dry organic matter of these transparent water-filled animals is probably not more than about 2 per cent of their living weight. The rate of growth for these actinians and for *Myriotrochus* is unknown, but actinians, even those inhabiting shallow water, are known to have a very long life. Ashworth and Annandale (1904) mentioned a *Sagartia troglodytes* kept in captivity for nearly 50 years. Hausding (1913) mentioned an observation by Dalyell that *Actinia equina* has lived in the aquarium for 66 years. Parker (1899, p. 48) reports that many actinians live longer than a man, and MacGinitie (1949) is of the opinion that actinians may live to 300 years. As cold-sea areas are already known to be inhabited by slowly growing, long-lived species, and as the

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deep sea is a cold sea, it seems reasonable to assume that deep-sea actinians may have a still longer life than the shallow-water ones.

If we accept Spärck's estimate of 1 g/m² wet weight for the deep sea as the absolute maximum, this corresponds to about 0.02 g dry organic matter per sq m, and it seems very probable that 50 years or more is required to produce this quantity of

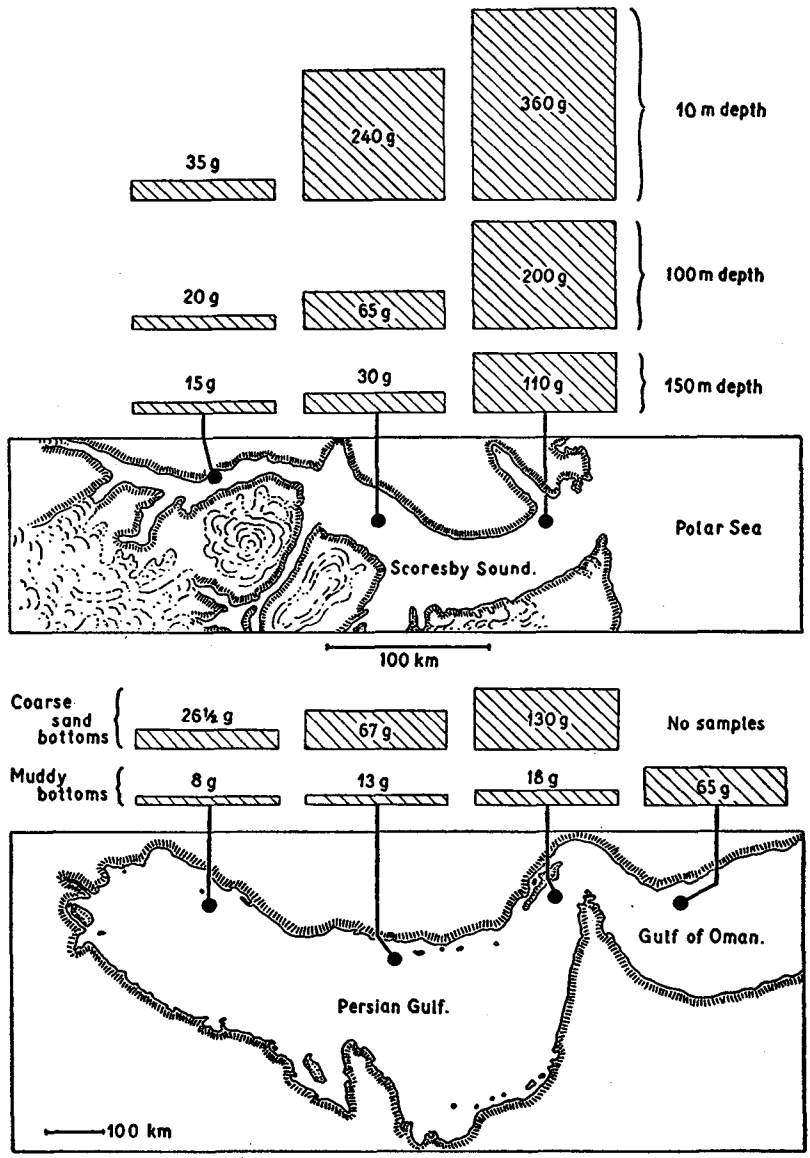

FIGURE 9.—*Diagram showing the parallelism in distribution of the "standing crop" between Arctic and tropical fjords and bays*

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organic matter. If so, the figure for the wet weight of the standing crop which Spärck considered "astonishingly high" actually indicates an extremely poor productivity—a productivity which at the greater depths is probably too low to support any stock of invertebrate macropredators. The greatest depths from which representatives of the different invertebrate groups have been recorded provide some interesting information in this context. (*See* Chapter 22.) If we focus upon the macropredators, we find the greatest depths so far recorded to be: for crabs about 5200 m, for brittle stars 6600 m, and for starfish 7630 m, while representatives of such groups as Actinia, Echinoidea, Holothurioidea, Lamellibranchia, Polychaeta, Amphipoda, Isopoda, Tanaidacea, Sipunculoidea, Crinoidea, and Gastropoda which are either nonpredatory, omnivorous, or at most micropredators or scavengers have been found significantly deeper—8210–10,190 m (information courtesy Dr. A. Bruun). The results of the recent Russian deep-sea investigations in the Kurile-Kamchatka trench (Zenkevich, 1954) show a similar tendency: the greatest depth registered for crabs ("Crustacea Decapoda") was 4600 m and for starfish 7700 m (ophiurans were not registered), while such nonpredatory groups as Octocorallia and the smaller Crustacea were still present at 8700 m, Actinia and Mollusca at 9200–9300 m, and Polychaeta and Holothuria at 9800 m depth.

This macropredator test again seems to strengthen the conjecture that growth and accordingly productivity is extremely slow in the deepest parts of the ocean.

ZoBell (1953), in his remarkable studies on deep-sea bacteria, has given a most interesting calculation of bacterial productivity in the Philippine Trench—a minimum of 8.76 g organic carbon produced per year per sq m in the topmost centimeter of mud. When compared with the figures for the productivity of deep-sea Metazoa, these figures for bacteria seem to be astonishingly high. This striking contrast seems to lead to the conclusion that these bacteria play an insignificant part as food for the Metazoa living there. The explanation for this may be rather complicated, and our recent knowledge does not permit the full answer. Several marine-bottom invertebrates do reject bacteria as food. Davis (1953, p. 349) has shown that none of the 13 species of marine bacteria tested to date was used as food by larvae of the American oyster, *Crassostrea virginica*. The possibility may also occur that several of the bacteria are eaten by Protozoa, and even if such Protozoa are again eaten by the Metazoa this means an extra link in the food chain, which is always a heavy waste.

ZoBell (1953) has proved the fundamental influence of water pressure on the growth and reproduction of his deep-sea bacteria. It therefore seems reasonable to consider whether this enormous pressure in the deep sea may radically increase their rate of growth of the Metazoa. If so, we may have underestimated their yearly production. For eggs of the fish *Fundulus*, pressure corresponding to about 140 kg/cm² (1900 pounds per square inch, Draper and Edwards, 1932, p. 106) causes no evident changes in the cell constituents but does slow down the rate of cell division, which would retard rather than increase growth. Apart from this, weighty reasons seem to speak against such a conjecture—above all, the fact that several species of deep-sea Metazoa, of exactly the same morphological appearance, are found in large numbers in high-arctic fjords at depths of 100 m or less (personal experience). Their rates of growth at these small depths are known to be slow, and although they may be represented in the deep-sea bottom in a different "physiological race" from that on the arctic shelf, their main structure is the same throughout their range. The writer's experience with other types of physiological races, for instance those adapted to different temperatures, seems to show only

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a gradation but no "revolution" in behavior from race to race (*cf.* Thorson, 1951): they may for instance double their metabolic rate or they may reduce it to half the average, but all "races" will tend to realize the "average responses" of their species in the milieu in which they live. Hence, it seems hardly possible that a "race" able to stand the conditions of pressure in the deep sea should have a rate of growth and productivity fundamentally different from that found in a shallow-water "race" of the same species in high-arctic regions.

It thus seems justified to conclude that the standing crop of bottom invertebrates in the very deep sea (calculated as dry organic matter) is very poor, and, because its rate of growth is extremely slow, the total yearly productivity is so small that, at the greatest depths, it is not sufficient to support a stock of invertebrate predators.

REVIEW OF LEVEL-BOTTOM ANIMAL COMMUNITIES AND THEIR DISTRIBUTION

Spärck attempted (1935; 1936) to give the first review of marine-animal communities, and Jones (1951) made a new attempt for the communities of the boreal area of the North Atlantic. These papers have proved most useful to the writer. Several papers in recent years have, however, widened our basis for comparison and accordingly also helped us and obliged us to revise some of our views.

Miyadi, Habe, and Yamamoto, working with small samples taken with Ekman-type grabs for a fairly large area of the Japanese coast, have often based their communities on the animals from less than 2 sq m. Such small samples also mean that the smaller animals (polychaetes, amphipods) are emphasized, and the animals which these authors regard as "characteristic" are quite different from those they might have chosen if a similar number of samples had been taken by a Petersen grab, and if their results had been compared with "parallel" samples from other seas. Thus Miyadi's (1941d, Fig. 3) "*Maldane sarsi-Terebellides* community" from Ago Wan is in reality a typical and well-defined *Amphiura* community (up to 250 *Amphiura rosea* m^2), and his "*Cardium hungerfordi* community" described in the same paper is an equally well-defined *Macoma incongrua* community (about 100 individuals m^2). Similarly, a series of small "associations" described by Miyadi (1940b) from Osaka Wan indicated a *Brissopsis luzonica* community when treated on a large scale using a Petersen grab. In such cases the writer has revised the communities described and in each case has given the reasons for the revision. In some cases it has also been necessary to discuss inadequately known communities; this has been done only to stimulate future students to learn more about them.

In the following review the word "Iso-community" has now and then been used in reference to communities which, though inhabited by other genera, are so closely related to the communities we are going to compare them with, in their morphological structure and their ecological characteristics, that they may be regarded as "ecological parallels". (*Cf.* Tischler, 1950, p. 39; 1951, p. 138; Caspers, 1950a, p. 58.)

This new attempt to review the level-bottom communities leaves, however, several questions unsolved, but for each new region examined the fact stands out more clearly—that the same types of bottom are everywhere inhabited by series of "parallel" animal communities, in which different species, of the same genera, replace one another as "characterizing species."

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MACOMA COMMUNITIES (Fig. 11)

General characteristics: Shallow-water communities mainly bound to estuarine conditions and found from the tidal zone to depths of 10–60 m or deeper. Characterizing genera: The lamellibranchs *Macoma*, *Mya*, and *Cardium* (in some cases also *Scrobicularia*), ± the polychaete *Arenicola*. On all types of mixed bottoms, increasing amounts of silt or mud will lead to dominance of the deposit feeders *Macoma* and *Arenicola*, increasing amounts of sand to dominance of the suspension feeder *Cardium*. The characterizing species seem to have a long life, a slow growth often arrested during winter, and a late maturity. The standing crop will therefore comprise several generations and give an impression of richer productivity than justified. Fluctuations from year to year are relatively small. Where there is a heavy population of young flounders, they preferably do not feed on the macrofauna but on the microfauna (especially harpacticoids) living in the same locality.

1. MACOMA CALCAREA COMMUNITY (Fig. 10) (The Arctic *Macoma* community). Described by Thorson (1933; 1934) from the East Greenland fjords. Characterizing animals: *Macoma calcarea, Mya truncata, Cardium ciliatum, Cardium* (= *Serripes*) *groenlandicum, Ophiocten sericeum, Pectinaria granulata* and *Astarte borealis, A. elliptica*, and *A. montagui*. From (0) 4 to 50–60 m depth. In the Barents Sea and around Spitzbergen to 100–130 m depth. Mixed bottoms. Increasing amounts of silt may lead to dominance of actinians (*Halcampoides*) or to transition to a *Portlandia* community. Increasing amounts of sand lead to a dominance of *Cardium groenlandicum* and *C. ciliatum* (the main food of the arctic walrus banks) or to a transition to a *Venus fluctuosa* community (*cf.* Zenkevich, 1930).

   DISTRIBUTION: Circumpolar. Barents Sea and White Sea, Kanin Peninsula, Murman coast (Zenkevich, 1927; 1930; Zenkevich *et al.*, 1928; Brotskaya and Zenkevich, 1932); Spitzbergen with surrounding banks (Brotskaya, 1930; Idelson, 1930); Jan Mayen, N.E. Greenland fjords, Angmagssalik (Thorson, 1933; 1934; Parat and Devillers, 1936; Bertelser, 1937); N.W. Greenland (Vibe, 1939, 1950); E., N., and W. Iceland, mostly in inner fjords (Spärck, 1929; 1937; Einarsson, 1941); Ramfjord, N. Norway (Soot-Ryen, 1924); the Faroes, mostly inner fjords (Spärck, 1929); Peter the Great Bay, Japan Sea (making here the inner border of a *Venus fluctuosa* community, Deryugin and Somova, 1940). Occurring, probably as a survivor from the glacial period, by Cape Lindesness and Oslo fjord, S. Norway (Petersen, 1915; Broch, 1927), in the southernmost part of the Danish Belts, and in the Baltic around Bornholm (Petersen, 1913; Hagmeier, 1926; 1930a).

2. MACOMA BALTICA COMMUNITY (Fig. 10) (The boreal *Macoma* community). Described by Petersen (1913; 1918) from inner Danish waters. Characterizing animals: *Macoma baltica, Mya arenaria, Cardium edule, Arenicola marina, Hydrobia ulvae*, and *Corophium volutator*. From the tidal zone to 8–10 m depth, in the Baltic as deep as 140 m. Mixed bottoms. Increasing amounts of silt lead to dominance of *Arenicola* and *Corophium* (and often *Scrobicularia plana*) or, in deeper water, to a transition to the *Syndosmya alba* community. Increasing amounts of sand lead to dominance of *Cardium edule* or to transition to a *Tellina tenuis* community (in quite shallow water) or a *Venus gallina* community (in deeper water). Certain large brackish-water areas (Zuidersee, Holland; Ringkoebing fjord, Denmark) show a great preponderance of *Mya*. The community obtains the best conditions for high weights and growth in wadden areas.

   DISTRIBUTION: the sea of Bothnia, the Åland sea, the Baltic (Hessle, 1923; 1924; Hagmeier, 1926; 1930a; Segerstråle, 1933); inner Danish waters (Petersen, 1911; 1913; 1918; Larsen, 1936); Ringkoebing fjord (Blegvad, 1935); Danish wadden sea (Thamdrup, 1935; Smidt, 1951); German wadden sea, Frisian islands, German bay, mouth of river Elben (Hagmeier, 1923; 1930b; Wohlenberg, 1937; Linke, 1939, Caspers, 1952); the Zuidersee (Havinga, 1922); the Norwegian coast from Oslo fjord (Petersen, 1915) to Ramfjord (Soot-Ryen, 1924); Scottish coast (Stephen, 1930; 1931; 1933; 1934), English North Sea coast (Blegvad, 1922; Mistakidis, 1951). It further occurs, probably as a survivor from a warmer period, along the west Murman coast (Guryanova *et al.*, 1930, p. 79–80), in the littoral of the Kola Fjord (Guryanova *et al.*, 1929), and in the White Sea (Zenkevich, 1927) and in the arctic part of the Pacific (Shantar Sea, Zachs, 1929). *M. baltica* still occurs as a nondominant member of the *Macoma nasuta* community in the Vancouver region.

3. MACOMA NASUTA-MACOMA SECTA COMMUNITY (The N.E. Pacific *Macoma* community) (Fig. 10). Described by Kirsop (1922) and by Shelford and Towler (1925) from the San Juan Archipelago in the Vancouver-Seattle region. Characterizing animals: *Macoma nasuta, M. secta, M. inguinata, M. baltica, Cardium corbis, Mya arenaria* (introduced), *Arenicola claparedei, Schizothaerus nuttalli*, and *Panope generosa*. From the tidal zone to 8–10 m. Mixed bottoms. Increasing amounts of mud give preponderance of *Macoma nasuta*. Increasing amounts of sand give a preponderance of *Cardium corbis*, and, as was also the case in the *Macoma baltica* community, the dominance of *Mya arenaria* is especially pronounced in brackish areas (MacGinitie, 1935, p. 656, 730).

   DISTRIBUTION: From the San Juan Archipelago (Kirsop, 1922; Shelford and Towler, 1925; Shelford, 1935; Wismer and Swanson, 1935; Clements and Shelford, 1946, p. 335); San Francisco Bay (Packard, 1918—probably much reduced by pollution in recent years), to Southern California (MacGinitie, 1935; 1939; Ricketts and Calvin, 1952, p. 300). Gislén (1931, p. 430) from Misaki in Japan mentions a littoral *Balanoglossus* community living on rather pure sand. Among the animals inhabiting this community is *Macoma nasuta*, which possibly might be taken for an indication of this community also in Japanese seas.

4. MACOMA INCONGRUA COMMUNITY (Fig. 11) (The N.W. Pacific *Macoma* community). Figured and described

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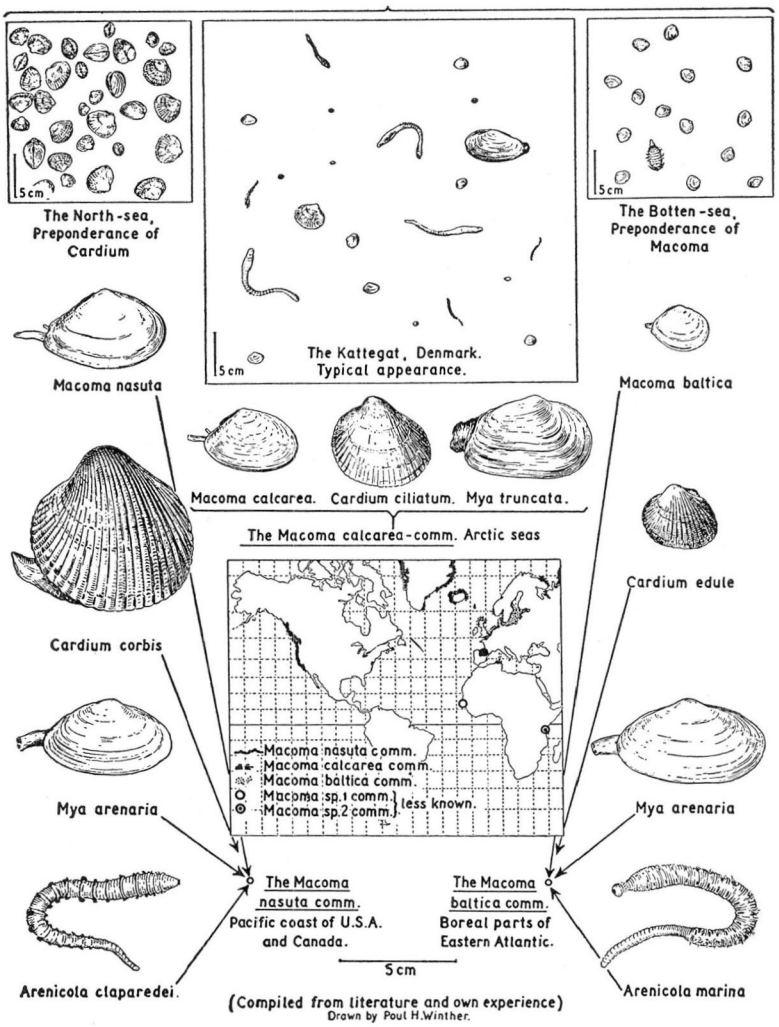

FIGURE 10.—*Diagram showing the parallelism between the Arctic, the boreal, and the Northeast Pacific* Macoma *communities*
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from Ago Wan, Japan, by Miyadi (1941d, Fig. 2; *cf.* also his list p. 179) as a "*Cardium hungerfordi-Dentalium octangulatum* community. Characterizing animals: *Macoma incongrua* (according to Fig. 2 about 100 individuals per sq m), *M. tokyoensis, M. awajensis, Cardium hungerfordi* (according to Fig. 2 about 650 individuals per sq m), *Dentalium octangulatum*. In shallow water, exact depth not indicated. Mixed bottoms.

DISTRIBUTION: Covering the majority of the bottom areas in the Ago Wan, Kii Peninsula, Japan.

Prof. R.Spärck found in 1951 indications of a *Macoma* community off Mombassa, E. Africa. A few quantitative samples were taken but have not yet been worked up. The writer found in March 1952 indications of another *Macoma* community in the outer estuary of Salumne, Senegal, French West Africa, but had neither time nor equipment to study it closer.

Besides these "pure" *Macoma* communities we often find communities from which some of the characterizing species are absent. The *Macoma baltica* community in its pure form does not seem to occur south of the Channel. *Mya arenaria* has its most southern occurrence off the French Atlantic coast, *Arenicola marina* and *Macoma baltica* are known to enter the Mediterranean but are rare here, and only *Cardium edule* occurs here in

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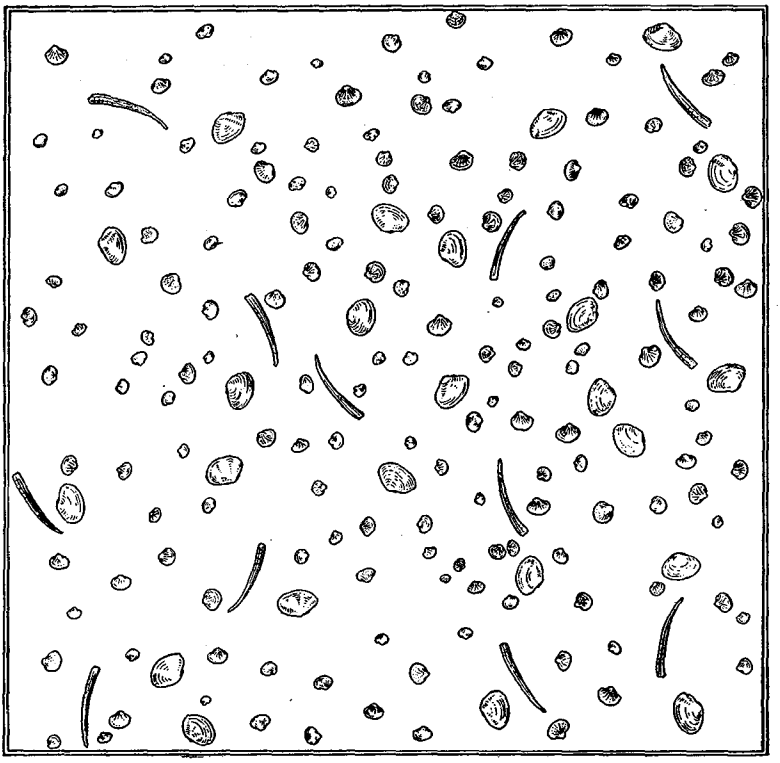

FIGURE 11.—*Northwest Pacific* Macoma incongrua *community*

The figure comprises the number of animals found per ¼ sq m level bottom. The characterizing species are: *Macoma incongrua*, *Cardium hungerfordi*, and *Dentalium octangulatum*. Calculated and redrawn on the basis of Miyadi (1941d, Fig. 2).

some quantity, making a *Cardium edule* community which probably must be regarded as a strongly "reduced" *Macoma* community, in which *Scrobicularia plana* often seems to replace *Macoma baltica*.

Thus a *Cardium edule-Scrobicularia plana* variety is known from Ria de Faro, Portugal, sandy-silty waddens (Vilela, 1947, with *Tapes decussatus*), a *Cardium edule-Hydrobia acuta* variety is known from the shore to 10 m depth off the coast of Romania, Black Sea (Borcea 1931; Caspers, 1951), and a pure *Cardium edule* variety seems to be indicated from estaurine waters at Tunisia (Bruun, 1940). The *Cardium lamarckii-Scrobicularia plana* community described by Vatova (1940a, Pls. IX, X) from Laguna Veneta, Adriatic Sea, shows a close similarity to the Portuguese variety, though the species of *Cardium* is different.

TELLINA COMMUNITIES

General characteristics: Shallow-water communities mainly inhabiting exposed beaches from the tidal zone to 5–10 m depth, or rarely deeper. Characterizing genera: The lamellibranchs *Tellina*, *Donax*, and *Dosinia*; the echinoderm *Astropecten*; and, in tropical regions, the prosobranchs *Terebra* and *Ancilla*. On pure bottoms of often very hard sand. The characterizing species seem to have a long life, a slow growth, and a rather late maturity; the standing crop thus comprises several generations. In fact these communities have a rather small productivity. Communities of this type seem to be absent from the arctic regions. Fluctuations from year to year are relatively small [except *Donax*, etc., on beaches; *see* Chapters 19 and 28. *Ed.*]

1. TELLINA TENUIS-TELLINA FABULA COMMUNITY (The boreal Lusitanian *Tellina* community). Described by Stephen (1930; 1933) from the Scottish coast. Characterizing animals: *Tellina tenuis*, *Tellina fabula*, *Donax vittatus*, *Nephthys coeca*. From the tidal zone to about 10 m depth. Pure sandy bottoms. In very hard pure sand there is a preponderance of *Tellina tenuis* and *Donax*, in looser sand with only a slight mixture of silt *Tellina*

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fabula will be in majority (in Scotland to about 40 m depth) and will in deep water form a transition to the *Venus gallina* community.

DISTRIBUTION: Danish North Sea coast (writer's observations), German North Sea coast off the mouth of the river Elbe and off the E. Frisian islands (Hagmeier, 1930b; Caspers, 1952), Scottish North Sea coast (*T. tenuis* in the very beach gradually replaced by *T. fabula* at somewhat greater depth, Stephen, 1930; 1931; 1933; 1934). A special variety of it with *Tellina tenuis, T. incarnata* (most common), and *Astropecten bispinosus* is found on the sand flats by Ria de Faro, Portugal (Vilela, 1947).

2. TELLINA DISTORTA-TELLINA DONACINA COMMUNITY (The Mediterranean *Tellina* community). Described by Vatova (1934; 1935; 1936; 1949) as a *Tellina* community and partially as a "*Loripinus fragilis* community," from the Adriatic Sea. Characterizing animals: *Tellina distorta, T. donacina* (in the Black Sea *Tellina exigua* replacing *Tellina distorta*), *Donax julianae, Ophiura albida*. From the shore (4 m) down to at least 24 m depth. Pure sandy bottoms.

DISTRIBUTION: Northern part of the Adriatic Sea (Vatova, 1949) and the coastal zone off Romania, Black Sea (Borcea, 1931). Too few samples and localities are known to give a general characteristic of this community.

3. TELLINA TENERA COMMUNITY (The N.W. Atlantic *Tellina* community). Described by Lee (1944) from Menemsha Bight, at the New England coast of U.S.A. Characterizing animals: *Tellina tenera* and the sand crab *Emerita talpoida*. From 2 to 5 m depth; pure yellow sand. Hitherto known only from the type locality. Further details on its composition highly desired. A community of the same type, consisting of, among others, species of *Tellina, Donax, Dosinia, Astropecten, Terebra*, and the crustacean *Emerita* is mentioned by Hedgpeth (1953, p. 185–188) from the inshore part of the Texas coast, but no quantitative data are given.

4. TELLINA LILACINA COMMUNITY (The New Zealand *Tellina* community). Described by Oliver (1923, p. 539–540) from New Zealand. Characterizing animals: *Tellina lilacina, Dosinia subrosa*, and the prosobranchs *Ancilla* (= *Baryspira*) *australis* and *Terebra* (= *Pervicacia*) *tristis*. In tidal zones with fine clean sand (Oliver, 1923; Powell, 1937). Hitherto known only from the type locality.

A community very similar to the New Zealand one described above and including the prosobranchs *Ancilla* (= *Olivancillaria*) *hiatula* and *Terebra micans* has been observed by the writer on the surf-beaten sand beaches of St. Louis, Cayar, and Yoff in Senegal, French West Africa, but no details are available.

VENUS COMMUNITIES

General characteristics: Communities associated with the open sea and found on sandy bottoms from 7–10 to 30–40 m depth. Characterizing genera: the lamellibranchs *Venus, Spisula* (or *Mactra*), *Tellina* and *Thracia*, the prosobranch *Natica* (= *Polynices*), the starfish *Astropecten*, and the polychaete *Ophelia* ± the irregular sea urchins *Echinocardium* or *Spatangus*. On loose sand *Spisula* will often be preponderant, and increasing amounts of silt will gradually lead to a *Syndosmya* community or an *Amphiura* community. Where the sand tends to harden *Tellina* will be the dominant species finally to form a pure *Tellina* community. Where the sand is coarse and more or less mixed with shell gravel (the so-called "*Branchiostoma* bottom") *Spisula* and *Tellina* will be represented by larger species with more solid shells, and *Branchiostoma* and a characteristic microfauna (*Polygordius, Caecum*, small nudibranchs) will appear. The productivity of these communities depends entirely on their composition. Where *Tellina* and *Venus* are preponderant, growth rate and rate of maturity are slow, and the productivity is only moderate even where the standing crop seems to be rich in individuals (several generations and therefore only small annual fluctuations). Where *Spisula* or *Mactra* is dominant, both having a quick upgrowth, an early maturity, and a short life, the productivity may reach figures which are among the greatest known from the sea bottom, and such areas, though the community may fluctuate enormously from year to year, are excellent growth centers for young flounders.

1. VENUS FLUCTUOSA COMMUNITY (The arctic *Venus* community). Described by Thorson (1934) from Scoresby Sound, E. Greenland. Characterizing animals: *Venus fluctuosa, Thracia truncata, Pandora glacialis, Euchone analis, Scoloplos armiger, Astarte borealis, A. elliptica. A. montagui*. From 3–7 m to 20–30 m depth or deeper (80 m, N. Pacific). Pure sandy bottoms near the open sea. Increasing amounts of silt will lead to an intermingling with *Cardium groenlandicum* and *Cardium ciliatum* and finally to a pure *Macoma calcarea* community.

DISTRIBUTION: Circumpolar. Matotschkin Schar and Nowaya Zemlya (Uschakov, 1930, p. 123); Scoresby Sound, Kangerdlugssuak, and Angmagssalik in E. Greenland (Thorson, 1934; Bertelsen, 1937); Shantar Sea, Arctic Pacific (up to 1375 adult and 369 juvenile *Venus fluctuosa* per sq m, with *Parasabella maculata, Ampharete grubei*, and *Arenicola marina schantarica*; (Zachs, 1929, p. 32–35, and diagram p. 46); Peter the Great Bay, Japan Sea (up to 700 *V. fluctuosa* and 14,500 crustaceans per sq m, preferably *Ampelisca macrocephalia*; Deryugin and Somova, 1940).

2. VENUS GALLINA COMMUNITY (The boreo-mediterranean *Venus* community) (Figs. 2, 12). Described by Petersen (1913; 1918) from inner Danish waters. Characterizing animals; *Venus gallina, Spisula elliptica, Tellina fabula, Mactra stultorum, Psammobia* (= *Gari*) *ferroensis* ± *Echinocardium cordatum*. From 8–10 m to about 40–50 m depth. Loose sand means dominance for *Spisula*, and a more hard sand dominance for *Tellina*. Where *Spisula* is nearly absent the community is constant, but rather

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poor. Where *Spisula* is dominant the community is fluctuating from year to year, but with an extremely high productivity (the flounder areas of the Dogger Bank, Davis, 1923; 1925).

DISTRIBUTION: Inner Danish waters (Petersen, 1913; 1918; Blegvad, 1930); German Bay and the E. Frisian Islands (Hagmeier, 1923; 1930b); Dogger Bank (Davis, 1923; 1925; Ursin, 1952; Birkett, 1953); large areas of the southern North Sea (Blegvad, 1922); Scottish area of the North Sea (*Spisula* nearly absent, Stephen, 1931); Cumberland Sound (indications only, Jones, 1952); Plymouth (transition to *Syndosmya* community, Ford, 1923); S. of the Isle of Man (Jones, 1951); off Faro, Portugal (indications only, Spärck, 1931); off Paestum and Salerno, S.W. Italy (indications only, with *Astropecten johnstoni*, Spärck, 1931); middle and inner part of the Adriatic Sea (Vatova, 1934; 1935; 1936; 1940b; 1949, p. 70), off the coast of Israel (Wirszubski, 1953), and off the coast of Romania, Black Sea (3–27 m, with *Spisula subtruncata*, *Pectinaria koreni*, *Corbula mediterranea*, and *Nassa reticulata* (Borcea, 1931, p. 661–662, 665; Caspers, 1951).

3. VENUS VERRUCOSA COMMUNITY (The mediterranean *Venus* community). Described by Vatova (1934) from the inner part of the Adriatic Sea; *see* also Bacci (1946). Characterizing animals: *Venus verrucosa*, *Venus ovata*, *Tellina balaustina*, *Natica millepunctata*, and *Astropecten aurantiacus*. Exact depth not indicated. Mixed to purely sandy bottoms. Further details unknown.

DISTRIBUTION: Gulf of Naples (Bacci, 1946); inner parts of the Adriatic Sea (Vatova, 1934; 1935; 1936).

4. VENUS FASCIATUM-SPISULA ELLIPTICA-BRANCHIOSTOMA COMMUNITY. Described by Ford (1923) from Plymouth as "the deep *Venus* community." Characterizing animals: *Venus fasciatum*, *Spisula elliptica*, *Branchiostoma lanceolatum*, *Echinocyamus pusillus*, *Syndosmya prismatica*, *Dosinia exoleta* or *D. lincta*, *Ensis ensis*, *Tellina crassa*, the fish *Ammodytes lancea*, and ± *Spatangus purpureus*, *Echinocardium pennatifidum*, and *E. flavescens*. From about 10 to about 300 m depth. On shell gravel ("*Branchiostoma* bottom") in shallow water and on sand at greater depths. On such sand in deep water (S.W. Iceland, the Faroes, and the North Sea) *Spisula elliptica* is preponderant (up to 1100 individuals per sq m, S.W. Iceland, Spärck, 1929), the upgrowth is quick, and the productivity is fairly large (Einarsson, 1941, p. 18–19; Spärck, 1929, 1937; Blegvad, 1922; Stephen, 1934). On coarse shell gravel with *Venus fasciatum*, *Dosinia*, *Ensis*, *Echinocyamus*, and *Spatangus* as the most numerous animals growth is slow, and productivity small.

DISTRIBUTION (except the *Spisula elliptica* variety already mentioned): Fladen and Hirtsholm in the Kattegat (unpublished); N.W. coast of Sweden (Gustafson, 1934); Heligoland deep (Hagmeier and Hinrichs, 1931; Caspers, 1938; Remane, 1940); off the Scottish North Sea coast (Stephen, 1923); off Plymouth (Ford, 1923; Smith, 1932; Holme, 1953); S. of the Isle of Man (Jones, 1951); off Faro, Portugal, 32 m (Spärck, 1931); middle and inner part of the Adriatic Sea (somewhat reduced, Vatova, 1934; 1935; 1936; 1949); Black Sea (*Branchiostoma*, *Ammodytes*, *Ophelia*, *Polygordius*, but no *Venus*, Zernov, 1913; Caspers, 1951).

A community quite parallel to the *Venus fasciatum-Spisula elliptica-Branchiostoma* community just described is known from the Persian Gulf and the Madras coast, associated with a shell-gravel bottom at 2–60 m depth. *Branchiostoma indica* may here occur in up to 390 individuals per sq m, and species of *Venus* (of the

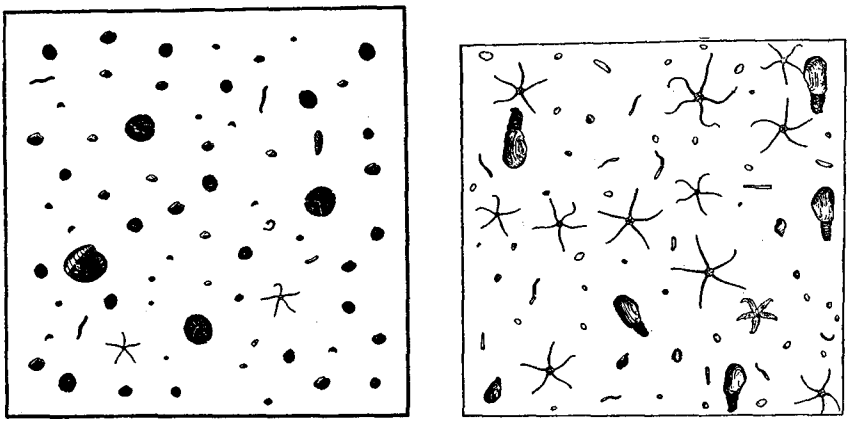

FIGURE 12.—*Boreo-mediterranean communities*

Left, the *Venus gallina* community, from a sandy bottom, 10–11 m depth, in the Kattegat. The figure comprises the number of animals found per ¼ sq m level bottom. The characterizing species are: *Venus gallina*, *Echinocardium cordatum*, and *Tellina fabula*. From Petersen (1918, Pl. III).

Right, the *Syndosmya* (= *Abra*) *alba* community, from a mixed bottom, 5–10 m depth, in the western Limfjord, Denmark. The figure comprises the number of animals found per ¼ sq m level bottom. The characterizing species are: *Syndosmya alba*, *Mya truncata*, *Cultellus pellucidus*, *Nucula nitida*, *Ophiura texturata*, and *Pectinaria koreni*. From Petersen (1911, Pl. III).

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"*fasciatum* type"), *Spisula*, and *Glycimeris taylori* plus the polychaete *Temnopleurus toreumaticus* occur in the same samples. Still not worked up in detail (Samuel, 1944; and the writer's investigations in the Persian Gulf in 1937).

An isocommunity to the *Venus* communities is described by Lee (1944) from Menemsha Bight, New England coast, 5–20 m depth, fine mixed sands. Characterizing animals are the lamellibranchs *Callocardia morrhuana* (belonging to the Veneridae), *Cyprina islandica*, and the polychaete *Clymenella torquata*.

Another isocommunity was found by the writer in the Persian Gulf, 4–50 m depth, sandy bottoms, with a venerid lamellibranch of the genus *Cytherea*, a *Spisula*, and a species of *Tellina*, *Ensis*, and *Cardium* as the characterizing species. The community is rather poor, but further details are not available at present (unpublished).

Syndosmya Community

General characteristics: Communities living in sheltered or estuarine areas, often with a somewhat reduced salinity and on a mixed to muddy bottom rich in organic material. From 5–10 to about 30 m depth. Characterizing genera: the lamellibranchs *Syndosmya*, *Cultellus*, *Corbula*, and *Nucula*, the polychaetes *Pectinaria* and *Nephthys*, ± the sea urchin *Echinocardium*. Increasing amounts of sand will lead to a *Venus* community, increasing amounts of silt to an *Amphiura* community. The characterizing species have a rapid growth, attain maturity at an early age, and have a short life (either "naturally" or because eaten by predators). The standing crop will comprise the production of little more than a year or, perhaps, only a fraction of it, and the total productivity is very large. Fluctuations of the quantitative composition of the community from year to year are enormous. A species dominating one year may be absent or nearly absent and replaced by another species the next year. Areas inhabited by *Syndosmya* communities are among the best feeding places for flounders.

1. Syndosmya alba Community (Figs. 12, 13). This is the only *Syndosmya* community known. Described by Petersen (1911; 1913; 1918) and Jensen (1919) from inner Danish waters. Characterizing animals: *Syndosmya alba*, *Cultellus pellucidus*, *Corbula gibba*, *Nucula nitida*, *N. nucleus*, *Pectinaria koreni*, *Glycera* sp., *Nephthys* sp., ± *Echinocardium cordatum*, *Ophiura albida*, and *O. texturata*. Mixed to muddy bottoms. In boreal seas from 8–10 to about 20 m depth, in the Mediterranean Sea and Black Sea from 5 to about 75 m depth. For general characteristics: *see* above.

Distribution: Bay of Kiel in Western Baltic (Hagmeier, 1926; 1930a); inner Danish waters (Petersen, 1911; 1913; 1918; Jensen, 1919; Blegvad, 1925; 1928; Spärck and Lieberkind, 1921), inner part of Ringkoebing fjord, W. Jutland (Blegvad, 1935), Grådyb off S.W. coast of Jutland (Blegvad, 1922), German Bay around Heligoland, Lister deep, and off the mouth of the river Elben (Hagmeier, 1923; Remane, 1940; Caspers, 1952); inner part of fjords and muddy coastal areas of Scotland (Stephen, 1923; 1934); Cumberland coast (transition to *Venus* community, Jones, 1952); Essex oyster grounds (Mistakidis, 1951); Plymouth (partially mixed with *Amphiura* community, Ford, 1923); Bay of Tunisia (Bruun, 1940); middle and inner part of the Adriatic Sea (Vatova, 1947; 1949); Black Sea off the coast of Romania (Borcea, 1931).

An indication of an isocommunity to the *Syndosmya* community is mentioned by Miyadi (1941b) from Beppu Wan, Japan, with the lamellibranch *Theora lubrica* (a close relative of *Syndosmya*), the amphipod *Ampelisca*, and the worms *Sternaspis* and *Glycera* as characterizing species.

Amphiura Communities

General characteristics: Communities inhabiting the soft bottom areas just outside the shallow water zones—*i.e.*, from 15–20 to about 100 m depth, in some cases deeper. Characterizing genera: *Amphiura* (often 400–500 individuals per sq m), *Turritella*, *Thyasira*, *Nucula*, *Nephthys*, *Terebellides*, *Lumbriconereis*, *Dentalium*, *Pennatula* (or *Virgularia*), and irregular sea urchins of one of the genera *Echinocardium*, *Brissopsis*, or *Schizaster*. A small increase of sand will often lead to a preponderance of *Echinocardium* and especially *Turritella*, a softening of the bottom often parallel to an increase in depth gives a preponderance of *Brissopsis*, *Thyasira*, and especially the sedentary polychaetes, and will finally lead to a *Maldane* community. Where *Amphiura* and irregular sea urchins are dominant, growth is rather slow, the standing crop is composed of several generations, and the content of dry organic matter is very poor. *Turritella* seems to have a slow growth and is only rarely eaten in the adult stage. The small lamellibranchs and especially the small polychaetes have a high content of dry organic matter and yield the most significant contribution to the productivity, which, however, when taken as a whole, is not very rich. Good feeding grounds for fish of the haddock, *Hippoglossoides*, and *Anarrhichas* types.

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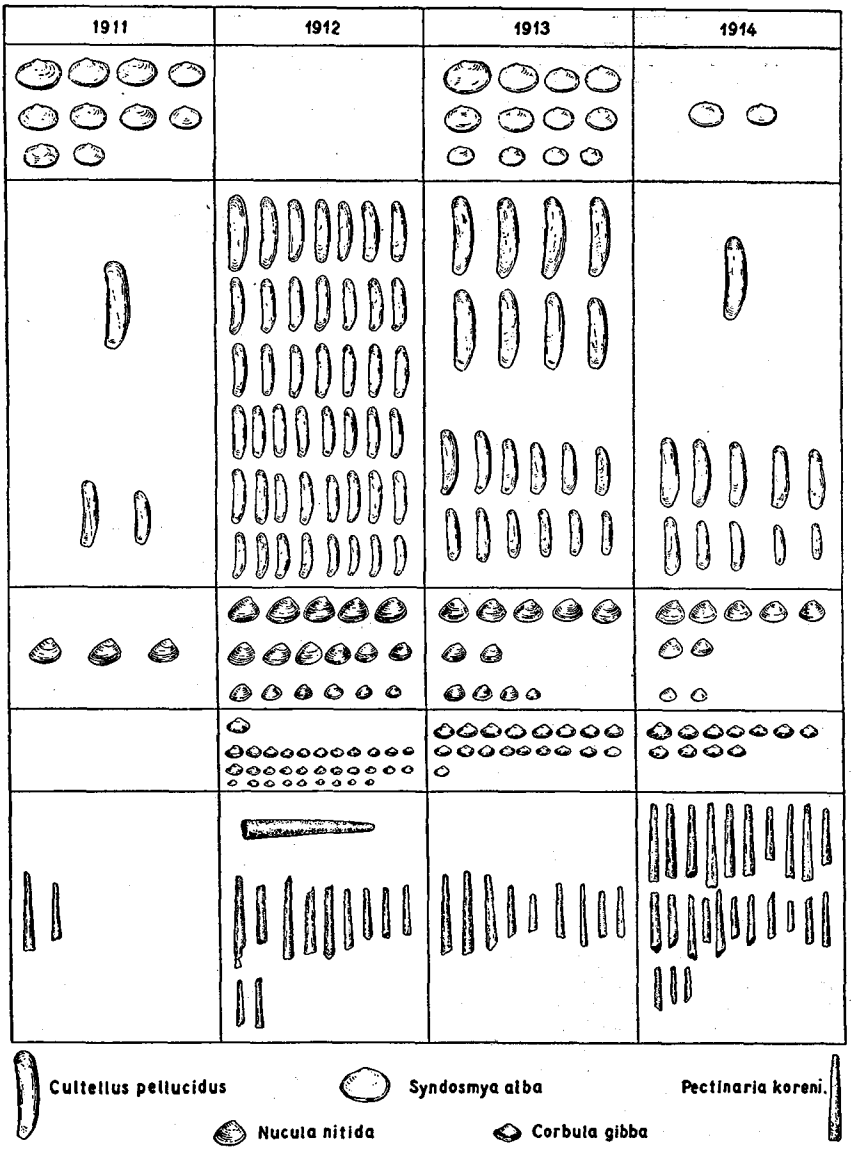

FIGURE 13.—*Photodiagram, showing the fluctuation in the amount of plaice food from year to year in the* Syndosmya (= Abra) alba *community from the western Limfjord, Denmark*

In each square the old stock, if present, is placed in the uppermost part, and the new brood in the lowermost part. From Boysen Jensen (1919).

1. AMPHIURA FILIFORMIS-AMPHIURA CHIAJEI COMMUNITY (Figs. 14, 15). (The boreo-mediterranean *Amphiura*-community). Described by Petersen (1913; 1918) as the "*Echinocardium filiformis* community" plus the "*Brissopsis chiajei* community." Characterizing species: *Amphiura filiformis* and (or) *Amphiura chiajei, Turritella communis, Aporrhais pes pelecani, Nucula tenuis* (or *N. nitida*, or *N. sulcata*), *Thyasira flexuosa, Syndosmya nitida, Terebellides stroemi, Nephthys* sp., *Lumbriconereis fragilis*, and ± the sea urchins *Echino-*

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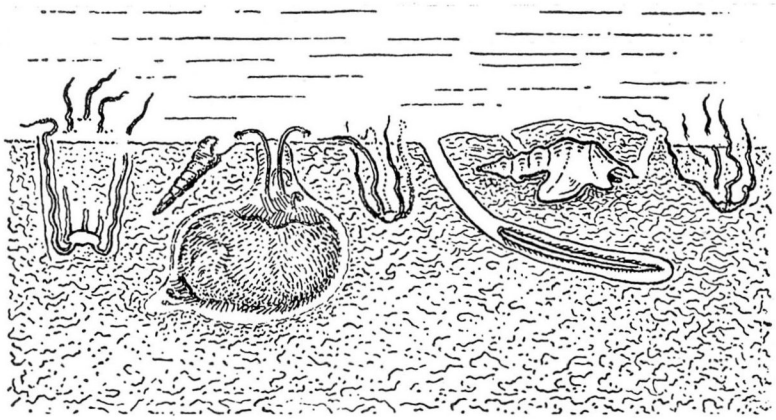

FIGURE 14.—*Boreo-mediterranean* Amphiura filiformis-Amphiura chiajei *community, seen in vertical section*

From a muddy bottom, at about 20 m depth, in the Kattegat, Denmark. The animals are (starting from the left): *Amphiura chiajei*, *Turritella communis*, *Brissopsis lyrifera*, *Amphiura filiformis* (2 specimens), *Nephthys ciliata*, and *Aporrhais pespelecani*. Drawn by Poul H. Winther, from G. Thorson (1950).

cardium cordatum, *Brissopsis lyrifera*, or *Schizaster canaliferus*. From 15–20 to about 100 m depth. On different kinds of soft bottoms, from clayey to silty. Its more clayey areas show preponderance of *Amphiura filiformis*, *Echinocardium cordatum*, and *Turritella*; its more silty and deeper areas show preponderance of *Brissopsis* (in the Mediterranean *Schizaster*), sedentary polychaetes, and the decapod *Calocaris macandreae*, but the conditions are so intermingled that it must be regarded one community.

DISTRIBUTION (of the typical community; for the variations *see* below): Northern part of the belts and the Kattegat, Denmark (Petersen, 1911; 1913; 1915; 1918; Blegvad, 1930); Gullmarfjord, Swedish W. Coast (Molander, 1928a; 1928b); off the Scottish North Sea coast (Stephen, 1923; 1934); eastern part of the southern North Sea (Blegvad, 1922); N. and N.W. of Heligoland (Hagmeier, 1923); Cumberland Sound (Jones, 1952); Plymouth (Ford, 1923, transition to a *Syndosmya* community), Cardigan Bay, Wales (Laurie and Watkin, 1922); South of the Isle of Man (Jones, 1951); off Faro, Portugal (Spärck, 1931); off the coast of Algeria (Spärck, 1931); off Salerno and Napoli (indications only, Spärck, 1931); middle and inner part of the Adriatic Sea (with *Schizaster canaliferus*, Vatova, 1934; 1935; 1936; 1940a; 1940b; 1949); off the coast of Israel (one variation with *Schizaster canaliferus* and one in deeper water with *Brissopsis lyrifera* and *Turritella*; Wirszubski, 1953). Variations are found in which the *Amphiura* species and the sea urchins are absent or nearly absent and where *Turritella communis* alone is preponderant: off Plymouth (Ford, 1923); off Naples (Bacci, 1946), and in the middle and inner Adriatic Sea (Vatova, 1949, p. 81, 85, 86). "Reduced" *Amphiura filiformis-chiajei* communities with more or less transitions to a *Maldane sarsi-Ophiura sarsi* community are known from Cumberland Sound (Jones, 1952), from south of the Isle of Man (Jones, 1951), from the Faroes (Spärck, 1929), and from S.W. Iceland (Spärck, 1929; 1937; Einarsson, 1941, p. 16).

2. AMPHIURA FLORIFERA COMMUNITY. Described by Borcea (1931, p. 671–672, dredgings only) from off the coast of Romania, Black Sea. Characterizing animals: *Amphiura florifera* ("tres commun et characteristique a ce niveau") with *Syndosmya alba* (a few only). From 47 to 50 m depth or more. Gray mud. At greater depths (65–75 m) *Amphiura florifera* gradually decreases, and *Syndosmya alba* increases in number until a pure *Syndosmya* community is established. Further details are highly desired.

3. AMPHIURA AESTUARII COMMUNITY (see Fig. 15, right). (The Japanese *Amphiura* community). Described by Miyadi (as a "*Maldane sarsi-Terebellides* community, 1941d, Fig. 3, and the table p. 180; *see* also Gislén, 1931, p. 429) from Ago Wan, Kii Peninsula, Japan. Characterizing animals: *Amphiura aestuarii* (to judge from Fig. 3 there are about 250 individuals per sq m), *Terebellides stroemi* (350 individuals per sq m), and *Maldane sarsi* (150 individuals per sq m). From (0) 15 to 40 m depth, on muddy or sandy bottoms. Miyadi mentions this community as if it were identical with the *Maldane sarsi-Terebellides* community he has described from a series of other Japanese bays. He seems, however, to neglect echinoderms as characterizing species, and it was only his Figure 3 which convincingly demonstrated a clear *Amphiura* community. So the *Maldane sarsi-Terebellides* communities mentioned in his other publications may well be *Amphiura* communities too, and, if so, the *Amphiura aestuarii* community seems to be widely distributed along the Japanese Islands.

4. AMPHIURA ROSEA COMMUNITY (The S.W. Pacific *Amphiura* community). Described by Powell (1937) from Auckland and Manukau harbors, New Zealand. (*See* also Dell, 1951; Fleming, 1951.) Characterizing animals: *Amphiura rosea*, *Echinocardium australe*, *Nucula hartwigiana*, *Dosinia lambata*, *Onuphis aucklandensis*, *Glycera americana*, *Lumbriconereis brevicirrata*, and *Pectinaria australis*. Between 10 and 23 m depth, soft

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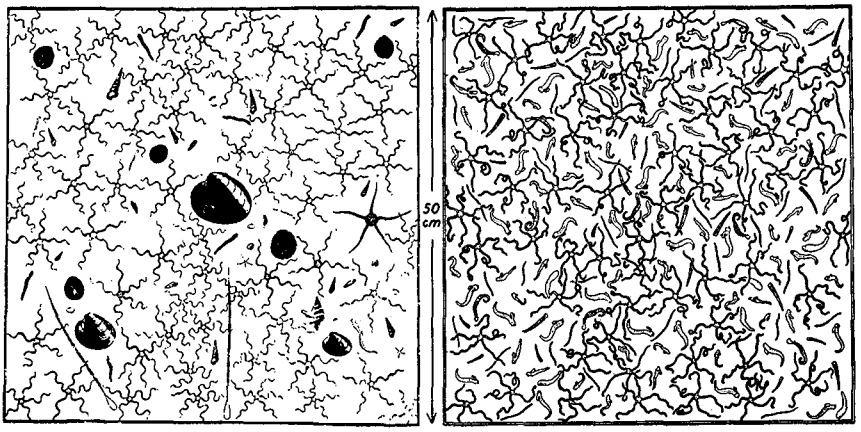

FIGURE 15.—"*Parallel*" Amphiura *communities*

Each figure comprises the number of animals found per ¼ sq m level bottom. Left: the boreo-mediterranean *Amphiura filiformis-Amphiura chiajei* community from a muddy bottom, 20–22 m depth, in the Kattegat, Denmark. Characterizing animals: *Amphiura filiformis* and *A. chiajei*, *Turritella communis*, *Aporrhais pespelecani*, the polychaetes *Terebellides stroemi* and *Glycera* sp. From Petersen (1918, Pl. IV).

Right: the Japanese *Amphiura aestuarii* community. From muddy and mixed bottoms, at about 15–40 m depth, in Ago Wan, Kii peninsula, Japan. Characterizing animals: *Amphiura aestuarii*, *Terebellides stroemi*, *Maldane sarsi*, *Glycera* sp., and *Dentalium* sp. Calculated and redrawn on the basis of Miyadi (1941d, Fig. 3).

bottoms; mud or mud with some sand; "deeper water community in more open waters" (Dell, 1951).

DISTRIBUTION: Hitherto known only from the fjords of Western New Zealand—*i.e.*, Auckland Harbor, Manukau Harbor (Powell, 1937; Fleming, 1951), and Queen Charlotte Sound (Dell, 1951).

On mixed bottoms in the Persian Gulf, 20–40 m depth, the writer found a *Brissopsis persica* community with a *Calocaris*-like decapod, a community which shows a close similarity to the outer part of the boreo-mediterranean *Amphiura* community (with *Brissopsis lyrifera* and *Calocaris macandreae*) as described above. The details on the Persian community are not worked out. Miyadi (1940b) from a very soft bottom, 6 to 64 m depth, at Osaka Wan, Japan, mentions some "associations" erected on the basis of a number of very small samples (Ekman grab, 80 samples in all, of 1/37 sq m each—*i.e.*, about 2 sq m bottom examined). Among the deeper samples were two rather large specimens of *Brissopsis luzonica*, and it seems likely that we here are concerned with an outer "zone" on the *Amphiura aestuarii* community described above.

AMPHIODIA-AMPHIOPLUS COMMUNITIES

In several parts of the Pacific soft-bottom communities occur which show close similarities to the *Amphiura* communities. The genus *Amphiura* seems, however, to be replaced here by two closely related genera—*Amphiodia* and *Amphioplus*—both of which are morphologicalically and ecologically nearly identical with *Amphiura*. This whole series of *Amphiodia-Amphioplus* communities may be regarded as iso-communities to the *Amphiura* communities, inhabiting the same type of bottom and replacing them in several areas of the Pacific. Characterizing genera: *Amphiodia*, *Amphioplus*, *Turritella*, *Schizaster*, *Nucula*, and the polychaetes *Sclerocheilus*, *Nephthys*, *Terebellides*, *Sternaspis*, and *Ammotrypane*. Productivity and rate of growth are unknown but are probably similar to the conditions outlined for the *Amphiura* communities.

1. AMPHIODIA CRATODERMA-TURRITELLA FENESTRATA COMMUNITY. Described by Deryugin and Somova (1940) from Peter the Great Bay, Japan Sea, depth 25 to 45 m, bottom type. Characterizing animals: *Amphiodia cratoderma* (up to 463 individuals per sq m), *Turritella fenestrata* (up to 35 individuals per sq m), *Axinopsis orbiculata*, *Magelona longicornis*, *Yoldia iohanni*. Further details lacking. A special variety of this community with more than 40 *Amphiodia* per sq m but with *Stegophiura brachyactis* (113 individuals per sq m) and the prosobranchs *Solariella varicosa* and *S. obscura* is found in the same locality at 80 to 200 m depth.

2. AMPHIODIA OCCIDENTALE COMMUNITY. Described by

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Weese and MacNab (1930) from East Sound, San Juan Archipelago, N.E. Pacific. Characterizing animals: *Amphiodia occidentale, Sclerocheilus pacificus,* and the lamellibranchs *Phacoides tenuisculpta* and *Pandora filosa.* Depth about 25–30 m, muddy bottoms. From the same region Shelford (1935, p. 266) mentions an area with *Amphiodia occidentale, Sclerocheilus,* and *Cucumaria populifera* as characterizing species, but regards it as part of the *Yoldia limatula* community.

3. Amphiodia sp.-Schizaster sp. Community from Chile. According to verbal information from Prof. H. Brattström and Dr. E. Dahl (Lund Univ. Chile Exped., 1948–1949) a community of this type inhabits the soft bottoms off the coast of the temperate part of Chile. Hitherto unpublished. To be described later.

4. Amphioplus macraspis Community. Described by Deryugin and Somova (1940) from Peter the Great Bay, Japan Sea, from soft bottoms and from depths exceeding 100 m. Characterizing species: *Amphioplus macraspis* (up to 53 individuals per sq m), *Ophiospenia tetracantha, Ophiura sarsi, Verticardia nadina.* The standing crop is rather rich. No further details known.

The writer has found that the soft bottoms of the Persian Gulf from 20 to 50 m depth were inhabited by a combined *Amphiodia-Amphioplus* community with a decapod of the *Calocaris* type, *Nucula, Nephthys, Ammotrypane aulogaster,* and several other sedentary polychaetes. Details still not worked up. Hitherto unpublished.

A *Schizaster lacunosus-Schlerocheilus* community with *Terebellides stroemi* described by Miyadi (1941c) from Ise Wan and Mikawa Wan, Japan, 29 to 46 m depth, muddy bottoms, should probably be mentioned here also, since at other occasions Miyadi seems to have neglected the brittle stars as characterizing species even when they were present in large numbers.

Turritella- and Cerithium Communities

It was shown that certain areas of the *Amphiura filiformis* community have so heavy a preponderance of *Turritella communis* combined with such a pronounced reduction in the number of *Amphiura* that they might have been regarded distinct *Turritella* communities had it not been for their rather narrow areas of occurrence and the gradual transitions to the surrounding "pure" *Amphiura* communities. We have, however, two Pacific communities in which respectively *Turritella* (= *Maoricolpus*) and its relative *Cerithium* are predominant, and for which at present we have no indications for the surrounding areas. We therefore mention them here and will await further information about their closer relations.

1. Maoricolpus (= Turritella) roseus Community. Described by Powell (1937) and Fleming (1951) from the fjords of the western Southland of New Zealand. Characterizing animals: *Maoricolpus roseus, Tawera spissa, Notocorbula zelandica, Nucula nitidula.* Within the range from 10 to 38 m depth. Sandy mud to muddy sand and coarse shell debris (the latter derived by dredgings only and, therefore, probably comprising epifauna as well as infauna). Only known from the type localities. No further details available.

2. Cerithium (= Proclavia) pfefferi Community (Fig. 16). Described by Miyadi (1938; 1940a; 1940c; 1941a, Figs. 2–3, *see* also Habe, 1949) from Tanabe Wan, Kii Peninsula, Japan. Characterizing animals: *Cerithium pfefferi* (from 500 to 1000 individuals per sq m), *Terebellides stroemi, Echinocardium cordatum, Nucula mirifica, Paphia undulata, Theora lubrica* (close to *Syndosmya*), *Pectinaria bocki, Sternaspis scutata,* and *Glycera* sp. No ophiurans. From 4 to 17 m depth. Muddy bottoms. The genus *Cerithium* seems in its morphological structure and in its mode of living to be so close to *Turritella* that this community must be regarded an isocommunity to the *Turritella* communities.

Maldane sarsi-Ophiura sarsi Community

General characteristics: Community inhabiting soft, fine mud bottoms in rather shallow estuaries, and at greater depths (about 100 to 300 m) in the open sea. Characterizing genera: the polychaetes *Maldane* and *Terebellides,* the brittle star *Ophiura sarsi,* the small lamellibranchs *Nucula, Syndosmya, Theora, Thyasira,* the gastropods *Philine* and *Cylichna,* the polychaetes *Aricia, Melinna, Praxilella, Clymenella, Glycera,* and *Pectinaria,* and the amphipod *Ampelisca* ± echinoderms of the genera *Ctenodiscus, Brissopsis,* or *Echinocardium.* From 4 to 18 m (Japanese fjords) to 80 to 220 m depth (Arctic and subarctic seas and Skagerrack). In Arctic seas at decreasing depths often transitional to a *Macoma calcarea* community. The standing crop is often rich in individuals and weight, and the preponderance of small polychaetes and lamellibranchs (high percentage of dry organic matter and probably a relatively rapid growth) point to a fairly large productivity.

1. Maldane sarsi-Ophiura sarsi Community (Fig. 16). This is the only known community of this type. Described by Spärck (1937) and by Deryugin and Somova (1940) from Iceland and from the Japan Sea, respectively, and (a variety of it) by Petersen (1915; 1918, Pl. IV) from the Skagerrack as "the *Brissopsis-sarsi* community". Characterizing animals: *Maldane sarsi* (in up to 7710 individuals per sq m, Zenkevich, 1927, st. 124, White Sea), *Ophiura sarsi, Terebellides stroemi, Mellina cristata, Clymenella gracilis, Pectinaria hyperborea, Nucula tenuis, Syndosmya nitida* (in the Pacific *Theora lubrica*), and species of *Philine* and *Cylichna* (for further animals and for depth and bottom, *see* the characteristics given above).

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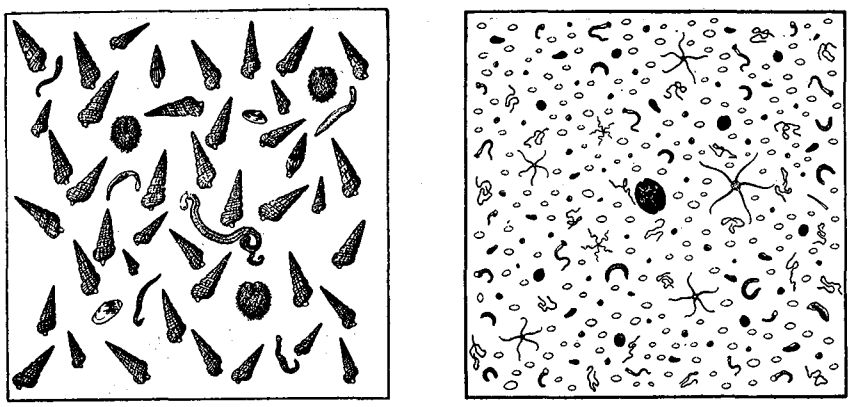

FIGURE 16.—*Japanese and circumpolar communities*

Left, the Japanese *Cerithium* (= *Proclavia*) *pfefferi* community, from a muddy bottom at about 12–13 m depth, Tanabe Wan, Japan. The figure comprises the number of animals found per $\frac{1}{50}$ sq m level bottom only. The characterizing species are: *Cerithium pfefferi, Theora lubrica* (close to *Syndosmya*), *Glycera* sp., and *Echinocardium cordatum*. From Miyadi (1941a, p. 476, Fig. 2).

Right, the circumpolar *Maldane sarsi-Ophiura sarsi* community (*i.e.*, "the *Brissopsis lyrifera-Ophiura sarsi* community" of Petersen). From a soft, muddy bottom, at 186 m depth, in the Skagerrack. The figure comprises the number of animals found per $\frac{1}{4}$ sq m level bottom. Characterizing animals: *Ophiura sarsi, Syndosmya nitida, Brissopsis lyrifera*, and several polychaetes (*Aricia, Melinna, Myriochele*, etc. From Petersen (1918, Pl. VI).

DISTRIBUTION: Circumpolar. It seems to inhabit the deeper areas of the Barents Sea and White Sea outside the *Macoma calcarea* community (indications in Zenkevich, 1927; Zenkevich *et al.*, 1928; Brotskaya, 1930); N., N.W., and S.W. Iceland (Spärck, 1937; Einarsson, 1941, p. 21 as "*Echinocardium flavescens*-community") Skagerrack (150 to 190 m, Petersen, 1915; 1918), deep parts of the Gullmarfjord W. Sweden (as "*Melinna tenuis*" and *Terebellides-flexuosa* associations", Molander, 1928a; 1928b), Peter the Great Bay, Japan Sea (Deryugin and Somova, 1940; at 200–600 m depth a variation with *Heliometra glacialis*), and Tanabe Wan, Beppu Wan, Mataya Wan, Gokasyo Wan, and Mutsu Bay, Japan (shallow water, Miyadi, 1938; 1940a; 1940b; 1940c; 1941a; 1941b; Habe, 1949; Yamamoto, 1950; 1951; 1952; Miyadi and Masui, 1942). The wide distribution of this community seems to be in accordance with the cosmopolitan distribution of most of the polychaetes characterizing it.

FORAMINIFERA COMMUNITIES

General characteristics: Poor communities inhabiting the deeper areas of Arctic and Boreal seas. Characterizing genera: the Foraminifera *Rhabdamina, Miliolina, Astrorhiza, Psammosphaera*, and *Saccamina*, the small lamellibranchs *Thyasira* and *Axinopsis*, the sedentary polychaete *Asychis*. From about 50 to about 700 m depth. Preferably muddy bottoms. The standing crop is often only a few g per sq m, and the productivity must also be regarded as extremely poor.

1. ARCTIC FORAMINIFERA COMMUNITY (Fig. 17, right). Described by Spärck (1933) and Thorson (1934) from the N.E. Greenland fjords. Characterizing animals: *Rhabdamina cornuta, Miliolina bucculenta, Asychis biceps, Axinopsis orbiculata*. From 50 to about 700 m depth. Muddy bottoms, often with some sand and stones. Standing crop very small. Productivity poor. Known from the type localities and from Jan Mayen (indications only, 210 m, Parat and Devillers, 1936).

2. BOREAL FORAMINIFERA COMMUNITY. Described by Stephen (1923; 1933; 1934) from the deepest part of the northern North Sea. Characterizing animals: *Astrorhiza arenaria, Saccamina sphaerica, Psammosphaera fusca, Thyasira flexuosa* (most common), and a few *Amphiura*. From depths slightly exceeding 100 m. Soft bottoms. Standing crop and productivity small, though, especially owing to *Thyasira*, significantly higher than in the corresponding arctic community.

Smaller spots inhabited by a closely related "community" with *Astrorhiza limicola* (*see* Fig. 17, left), as the predominant form is known from quite shallow water (5 m depth or less) off Helgoland in the southern North Sea. Sandy bottom (Caspers 1950b, p. 158, Fig. 15).

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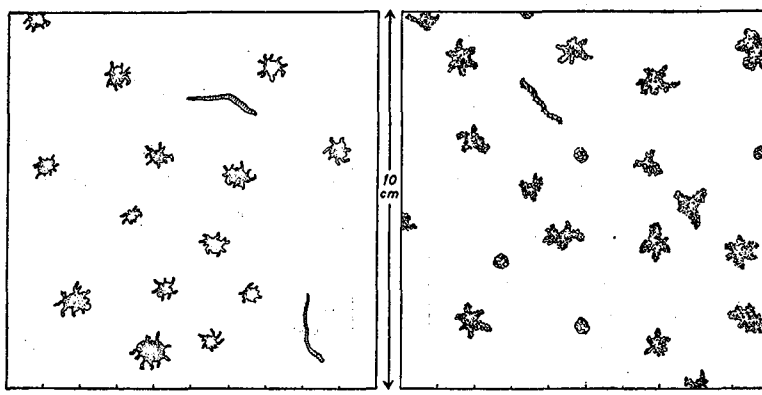

FIGURE 17.—*"Parallel" Foraminifera communities*

Each figure comprises the number of animals found per $\frac{1}{100}$ sq m level bottom only.

Right: The Arctic Foraminifera community, from a muddy bottom, at about 50–700 m depth, in the Franz Joseph Fjord, East Greenland. Characterizing animals: *Rhabdammina cornuta, Psammosphaera fusca,* and a maldanid. Redrawn from Spärck (1933, Pl. 6).

Left: The boreal Foraminifera community. From a spot on sandy bottom, at 5 m depth, in the southern North Sea. Characterizing animals: *Astrorhiza limicola* and the polychaete *Nephthys* sp. Redrawn from Caspers (1950b, Fig. 15).

AMPHIPOD COMMUNITIES

General characteristics: Communities mainly associated with estuarine conditions or with brackish waters and with relatively soft bottoms. Different species of *Amphipoda* occur, normally in large numbers. In spite of this the weight of the standing crop is often small. The productivity is, however, larger than indicated by the weight, since most of the *Amphipoda* have a short life and grow to maturity rather quickly. The males may have a shorter life than the females, and these communities may therefore show large fluctuations even within the different seasons of the same year.

1. PONTOPOREIA COMMUNITY (Pl. 4 in Chapter 24). (The boreo-arctic brackish-water community). Described by Hessle (1923; 1924) from the Baltic and by Spärck (1937) from Hornafjord, S. Iceland. (*See* also Segerstråle, 1937; 1938.) Characterizing species: the amphipods *Pontoporeia femorata, P. affinis,* and *Bathyporeia pilosa* ± the large isopod *Mesidothea entomon* and the gephyrean *Halicryptus spinulosus* and larval *Chironomidae.* From 10–20 m to about 200 m depth (at Iceland at 1 to 4 m depth only). Fine silty bottoms with more or less sand. Where the bottom is most sandy and at more shallow depths *Pontoporeia affinis* and *Mesidothea entomon* seem to be most common. On pure silty bottom and deeper, *Pontoporeia femorata* is most preponderant. In the southern Baltic we find all transitions to the *Macoma baltica* and the *M. calcarea* communities. For density and productivity, *see* the general remarks above.

   DISTRIBUTION: Hornafjord, S.E. Iceland, brackish water, only *Pontoporeia femorata* and *Halicryptus* (Spärck, 1937); Sea of Bothnia and Northern part of the Baltic down to Gottland and the bay of Danzig (Hessle, 1923; 1924; Hagmeier, 1926; 1930a).

2. BOREO-ARCTIC AMPELISCA COMMUNITY. Described by Miyadi (1940a; 1940c; 1941a; 1941b; 1941c) from Tanabe Wan, Beppu Wan, Ise Wan, and Mikawa Wan, Japan. Characteristic animals: large numbers of different species belonging to the amphipod genus *Ampelisca* (a close relative of *Haploops*; *see* next community). In Japan often with the sand dollar *Echinarachnius mirabilis,* the lamellibranchs *Theora lubrica,* and polychaetes of the genera *Sternaspis* and *Glycera.* The character and distribution of this community is not at all clear. It seems to occur in patches within other communities: in Japan within the *Amphiura aestuarii* and the *Maldane sarsi-Ophiura sarsi* communities, in Peter the Great Bay, Japan Sea, within certain areas of the *Venus fluctuosa* community (up to 14,500 *Ampelisca macrocephala* per sq m, Deryugin and Somova, 1940), and even in the *Syndosmya alba* community in Danish seas many species of *Ampelisca* occur in large numbers (Blegvad, 1925, p. 34). It is yet to be determined whether this is a "good community." Further details are highly desired.

3. HAPLOOPS TUBICOLA COMMUNITY (Fig. 18). Described by Petersen (1913; 1918, Pl. VIII) from a small area in inner Danish waters. Characterizing animals: the amphipod *Haploops tubicola* (up to 3000 to 4000 individuals per sq m), *Pecten septemradialus, Lima loscombi,* and several polychaetes with *Eumenia crassa* as the most common form. From 20 to about 40 m depth. On a tough clay bottom. This community is known only from the type locality and seems to have a rather local distribu-

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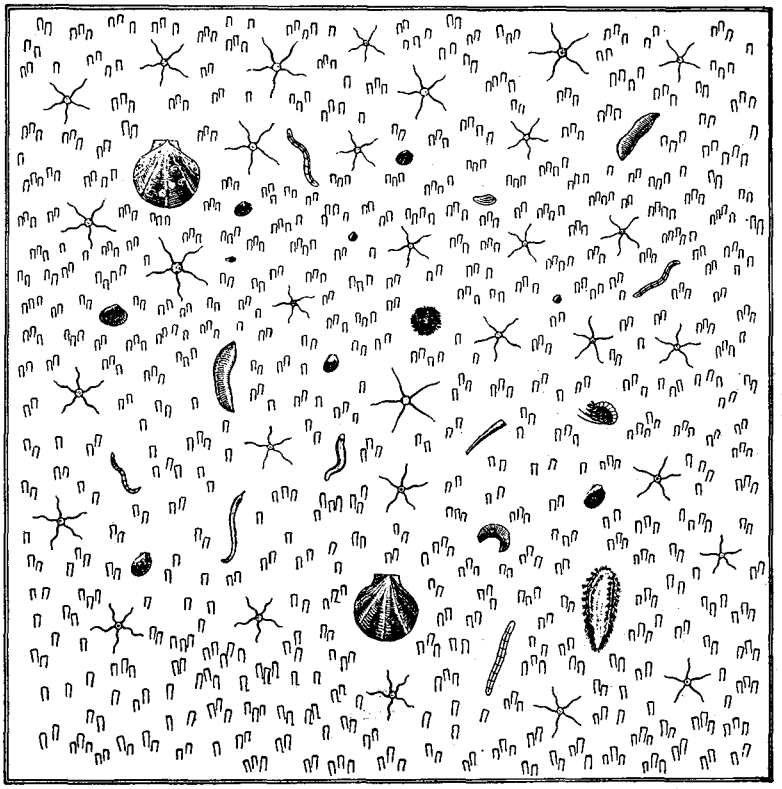

FIGURE 18.—Haploops tubicola *community*

From a tough clay bottom, at 27 m depth, SE. Kattegat. Characterizing animals: the amphipod *Haploops tubicola* (only the tubes are indicated on the picture), *Ophiura robusta*, *Pecten septemradiatus*, and the polychaetes *Eumenia crassa* and *Aphrodite aculeata*. The figure comprises the number of animals found per ¼ sq m level bottom. From Petersen (1918, Pl. VIII).

tion; only small patches of it seem, however, to occur in the Cumbrae Deep, Scotland (Allen, 1953, p. 243). Its standing crop is rather rich, and, since rapidly growing lamellibranchs, polychaetes with a high percentage of dry organic matter, and short-lived amphipods are its main inhabitants, the productivity must be assumed to be considerable.

Besides the communities mentioned here, Vibe (1939, p. 35) has described a *Mesidothea sabini* community with a rich number of *Amphipoda* from the banks directly below the large N.W. Greenland bird cliffs. Muddy bottoms. Supposedly this special community is dependent on the large quantity of guano produced by the birds. Further details are, however, needed before we may judge whether this is a "community", in the sense of Petersen, or a local phenomenon only.

A brackish-water community described by Caspers (1951) from the Black Sea off Varna, Romania, with larval Chironomidae, Hydrobia, and large numbers of amphipods (Gammaridae and Corophium) may probably be regarded as the isocommunity to the *Pontoporeia* community in the Baltic.

TYPES OF COMMUNITIES KNOWN EXCLUSIVELY FROM ARCTIC WATERS

1. PORTLANDIA ARCTICA COMMUNITY. Described by Thorson (1934) from Scoresby Sound, E. Greenland. Characterizing animals: *Portlandia arctica*. No other animals of importance. From 10–15 to 50–60 m depth. Only off the mouth of glacial rivers and large glaciers, on a very soft, milky-colored to light-gray mud. Very specialized community occurring only locally and over small areas. Transitions to a *Macoma calcarea* community (Zenkevich, 1927, Barents Sea) and to a *Venus fluctuosa* community (Bertelsen, 1937, p. 25) are known. Productivity unknown, but probably poor.

DISTRIBUTION (in its "pure" form): Known only in its type locality and from Nordfjord in Franz Joseph fjord, E. Greenland (Thorson, 1934), and perhaps from

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Storfjord, Spitzbergen (indications only, Brotskaya, 1930).

2. ARCA GLACIALIS-ASTARTE CRENATA COMMUNITY (Fig. 19). Described by Spärck (1933) and Thorson (1934) from the large N.E. Greenland fjords. Characterizing animals: *Astarte crenata, Arca glacialis, Thyasira flexuosa, Pecten groenlandicus, Ophiopleura borealis,* ± *Ctenodiscus crispatus.* From 30–40 to about 550 m depth. Muddy bottoms. Purely arctic community living at a constantly negative temperature. All species inhabiting it have a nonpelagic development and live their whole life in the same area. Standing crop rather poor, comprising many generations. Productivity accordingly small. Fluctuations from year to year insignificant. Probably the most constant of all level-bottom communities known.

DISTRIBUTION: Central and northern Barents Sea, and Kara Sea (Zenkevich *et al.*, 1928); the Spitzbergen banks (indications only, Idelson, 1930); Ramfjord, Northern Norway (10–40 m, *Arca glacialis* lacking, Soot-Ryen, 1924); Jan Mayen (Parat and Devillers, 1936); Franz Joseph Fjord, Scoresby Sound and Miki's fjord, E. Greenland (Spärck,1933; Thorson, 1933; 1934; Bertelsen, 1937).

TYPES OF COMMUNITIES KNOWN EXCLUSIVELY FROM SUBARCTIC WATERS

1. YOLDIA HYPERBOREA COMMUNITY. Described by Spärck (1937) from W., N., and E. Iceland. Characterizing species: *Yoldia hyperborea* (= *Yoldia limatula*), *Pectinaria hyperborea, Sternaspis fossor, Leda pernula,* and *L. minuta,* different species of *Nucula* and of the polychaete species *Clymenella, Amphicteis, Maldane,* and *Scalibregma.* From about 10 to about 70 m depth. On muddy bottoms. Standing crop fairly rich. Productivity probably of medium size owing to the large content of dry organic matter in the numerous polychaetes.

DISTRIBUTION: White Sea (Zenkevich, 1927); Southern Greenland (Spärck, 1936, p. 138); Iceland (Spärck, 1937); San Juan Archipelago, N.E. Pacific (variation with *Pandora filosa,* Shelford, 1935; Clements and Shelford, 1946, p. 339).

TYPES OF COMMUNITIES KNOWN EXCLUSIVELY FROM WARM SEAS

CRAB COMMUNITIES

As the arctic and subarctic seas seem to have a few characteristic communities, so also have the warm seas, and some are even extremely specialized ones—*viz.*, the crab communities.

General characteristics: Communities associated with loose, sandy bottoms at depths of about 10–30 m. Characterizing animals: small filter-feeding crabs in enormous quantities dominating the samples. Also a few lamellibranchs and polychaetes, but so scattered in their occurrence that their quantitative significance is very small. The crabs, having no other animals to feed upon in the bottom, must take their food from the plankton. This is possible only in a shallow-water region with turbulent water where a rich productivity of plankton may take place throughout the year, and the basis for such a constant high productivity might only be found in areas where the light conditions allow photosynthesis to take place throughout the year.

1. PINNIXA RATHBUNI COMMUNITY (Fig. 20, right). Described by Miyadi (1941c, with figure) from Ise Wan and Mikawa Wan, Japan. Characterizing species: the crab *Pinnixa rathbuni* (more than 3000 mature individuals per sq m). Besides this species only a few specimens of *Tellina pallidula, Limopsis multistriata,* and *Corbula* (= *Aloidis*) *venusta* without any quantitative significance. From 7 to 37 m depth, gravel, sand, and muddy sand. Miyadi's view: that "it is obvious that such large numbers of crabs cannot occupy the bottom for a long time, and the present association may perhaps be a temporal or a seasonal one" seems hardly to agree with the writer's experience from the Persian Gulf. The standing crop is rich, and the productivity probably extremely high.

DISTRIBUTION: Known only from the type locality.

2. XENOPHTHALAMUS PINNOTHEROIDES COMMUNITY (Fig. 20, right). Found (hitherto unpublished) by the writer (1937) in the Persian Gulf. Characterizing species: The crab *Xenophthalamus pinnotheroides* (more than 1500 mature individuals per sq m) plus a few Polychaeta without any quantitative significance. Depth about 20 m. Loose sand. The samples showed a good constancy as to the density of the crabs and were distributed over an area of several square kilometers. The standing crop was rich, and the productivity probably very high.

A hermit-crab community described by Mary Samuel (1944) from the Madras coast, muddy bottom, at a depth of 20–35 m and totally dominated by *Diogenes rectimanus* and *Diogenes costatus,* no other animals playing any quantitative part within the said area, must probably be regarded an isocommunity to the crab communities mentioned above. Also here the bottom seems poor in food for the hermit crabs, which accordingly must either be deposit feeders or take their food directly by filtering the plankton. Also the sand crab (*Emerita*) communities described from the Californian beaches by MacGinitie (1949) may probably be regarded isocommunities to the crab and hermit-crab community just mentioned, but, since the *Emerita* community is intertidal only, it is not discussed in detail here.

OTHER COMMUNITIES INSUFFICIENTLY KNOWN AND WITHOUT KNOWN PARALLELS

1. AMPHILEPIS NORVEGICA-PECTEN VITREUS COMMUNITY. Described by Petersen (1915; 1918, Pl. VII) from the deepest part of the Skagerrack and the Oslo fjord, S. Norway. Characterizing animals: the brittle star *Amphilepis norvegica* (up to 60–70 individuals per sq m), *Pecten vitreus* (30–40 individuals per sq m), *Thyasira flexuosa* (60–70 individuals per sq m), and different small polychaetes. From 300 to 400 m depth and deeper. Soft

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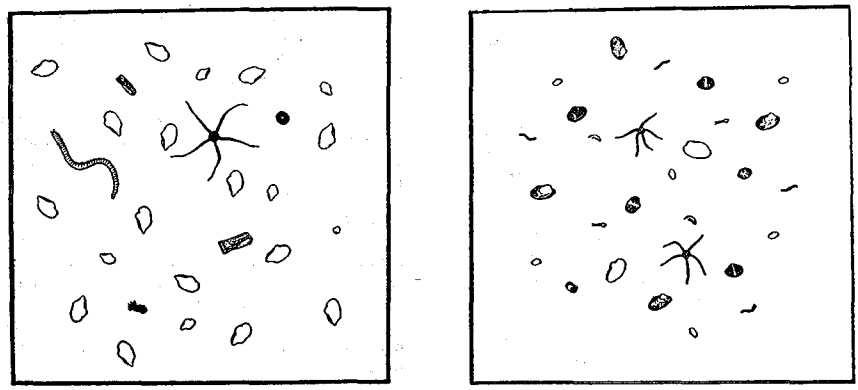

FIGURE 19.—*Arctic communities*

Left, the *Portlandia arctica* community. From light-gray mud, at about 30 m depth, Scoresby Sound, East Greenland. The figure comprises the number of animals per ¼ sq m level bottom. Characterizing animals: the lamellibranch *Portlandia arctica*, the holothurian *Myriotrochus rinki*, and the brittle star *Ophiocten sericeum*. From Thorson (1934, Pl. 3).

Right, the *Arca glacialis-Astarte crenata* community. From a muddy bottom, at about 200 m depth, in the Franz Joseph Fjord, East Greenland. The figure comprises the number of animals per ¼ sq m level bottom. Characterizing animals: the lamellibranchs *Arca glacialis* and *Astarte crenata* and the brittle star *Ophiocten sericeum*. From Spärck (1933, Pl. 5).

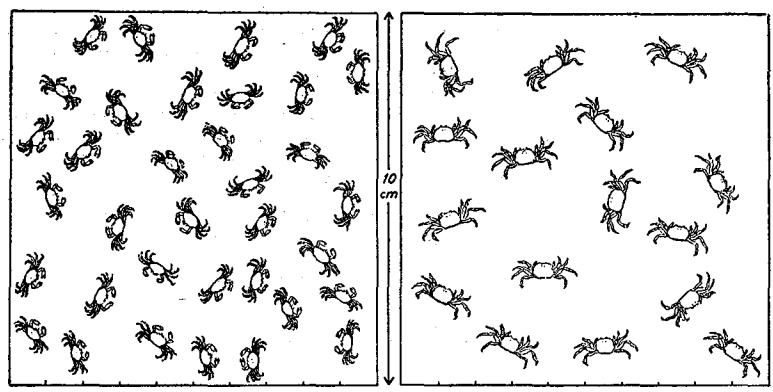

FIGURE 20.—*"Parallel" crab communities*

Each figure comprises the number of animals found per $\frac{1}{100}$ sq m level bottom only.

Left: the Japanese *Pinnixa rathbuni* community. From mixed bottom, at about 14 m depth, at Ise Wan, Japan.

Right: the Persian *Xenophthalmus pinnotheroides* community. From a loose sandy bottom, at about 20 m depth, in the S.E. part of the Persian Gulf. Drawn by Poul H. Winther, orig.

muddy bottoms. Standing crop a few g only. Productivity unknown, but to judge from the preponderance of the brittle stars and the scarcity of lamellibranchs and polychaetes it must be very poor. Besides the *Foraminifera* communities (and perhaps the *Arca glacialis-Astarte crenata* community) this is probably the only deep-sea community hitherto adequately described, and it is probably widely distributed in areas still not examined with quantitative instruments.

The rest of these communities, still very poorly known, shall be only summarily treated here, but must be kept in mind until "parallels" turn up and allow us to judge their "validity" and relationships. They are (Atlantic first, then Pacific):

1. DITRUPA SUBULATA COMMUNITY with a few *Amphiura filiformis* and *A. chiajei*. North Sea off Scotland, depth and bottom unknown (Stephen, 1923).

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2. TROPHONIA AFFINIS-VENERICARDIA BOREALIS COMMUNITY. Off Martha's Vineyard, New England coast of U.S.A. From 10 to 14 m depth. Mud with stones. Covering a very small area only (Lee, 1944).

3. TAPES AUREUS COMMUNITY WITH NUCULA NUCLEUS AND NASSA MAMMILLATA. Laguna Veneta, the Adriatic Sea, Depth?, preferably on sandy bottoms (Vatova, 1940b).

4. UPOGEBIA LITORALIS-MELINNA PALMATA COMMUNITY. With *Nassa reticulata, Capitella capitata, Spisula subtruncata, Glycera* sp., nereids, and *Ampelisca diadema*. Black Sea off the coast of Romania. Deeper than 15 m. Muddy bottom (Caspers, 1951). The writer has seen a community of this type in a muddy estuary, 0 to 2 m depth, on the island of Lanzarote, Canary Islands.

5. ASABELLIDES SIBIRICA-NUCULA TENUIS COMMUNITY. With *Yoldia johanni* and *Axinopsis orbiculata*. Peter the Great Bay, Japan Sea, 22 m depth. Bottom ? (Deryugin and Somova, 1940).

6. PRIONOSPIO PINNATA COMMUNITY. With *Theora lubrica* and *Ammotrypane aulogaster*. Beppu Wan, Ise Wan, Mikawa Wan, Japan. From 19 to 61 m depth. Muddy bottoms (Miyadi, 1941a, 1941b; 1941c).

7. LUCINOMA ACUTILINEATA COMMUNITY. With *Prionospio pinnata, Philine japonica*, and *Echinocardium cordatum*. Beppu Wan, Japan. Deeper than 60 m. Soft blackish mud (Miyadi, 1941b).

8. ARACHNOIDES PLACENTA (= "SAND DOLLAR")-COMMUNITY. With numerous specimens of the prosobranch *Zethalia* (= *Umbonium* = *Rotella*) *zelandica*. (For illustrations *see* Seilacher, 1953, p. 269.) Manukau Harbor, New Zealand, on a hard ferruginous mud, from 10 to 38 m depth (Powell, 1937). Probably a parallel to a sand-dollar community, not described, occurring off the coasts of California.

9. LIOMIA MEDUSA-SABELLARIA SPINULOSA COMMUNITY. With *Thelepus cincinnatus* and *Troglopagurus jausseaumei*. Madras coast, from 20 to 28 m depth. On sandy clay (Mary Samuel, 1944).

GEOGRAPHICAL SUMMARY OF LEVEL-BOTTOM COMMUNITIES*

1. ARCTIC PART OF THE ATLANTIC
   a. NOVAYA ZEMLYA-BARENTS SEA-WHITE SEA-MURMAN COAST: *Macoma baltica* community, *Macoma calcarea* community, *Venus fluctuosa* community, *Arca-Astarte crenata* community (reduced), and *Yoldia hyperborea* community.
   b. ARCTIC NORWAY: *Macoma baltica* community, *Macoma calcarea* community, *Arca-Astarte crenata* community (reduced).
   c. SPITZBERGEN AND THE BANKS AROUND IT: *Macoma calcarea* community, *Arca-Astarte crenata* community, and small indications of a *Maldane sarsi* community and a *Portlandia artica* community.
   d. EAST GREENLAND COAST AND JAN MAYEN: *Macoma calcarea* community, *Venus fluctuosa* community, *Arca-Astarte crenata* community, Foraminifera community, *Portlandia arctica* community.
   e. N.W. GREENLAND COAST: *Macoma calcarea* community, *Chiridota sabini* community.

2. NORTH ATLANTIC ISLANDS AND E. COAST OF U.S.A.
   a. ICELAND: *Macoma calcarea* community, deeper *Venus* community (reduced), *Amphiura filiformis* community, *Maldane sarsi* community, *Yoldia hyperborea* community, *Pontoporeia* community.
   b. THE FAROES: *Macoma calcarea* community, deep *Venus* community (reduced), *Amphiura filiformis* community.
   c. MENEMSHA BIGHT, N.E. U.S.A.: *Tellina tenera* community, *Cyprina-Clymennella torquata* community, *Venericardia borealis-Trophonia affinis* community.
   d. NORTHERN GULF OF MEXICO: *Tellina* spp. community, *Mulinia lateralis* community.

3. SCANDINAVIA, N.W. GERMANY, AND HOLLAND
   a. THE BALTIC AND THE SEA OF BOTHNIA: *Macoma baltica* community, *Macoma calcarea* community (survivor), *Syndosmya alba* community (Only in W. Baltic), *Pontoporeia* community.
   b. INNER DANISH WATERS: *Macoma baltica* community, *Macoma calcarea* community (survivor), *Venus gallina* community, deep *Venus* community, *Syndosmya alba* community, *Amphiura filiformis* community, *Haploops* community (local only).
   c. SWEDISH W. COAST, NORWEGIAN S. COAST, SKAGERRACK: *Macoma baltica* community, *Macoma calcarea* community, deep *Venus* community, *Amphiura filiformis* community, *Maldane sarsi-Ophiura sarsi* community, *Amphilepis norvegica-Pecten vitreus* community.
   d. DANISH, GERMAN, AND DUTCH NORTH SEA COASTS: *Macoma baltica* community, *Venus gallina* community, deep *Venus* community, *Tellina fabula* community, *Syndosmya alba* community, *Amphiura filiformis* community.

4. DEEPER NORTH SEA, GREAT BRITAIN AND IRELAND
   a. NORTH SEA BASIN: *Venus gallina* community, deep *Venus* community, *Amphiura filiformis* community, *Foraminifera* community, *Ophiura affinis-Echinocyamus* community.
   b. SCOTTISH COAST: *Macoma baltica* community, *Tellina tenuis-T. fabula* community, *Syndosmya alba* community.
   c. ENGLISH COAST AND COAST OF WALES: *Macoma baltica* community, *Venus gallina* community, deep *Venus* community, *Syndosmya alba* community, *Amphiura filiformis* community (= *Turritella*).
   d. W. COAST OF IRELAND: Indications of an *Amphiura filiformis* community (Southern, 1915).

5. LUSITANIAN PART OF THE ATLANTIC
   a. COAST OF PORTUGAL: *Venus gallina* community, deep *Venus* community, *Tellina tenuis* community (With *T. incarnata*), *Cardium edule-Scrobicularia* community (= reduced *Macoma* community).

6. THE MEDITERRANEAN
   a. ITALIAN W. COAST: *Venus verrucosa* community, indications of *Venus gallina* community, indications of *Amphiura filiformis* community (= *Turritella*).

* Includes only references not cited in the preceding section [Ed.].

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b. ADRIATIC SEA: *Venus verrucosa* community, *Venus gallina* community, deep *Venus* community, *Tellina distorta* community, *Syndosmya alba* community, *Amphiura chiajei-Schizaster* community (= *Turritella*).

c. NORTH AFRICAN COAST: *Syndosmya alba* community, *Cardium edule* community (= reduced *Macoma* community), *Amphiura filiformis* community.
Off the coast of Israel: *Venus gallina* community; *Amphiura chiajei-Schizaster* community (in deeper water with *Brissopsis lyrifera* and *Turritella*.

7. BLACK SEA
Cardium edule community (= reduced *Macoma* community), *Venus gallina* community, deep *Venus* community (indications only), *Amphiura florifera* community, *Upogebia-Melinna* community.

8. ARCTIC PART OF THE PACIFIC
Macoma baltica community, *Venus fluctuosa* community, *Amphiodia cratoderma* community, *Amphioplus* community, *Maldane sarsi-Ophiura sarsi* community, *Asabellides siberica* community.

9. PACIFIC COAST OF NORTH AMERICA
a. SAN JUAN ARCHIPELAGO: *Macoma nasuta* community, *Yoldia hyperborea* community, *Amphiodia occidentale* community.
b. CALIFORNIA: (tidal flats only) *Macoma nasuta* community.

10. PACIFIC COAST OF SOUTH AMERICA
Nothing has been published, but verbal information from Prof. H. Brattström and Dr. Erik Dahl (Lund Univ. Chile Exp. 1948–1949) seems to indicate an *Amphiodia-Schizaster* community.

11. COASTAL AREAS OF JAPAN (from 37°N. Lat.: Nanao Wan to 33°40′N. Lat.: Tanabe Wan): *Macoma incongrua* community, indications of *Macoma nasuta* community, *Amphiura aestuarii* community (? with *Brissopsis luzonica* zone), *Ophiura sarsi-Maldane sarsi* community, *Cerithium pfefferi-Terebellides* community (Isocommunity to the *Amphiura-Turritella* community), *Ampelisca* community, *Prionospio* community, *Pinnixa* community. Numerous papers were published in Japan during and immediately after the war: Habe (1943; 1945), Masui (1943), Miyadi *et al.* (1943; 1944) in J. Ocean. Soc. Japan, vols. 2–4; by Kawaguchi *et al.* (1944; 1946) and Namibe *et al.* (1946a, 1946b) in Physiol. Ecol. Contr. Otsu Hydrobiol. Exp. Stat. Kyoto Univ., vols. 8, 55, 56, 58; by Habe *et al.* (1945a; 1945b; 1945c) and Miyadi *et al.* (1944; 1945; 1946) in Rep. on Physiol. & Ecol. Kyoto Univ., nos. 3, 21, 22, 31, 32, 54, 55, 56, 57 (mimeographed only); by Masui (J. Fish., no. 49, 1941), Miyadi and Masui (J. Oceanogr., vol. 13, 1942, and Sea & Sky, vol. 22, 1942), and by Miyadi and Habe etc. (in Okada: *Studies on aquatic animals of Japan*, vol. 1, 1950). Most of these papers are partially or entirely in Japanese, and none has been accessible to the writer.

12. COASTAL AREAS OF NEW ZEALAND
Tellina lilacina-Ancilla community, *Amphiura rosea-Echinocardium australe* community, *Maoricolpus* community (= *Turritella*) (Isocommunity to the *Turritella* zones of the *Amphiura* community), *Arachnoides-Zethalia* community.

13. COASTAL AREAS OF INDIA
Branchiostoma-Temnopleurus community (= reduced deep *Venus* community), *Liomia medusa-Sabellaria* community, Diogenes community (Isocommunity to the tropical crab communities?).

14. PERSIAN GULF
Information based upon about 300 bottom samples with the 1/10 sq m. Petersen grab taken by Dr. B. Løppenthin and the writer during 1937–1938 (hitherto unpublished): *Venus* (= *Cytherea*)-*Spisula* community, deep *Venus* community (*Branchiostoma indica* community), *Amphiodia-Amphioplus* community, *Xenophthalamus pinnotheroides* community (= crab community) and *Zethalia* (= *Umbonium*, = *Rotella*) community.

CONCLUSION

This review is a further indication of the uniformity of the level sea bottom and its fauna. Thus we may now compare series of "parallel communities" inhabiting the same type of bottom at similar depths, characterized by different species of the same genera, but replacing each other in accordance with the geographical regions. We know of four *Macoma* communities and have indications of two more. We know of four *Tellina* communities, three *Venus* communities, four *Amphiura* communities, four *Amphiodia-Amphioplus* communities, two Foraminifera communities, and so on.* We also see that only a rather small number of genera are really dominant among the infauna of Recent seas, and a closer study of the biology and ecology of these genera will be of the greatest value. In fact, it already seems possible to point out the genera which will be the characteristic "index fossils" for our period, as the ammonites, belemnites, and trilobites are for earlier geological periods.

The value of these "parallel communities" for future scientific level-bottom re-

* For "parallel communities" from W. Africa, published after this manuscript was finished, *see* Longhurst, 1957, and Thorson, 1955).

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search can hardly be overestimated. Teams of ecologists in Japan, New Zealand, California, the Mediterranean, and Scandinavia, for example, may study such a series of "parallel communities" occupying in all places about the same type of substratum, and having the same rate of competition among members of the same genera. Strong evidence suggesting that the replacing species of these level-bottom genera are totally or nearly adapted to the temperatures under which they live is now available (*see* Thorson, 1951, p. 309–316, and Bullock, 1955), and, as we have emphasized, temperature seems to be the principal variable factor for the infauna. Scholander *et al.* (1953) consider climatic adaptation in arctic and tropical poikilotherms and state, concerning marine animals, that ". . .hence there is a very considerable, although not complete, metabolic adaptation in the arctic forms relative to the tropical forms" (p. 90). It seems reasonable to assume that the level-bottom species of the same genera replacing each other from the Arctic to the tropics will be among those which have the most nearly complete adaptation.

These "parallel communities" make it possible for us to build a solid framework for future studies on level-bottom ecology. Observations on habits of species of, for instance, *Macoma*, *Venus*, or *Amphiura* in Scandinavian seas may help to explain the influence of other species of the same genera in "parallel communities" in other seas, and thus valuable generalizations may be made. After the problems of feeding, growth, reproduction, and competition are outlined for these "parallel communities" of the macrobenthos, the next step should be to examine in detail the meio- and microbenthos within the macro communities and to determine their significance for the community as a whole. The recent work carried out by Remane and his collaborators on the microbenthos of shallow water and beaches seems to indicate that the distribution of the microfauna within the macrofauna communities will also show a pronounced uniformity.

Discussions have shown a large gap between marine level-bottom ecologists and terrestrial soil-fauna ecologists in their points of view as well as in their mode of working and of problem solving. Most soil-fauna ecologists have had to postpone the use of quantitative methods for practical reasons and seem unable to cope with their most complicated microclimatic problems, which makes generalizations from conditions found in the individual microbiotopes nearly impossible.

The marine level-bottom ecologist is in a much more favorable position; he can use the large uniform bottom flats and the "parallel communities" for well-founded generalizations, but he must not forget the responsibility which this privilege gives him in finding ways to fill the gap from marine to terrestrial ecology.

All life started in the sea, and several millions of years passed before the organisms conquered land. Nevertheless, today only about one-sixth of all recent species of animals live in the sea. The terrestrial microlandscapes with their huge variations have had an enormous selective effect as compared with that of the marine landscapes, and the nearly utopian problem which the terrestrial soil ecologist has to tackle is to examine and evaluate all the factors of these varying microlandscapes which led to the specialization and, then, to apply his results in relation to the animals inhabiting them.

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How can a marine ecologist help to bridge the gap to terrestrial ecology? The best method probably should be to do just as the animals did long ago: to start from purely marine conditions and then to make a slow approach to land, meeting gradually one terrestrial factor after the other to see what happens. A *Macoma baltica* community which seems to be rather uniform and constant over large areas, when totally submerged, tends to divide into several distinct "zones" on the tidal flats in accordance with the changing degrees of water covering and exposure to the air (Hagmeier and Kändler, 1925, p. 38; Thamdrup, 1937; Wohlenberg, 1937). This is the result of meeting the first terrestrial factor only. These fascinating biotopes forming all gradations from sea to land may prove to be the first key to a quantitative approach to terrestrial soil-fauna problems. Remane and his pupils, working in this zone, have recently described even a subterranean marine microfauna. The next terrestrial factor we meet would probably be the first traces of terrestrial vegetation, which again complicates the conditions.

C. G. Joh. Petersen apologized for his audacity in publishing the first hypothetical maps of the animal communities of the North Atlantic (1914, p. 6): "I venture to make this attempt well knowing how imperfect it must be, because it will have to be made sooner or later, and the sooner it is made, the sooner I trust, will it be repeated to better effect." Let his words be the motto also for this chapter.

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ARCTIC OCEAN

BEAUFORT SEA

BARENTS SEA

NORTH PACIFIC OCEAN

NORTH ATLANTIC OCEAN

INDIAN OCEAN

SOUTH PACIFIC OCEAN

SOUTH ATLANTIC OCEAN

Great Shantar Is.

Peter the Great Bay

Misaki

Tokara Is.

Do-Son

Eniwetok

Bikini

Ifaluk

Arno

Kapingamarangi

Onotoa

Hawaii

Raroia

Sidney

Kangaroo Is. (American River)

Tasmania

Poor Knights Is.

Wellington

Puget Sound

Oregon (Brookings)

San Francisco

Monterey (Mussel Pt.)

Port Aransas

Marineland, Fla.

Miami

Beaufort

Woods Hole

Nova Scotia

Baia de Guanabara

Kola Fjord

Murmansk

Gullmar Fjord

Anglesey

Lough Ine

Plymouth

Fiume

Varna

Sebastopol

Senegal

After Zubov, 1947; localities indicated are sites of recent ecological studies (see text, esp. Table I)

LEGEND

semidaily tide

irregular semidaily

irregular diurnal

regular diurnal

2.2 = maximum range in meters

CHARACTER AND MAXIMUM RANGES OF VARIOUS TYPES OF TIDES ON THE SHORES

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Chapter 18

Rocky Intertidal Surfaces

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INTRODUCTION

Summarizing our information on this subject and the pertinent information to be found through the huge bibliography are not the only objectives of this chapter. An organization has been attempted which seems potentially of service in pointing out variables or factors, the study of which, through application of the experimental method, may facilitate better understanding of the various problems and encourage the formulation of new, testable hypotheses.

This goal is sought by organizing the material presented around what seem to be the major aspects of realms in the variation of the environment. For the reporting of observations, the environment lends itself to measurement as variations (or duration) through *space*, *time*, and *numbers*, and *in* C. G. S., or related, units.[1] Most of the points outlined by Michael and Allen (1921) in their outline of the problems of marine ecology are covered but have been reorganized with the above variables in mind.

The environmental variables delimit a form in space, time, and numbers peculiar to each species, group of species, or other biological unit being treated. For this form we shall use the term *biospace*, though in deference to the usual three-dimensional conception of "space" some other term might well be more appropriate for a form having more than three dimensions. Järnefelt (1940), Reijne (1948), and Detling (1951) present possible methods of illustrating these polydimensional biospaces (Fig. 16) within the restrictions imposed by two-dimensional printing.

A simple sample of, or section through, a biospace would be provided by a uniformly exposed and vertical plane shore. Such a two-dimensional plane section would be expected to have ends which are more or less attenuated in some respect. A third dimension would be simply represented and sampled when, or if, the section were curved. A series of jetties or breakwaters would provide on their intertidal surfaces a series of plane sections through the different biospaces that form the essential substance of this chapter (though there has been no hesitation in bringing in occasional examples from other habitats). A series of large boulders protruding into the air and scattered over a subtidal bottom would provide a somewhat more complicated sampling through a set of local intertidal biospaces. Temporal and numerical distribution provide additional dimensions. If enough samples were available one should be able to calculate the extent of these biospaces and predict where particular

[1] Papers extensively utilizing means of exposition other than such specific units (*e.g.*, centimeters, grams, seconds) have been found to be of little use though they may be artistic or literary masterpieces. The relegation of a host of them to the great list of papers that might have been cited herein is manifest.

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organisms would grow, for example, on a new breakwater to be installed in the region.

The presence or absence of such boulders or other suitable surfaces as required by a particular organism for existence are what Chapman (1943, p. 243) has emphasized as "presence or absence" factors. The common mussel of the west coast of North America, *Mytilus californianus*, develops only on solid surfaces: *substratum*, for this organism, is a presence or absence factor.

This chapter is restricted to an analysis of the vertical and certain longitudinal factors of distribution on solid surfaces and to a discussion of probable causes of such distributions. The factors governing horizontal, temporal, and numerical distribution on intertidal solid surfaces are in the main left to other chapters (especially Chapter 13) except in so far as their utilization appears useful in the development of hypotheses in this discussion.

BASIS FOR CRITICISM AND THE SUBSTANCE FOR A POINT OF VIEW IN PRESENT-DAY INTERTIDAL ECOLOGY

The element of chance must be recognized in natural history, and the viewpoint taken here is that any particular organism arrived where it is by chance and remains there because it could grow there and nothing has killed or removed it. Colman (1933) is one of the few intertidal ecologists acknowledging the importance of this viewpoint. Though probably valid for individuals, this does not seem to be strictly true for species. The detailed papers on the settlement of invertebrate larvae by Thorson (1946; 1950) and D. P. Wilson (1952) should be seen for reviews of a wealth of information in reference to the aspects of nonrandom settling. (*See* also Chapter 17.) Apparently some kinds of larvae do not metamorphose, settle, or attach except in the presence of, for example, a certain substratum. Wilson presents an experimental study of a sand-dwelling polychaete worm showing great specificity for the substratum. In such cases, however, the element of chance is certainly still true in reference to the individual and, if the definition of chance includes either a hypothetical, complex, or unknown element, these worms still settle by chance although immediately governed by regulatory factors.

One should be surprised if a cause-and-effect relationship were revealed from the measuring of vertical distribution on surfaces with exposures varying in respect to several environmental elements, the variations of which had not been studied in their historical relationship to the observed distribution. The results of studies made without any knowledge of the history of the environment, and made at *a priori* chosen places or at places having irregular surfaces, or surfaces not uniformly exposed to the sea, have given results that (1) do not show sharp zonation, or (2) show no correlation with any known factor or combination of factors. The attenuation of distributions shown by Hewatt (1937, Fig. 1) and Broekhuysen (1940, Fig. 1) are interpretable on this basis. Dellow's (1950, Fig. 7) random distribution (Fig. 8) of range limits could have been expected on this basis. These specific bits of information are thus treated as negative evidence in so far as zonation or its causes and effects are concerned.

The chance sampling methods of the terrestrial ecologist or of the plankton oceanographer must be modified in the intertidal region with respect to the steep

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gradients and the relatively small distances. Habitats might well be chosen which are relatively uniform except for the variable, or variables, being considered. This has long been recognized as advisable by experimental scientists and for equally long this has been generally ignored by field ecologists.

The trend initiated by such students as W. H. Johnson (*e.g.*, 1933) and Hardin (1944), who have investigated the relationships of two or a few micro-organisms in a completely controlled environment, is encouraging. The dictum of Richards (1932) should be carefully considered: ". . .study exceptional habitats, . . . where the influence of certain factors is shown in an extreme degree." While at one time such extremes can be expected to be functioning as limiting factors (Liebig's law of the minimum) they can at other times be expected to be functioning in the somewhat reciprocal manner of inhibiting factors. This does not mean overlooking average conditions, but, as Allee (1922, p. 236) suggests, one desires these *and* the extremes. Certainly the simplest situations in nature are not now well understood, and it would be easier to gain an understanding of the environment by beginning in general with the simplest situations that can be found and working toward the more complex.

Many recent papers have yielded only negative evidence, and yet they have been published, some with inferences. An example frequently seen is the paper reporting observations in the vertical aspects of intertidal ecology, based on study of a convenient shore or a shore chosen otherwise than for pronounced vertical distribution. The vertical aspects of the particular shore are not conspicuous, and the results are correlated with but few other factors (or dimensions) of known variability. In our present state of knowledge one short visit to a site is not enough to reveal the causal relationships of what is observed. The effects seen cannot be expected to show any more than a coincidental relationship with the *predicted* values or the *concurrent* values of putative causal agencies. Such additions to our already massive literature reporting uninterpretable complex observations have been found to be of little use in our search for better explanations of the problems of intertidal ecology, and such papers for the most part have been ignored here.

The beautifully done historical account by Gislén (1929; 1930) has long been the standard reference for the history of intertidal and subtidal ecology. There are also the reviews by Fischer-Piette (1940); Stephenson and Stephenson (1949), Chapman (1946b), and Feldmann (1937 p. 101 ff.; 1951). Citations for this chapter have been selected with the hope of giving the interested student entry into the literature. Thus many of the references cited for a particular topic are either very recent or very old.

VERTICAL ASPECTS OF DISTRIBUTION

Historically we find that early biologists such as Charles d'Orbigny (1820) and Jean Vincent Felix Lamouroux (1824), in 1816, wrote about vertical distribution. The former said, "I believe I am the first who has indicated the zones or bands which each species of marine plant inhabits under the waters of the sea . . . " The latter is reputed (Gislén, 1930, p. 46) to have presented a scheme for subdividing the intertidal area according to the time of immersion and vertical range of the tide.

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Wahlenberg (1812) had given an even earlier account of zonation along the coast of Norway. Even earlier someone else may have said essentially the same things; many have since. Indeed, reporting the intertidal distribution of organisms has been an occupation attractive to many authors.

Vertical distribution as treated here is the vertical distribution on that part of solid shores affected by movements of the water surface, such as tidal action, wave action, and currents, and as affected by the differences due to such factors as adsorption (capillarity) and diffusion related to the air-water interface. The general observation is that throughout the world in the intertidal region, horizontally extensive, biotically distinct areas may be recognized, one above the other. These are (Johnson and York, 1915) narrow vertically but hardly less sharply distinct from one another in regions where the tide range is small, and they are correspondingly wide verti-

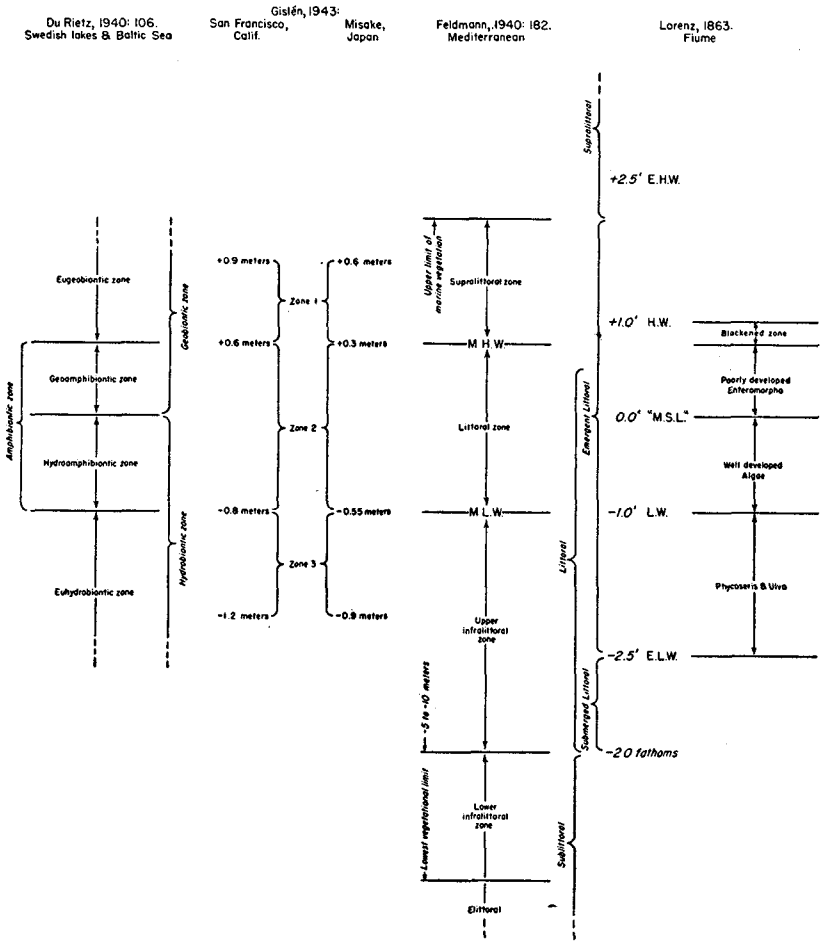

FIGURE 1.—*Intertidal zonation on different shores*
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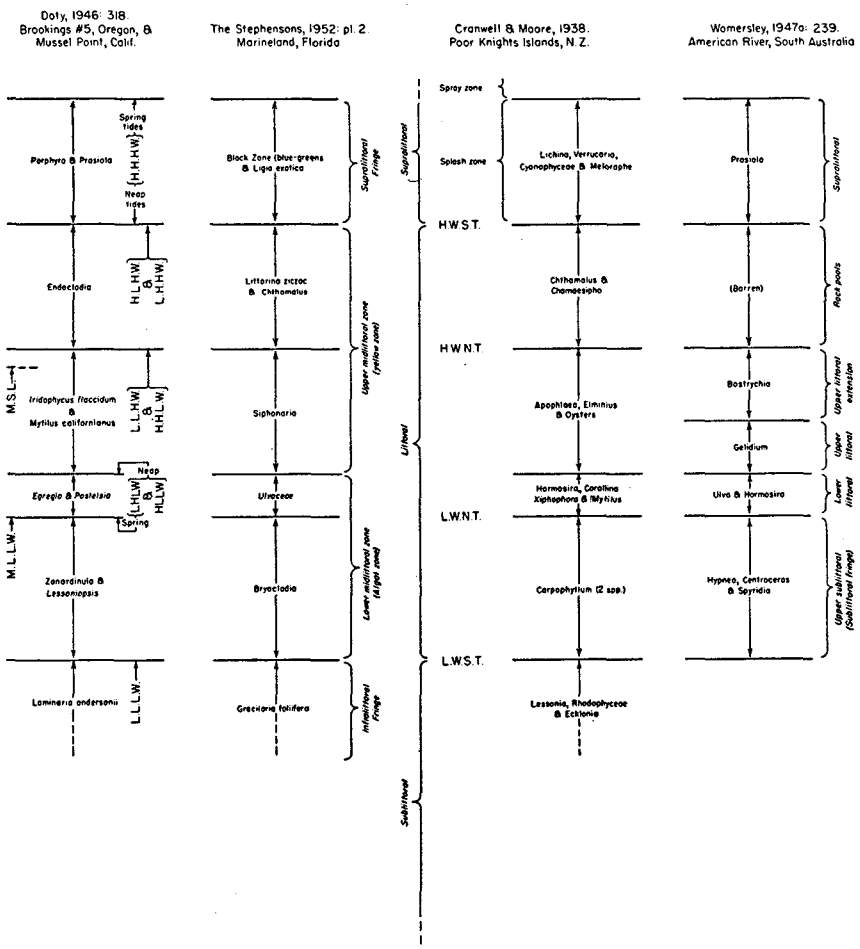
cally where the tide range is great. While these areas are usually called zones, they have often been called "girdles" and "belts". The zones may be thought of as two-dimensional samples of the biospaces discussed above. Zonation is found along shores where there is great or little tidal action, wave action, or current. In general the same series of zones, essentially of the same proportional heights, appears throughout areas having similar tides (Fig. 1). The different specific taxonomic entities, throughout their geographic ranges, appear consistently in the same zones (Doty, 1946, Fig. 2; Womersley, 1947, Fig. 3). In some cases this is for a relatively small geographic area—British Columbia to Central California (*e.g.*, *Postelsia palmaeformis* [G. M. Smith, 1944, p. 142]) or a very great one (*e.g.*, *Rivularia atra* from New England [Doty, 1948, p. 256], to South Australia [Womersley, 1947, p. 246]). Such zonation has been reported widely. Table 1 gives a set of key references to descriptions of intertidal vertical distribution by geographic areas.



GURE 1.—*Continued*

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TABLE 1.—*Geographical index of papers on rocky shore ecology*
(Primarily of those considered in this chapter)

NORTHWESTERN PACIFIC

Deryugin (1939)
Gislén (1931; 1943)
Tokioka (1953)
Yendo (1914)
Zachs (1927; 1929

NORTHEASTERN PACIFIC

Doty (1946)
Gislén (1943; 1944)
Hewatt (1935; 1937)
Northcraft (1948)
Ricketts and Calvin (1952)
Rigg and Miller (1949)
Shotwell (1950a; 1950b)

PACIFIC ISLANDS

Doty and Morrison (1954)
Kanda (1944)

SOUTH AMERICA AND CENTRAL AMERICA

*(Pacific)
Dansereau (1947)
Galtsoff (1950)*
Joly (1952)
Monod (1950)
Nonato (1951)
de Oliveira (1947; 1950)
Oliver (1944)
Skottsberg (1941)*

AUSTRALIA AND NEW ZEALAND

Bennett and Pope (1953)
Carnahan (1952)
Chapman (1949; 1950)
Cranwell and Moore (1938)
Dakin, Bennett and Pope (1948)
Dellow (1949; 1950)
Guiler (1950; 1954)
Womersley (1947)
Womersley and Edmonds (1952)

NORTHWESTERN ATLANTIC

Boergesen (1904; 1908)
Chapman (1946a)
Johnson and Skutch (1928a)
Pearse (1913; 1914)
Prat (1936; 1940)
Stephenson and Stephenson (1952; 1954)
McDougall (1943)
Williams (1949)

GULF OF MEXICO

Hedgpeth (1953)
Taylor (1954)
Stephenson and Stephenson (1950)
Whitten *et al.* (1950)

WEST AFRICA

Sourie (1954)

SOUTH AFRICA

Baardseth (1941)
Bokenham (1938)
Broekhuysen (1940)
Isaac (1937)
Stephenson (1947)

NORTHEASTERN ATLANTIC

*(Baltic)
Colman (1933)
D'Orbigny (1820)
Du Rietz (1947)*
Evans (1947a; 1947b; 1949)
Fischer-Piette (1934)
Gislén (1930)
Kitching (1935)
Levring (1937)
Lewis (1953)
Moore and Sproston (1940)
Morton (1954)
Southward (1953)
Southward and Orton (1954)
Steeman Nielsen (1951)
Davy de Virville (1940)
Waern (1952)*
Wahlenberg (1812)*
Zaneveld (1937)

MEDITERRANEAN AND BLACK SEA

Antipa (1933; 1941)
Delamare and Bougis (1951)
Ercegovič (1932–1934)
Feldmann (1940)
Huvé (1953)
Huvé and Huvé (1955)
Lorenz (1863)
Nasr and Aleem (1949)
Zernov (1913)

ARCTIC

Guryanova *et al.* (1930)
Madsen (1936; 1940)

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The levels between the zones are sometimes referred to as "breaks". They are recognizable as sudden changes in the dominant species present. The elevations at which these breaks occur are usually referred to as "critical levels" and are often correlated with features of the tides or with the distribution of key organisms. Such biological features as "physiological high tide", "litus line", and other terms have been used for particular elevations recognizable by the distributions of intertidal organisms. Guiler (1950, p. 188) equates his earlier term "lethal level" with critical level—*i.e.*, the tide level at which "very great diminution in numbers . . . takes place." Lewis (1953) presents one of the most recent discussions of variations in biological critical levels. Tidal datum points are used as reference points from which elevations are measured physically. These are usually mean lower low water (where there are semidiurnal mixed tides), mean low water (semidiurnal and diurnal tidal regions), or mean sea level.

It has been observed (Lamouroux, 1824 [1816]; Gislén, 1944; Knight, 1947; Zenkevich, 1947); and expected (Chapman and Trevarthen, 1953), though not yet studied satisfactorily, that the actual levels in reference to mean sea level change with latitude. The general observation is a lowering with nearness to the equator.

Upward shifts of zones are widely found with increased wave action. Hewatt (1937) recognized such shifts along his transect but made no allowance for them. Colman (1933), Johnson and Skutch 1928a, p. 191), and Broekhuysen (1940, Fig. 1) all discuss allowances for wave action and usually suggest an allowance of about 2 feet. Stephenson (1944, Fig. 310) and Lewis (1953, Figs. 7, 13) illustrate nicely the shift one sees upon levelling from a wave-exposed to a wave-protected area (Fig. 14). A formula for analyzing and predicting this effect of wave action has been proposed by Guiler (1950). Lewis presents a bimodal graph (his Fig. 9) that represents wave action to be most intense between LWS and LWN and again between HWN and HWS.

Particularly because of the current interest in economic seaweeds and because of our interest in the way marine organisms contribute to the corrosion and corrasion of shores, the protection from erosion and to the positive upbuilding of beaches, reefs and shores, we should like to know something of the quantitative distribution of organisms. Unfortunately very little has been done in this respect in the intertidal region, with the exception of some work at Murmansk (Zenkevich, 1947, p. 73). The subtidal region has received considerable attention through the work of such authors as Gislén (1930) and, currently, the work at the Institute of Seaweed Research, as summarized in the Annual Reports of that institution. It would be interesting to know if the distribution of mass and numbers follows the distribution of life forms to be expected in associations of terrestrial organisms.

In some cases certain genera or life forms (*e.g.*, *Calothrix*, littorines, barnacles, or mussels) are used as indicators of certain zones throughout the world. Others are so used in the Northern Hemisphere (*e.g.*, *Laminaria*) or Southern Hemisphere (*e.g.*, *Cystophora* or *Hormosira*) or only in the tropics (*e.g.*, *Padina* and *Bostrychia*). Johnson and Skutch (1928b) consider and reject the naming of zones according to these local dominants. Stephenson and Stephenson (1949, p. 297 ff.) have recently rejected such naming on a world-wide basis as neither descriptive nor consistently

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applicable. For example, "balanoid" recalls nothing in the way of position or form when used in the combination "balanoid zone", and there are places where balanoids are absent. As a subexample, at Woods Hole the barnacles are removed by ice during many winters, and there are none in many portions of what might be called a balanoid zone until the next period of *Balanus* setting. To extend this: in the British Isles one would be inclined to accept the terms fucoid zone and laminarian zone. The former would be in the upper portion of the littoral region, and the latter in the sublittoral. In the Southern Hemisphere, the term fucoid is used to refer to such genera as *Cystophora* and *Carpophyllum* instead of to the Fucaceae. These two genera characterize the sublittoral, a zone that would be characterized by the Laminariaceae and called laminarian zone in the Northern Hemisphere.

The major zones or regions, since the time of Forbes (1843, 1844) and Lorenz (1863), have been named I, II, III (etc.) by various people and named in the reverse order by others. For detailed discussions of these names see, *e.g.*, Ricketts and Calvin (1952), Northcraft (1948, p. 396), Gislén (1943, p. 22), Du Rietz (1940), Feldmann (1937, pp. 101 ff., Table 5). Numbers by themselves are perhaps the least significant of all systems, though convenient for local field work. Isaac (1937) referred to the zones he found in South Africa by the letters A through H, but also named them according to the dominant algal species.

Zones might be recognized according to the tide factors (Doty, 1946) which may delimit them. This system is too complex to be satisfactory and is at present unusable; rarely have authors given sufficient correlated tidal and distributional data for an analysis on this basis.

Zonation at the seashore has been presented in many ways and, unfortunately, often without a description or without explaining just how the data were obtained. One suspects, after some experience in the matter, that most authors fuse into a report on observations at one station measurements taken from a region so horizontally broad that areas of nonuniform physiography are recorded, and thus a great many overlapping ranges appear in their results. Sampling nonplane nonuniformly exposed shores gives the same type of results.[2] We are not concerned here with such types of shores for they yield results too complicated for an attempted explanation at our current level of interpretation of intertidal phenomena. Figure 1 illustrates a few sets of data (*see also* Ricketts and Calvin, 1952, Figs. 131–132), chosen to illustrate some of the different types of zonation presented. In intertidal regions three to seven zones have been distinguished. In places more than seven may be distinguished.

While we are not concerned here in detail with more than the uppermost of the sublittoral region and the lowermost parts of the supralittoral region, we feel that some effort toward development of a uniform explanation of these observations should be made. Perhaps the clues leading to the explanation proposed here are in the statement of Womersley and Edmonds (1952, p. 89) who in discussing subzonation within their "littoral zone" say that it *may be* "divided into sub-zones as required," and in Du Rietz's (1940; 1947) papers, which in themselves are efforts

[2] The excellently documented study by Morton (1954) on faunas of crevices in the intertidal zone appears to be the best study to date of the distribution of organisms on an irregular surface.

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toward a better and more nearly uniform explanation of zonation. Especially to be noted are the views of Stephenson and Stephenson (1949), who after many years of ocean-shore study have concluded that the intertidal zones are caused by the same factors that cause zonation around bodies of water such as fresh-water lakes.

From examination of Figure 1 it is certain that one inelastic set of names or numbers is not satisfactory as a basis for a uniform nomenclature. It has been thought that perphaps a consideration of the nature of zonation in reference to the possible causal factors might be a profitable way of bringing forth a "uniformity theory" for the differences observed between zonation on one shore and another. Study of the scheme proposed by Du Rietz (1940), devised from a consideration of the variables along the shores of Swedish lakes and the ocean (Baltic Sea), provides clues as to the integration of the lake-shore and ocean-shore phenomena of interest both to the limnologist and to the marine biologist.

Possibly the factors involved in zonation both on fresh- and salt-water shores are those related to the movement of materials at the air-water interface. This movement is by diffusion, convection, and mass action. The gradient of humid air above the water surface is a diffusion phenomenon, as are the gradient rates of gas exchange in the near-surface water below. The winds which may significantly alter these diffusion phenomena, and which provide the waves, are essentially convection movements. The tides and the waves are the most notable of the mass-action phenomena. Admittedly the actual degree of penetration of energy through radiation (light and heat) or materials by diffusion, and so on, is important, as are other physical and chemical phenomena. Adsorption and its relative, capillarity, cause movement of water into the soil above the water line or into the surface of the rocks there. Wave action provides a very frequently wet (or very frequently dry) expansion of the meeting place of the land and sea. Tides are like long-period waves but distinct from them in their regularity and certain predictable (repeating) peculiarities of elevation and duration. In view of the great preponderance of opinion as to the importance of tides in intertidal zonation, it is worth while to consider their major variations and the possible relationships of these variations to intertidal organisms, although it is well recognized that tides are not the only factors involved.

The major variation of the tides is a shifting upward and downward of the surface of the sea. If this shift from high water to low water occurs once every lunar day (24.84 hours) (Fig. 2*A*, upper abscissa, and Fig. 3*A*) the tides are said to be diurnal.[3] If this shift takes place twice a day, and successive high tides and successive low tides are similar in height (Fig. 2*A*, lower abscissa, and Fig. 3*B*, at least in reference to low tides), the tides are said to be semidiurnal. If the variation in elevation takes place twice a day but successive high tides and successive low tides are quite different in height (Fig. 2*B* and Fig. 3*C*) the tides are said to be mixed. In some localities the type of tidal variation changes from time to time. Plate 1 shows the distribution of these tidal types on the ocean shores of the world. The high tides are a certain number of hours behind the transit of the moon, depending upon the locality.

When sun and moon are in syzygy (conjunction or opposition) their combined effect on the tides is great, and spring tides of larger range (*e.g.*, 20 per cent over mean range) result. When the moon

[3] Hydrographic terms and abbreviations used in this chapter are those used and defined in special publications 135, *Tidal Datum Planes*, and 228, *Tide and Current Glossary*, of the U. S. Department of Commerce, U. S. Coast and Geodetic Survey, or are derivatives from them.

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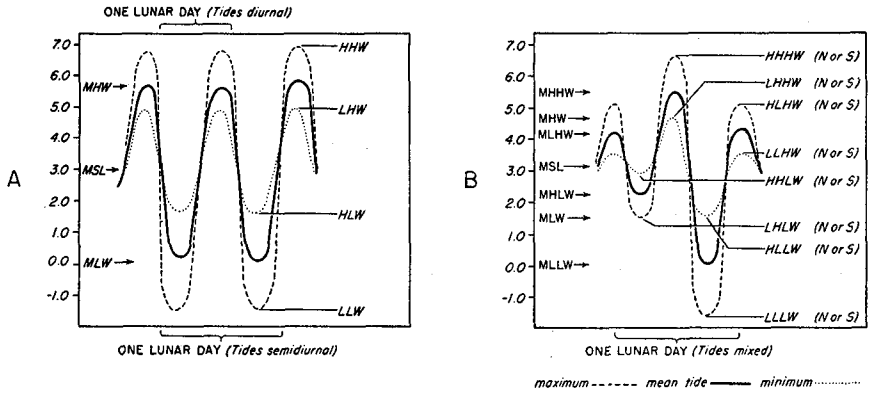

FIGURE 2.—*Tidal levels and types*

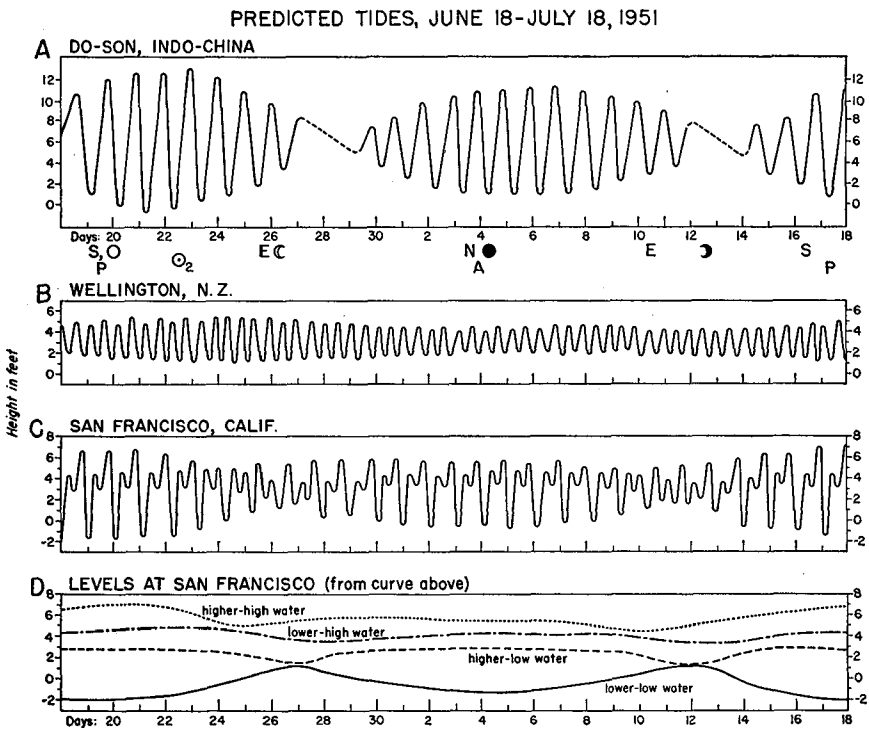

FIGURE 3.—*Predicted tides of different types plotted for 30-day periods at the designated localities*
Compiled from U. S. C. & G. S. Tide Tables.

is in its quarter phases the tidal effect is least, and neap tides occur (*ca.* 20 per cent less than the mean).

On most shores, with a change in the moon's declination away from the equator, succeeding high waters are at different heights (Figs. 2, 3), as are succeeding low waters. During such periods the moon is said to be in the tropics, and tropic tides occur, *i.e.*, tides with the diurnal or declinational inequalities

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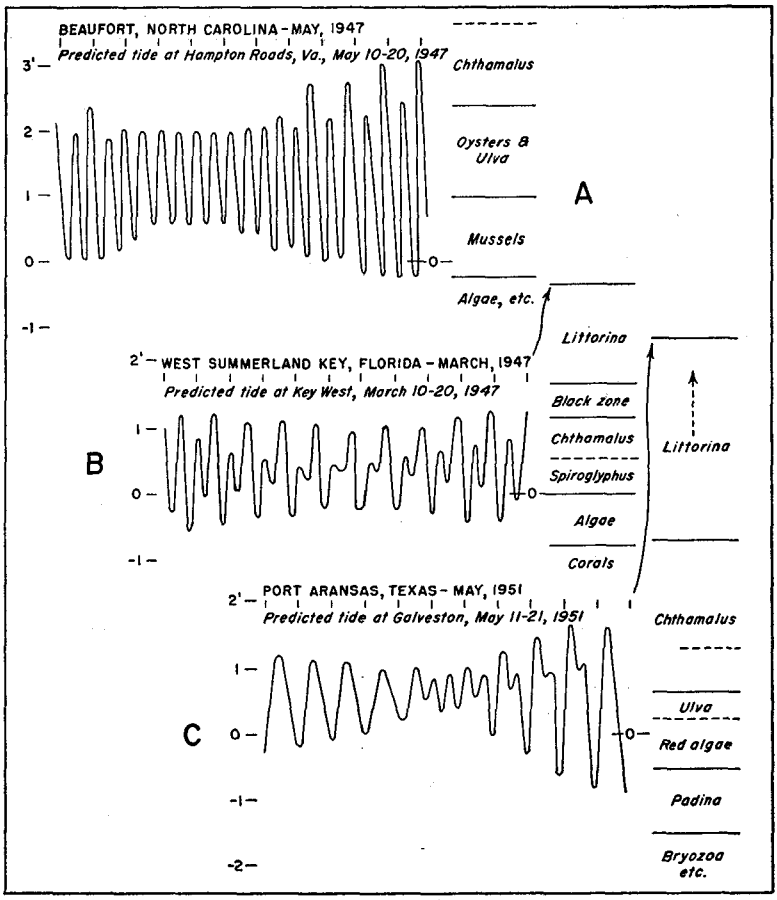

FIGURE 4.—*Zonation and predicted tides for the month preceding observation*
From Hedgpeth (1953).

of elevation mentioned. When the moon is over the equator one expects equatorial tides (Fig. 4, for May 11–14 at Port Aransas and Beaufort), *i.e.*, those with little diurnal inequality. That is to say, when the moon is at 90°, or immediately over the equator, successive high tides occur at similar elevations, and successive low tides are at similar heights.

A tropic tide during a spring period may be 10–30 per cent lower or higher than a mean low tide or a mean high tide. During neap periods equatorial tides are 10–30 per cent less in range than the mean values. These two conditions occur at about 7-day intervals, and they are repeated at about 14-day intervals. The presence of significant tropic tides means the shore has mixed tides. Without them the tides will be diurnal or semidiurnal.

The moon moves in its eccentric orbit about the earth every 27½ days, and the tides produced when the moon is closest to the earth (perigee) are about 20 per cent greater than when the moon is farthest away (apogee). Thus there is a 27½-day rhythm in the tides (Fig. 3*D*). The tidal phenomena of the first half of a year, *e.g.*, of the period of December 22 through June 22, are repeated roughly in reverse order during the last half of the same year, *e.g.*, the period of June 22 to December 22. There is also variation through the year, for example, the period of solar perigee (December) is characterized by tides of greater amplitude than periods of solar apogee (June).

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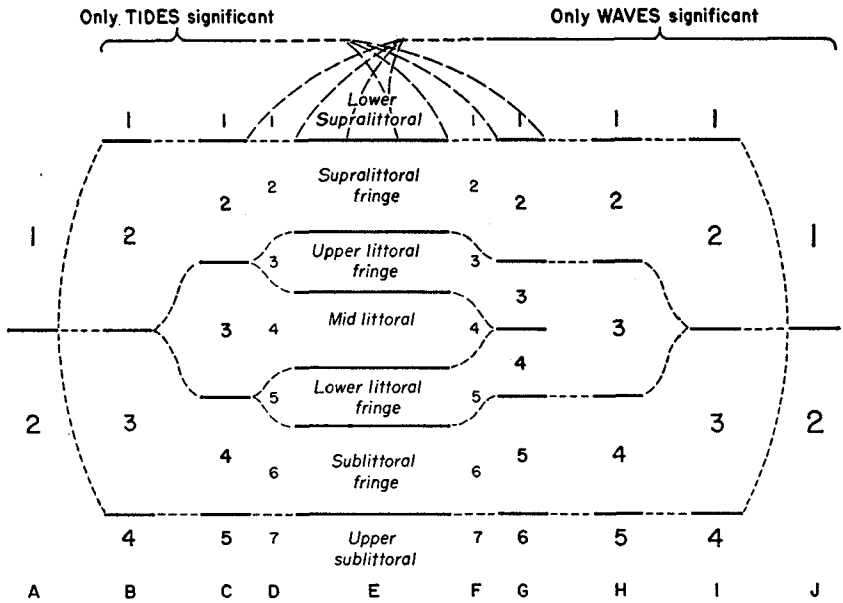

FIGURE 5.—*Types of zonation to be expected under varying conditions of tide and wave action*

BASIC VERTICAL ZONATION SCHEME

Shores without a littoral zone.—With the simpler aspects of the tides in mind we can proceed to a discussion of the patterns of zonation generally found on plane surfaces uniformly exposed to the sea. The simplest situation in the way of a biotic arrangement at the air-water interface would be that to be expected on a shore where there were none of the factors operating to produce gradient or other changes as this interface is approached from above or below. One could expect then a sharp line between a sublittoral and supralittoral region, perhaps appearing as a sharp line between the fishes and the flowers. Such a situation is diagrammed at *A* and *J* in Figure 5.

With the presence of such factors as adsorption and diffusion (of water, solutes, gases, radiant energy) one would expect the biota to differ as the interface was approached and the situations diagrammatically presented in Figure 5 at *B* and *I* to prevail. Perhaps if these factors were lacking but there were random wetting of zones 1 and 2 by random wave action (*i.e.*, nonregularly occurring wave action as by storms) this pattern would prevail. Note that it is essentially that of Du Rietz (Fig. 1) wherein zones 1 and 2 of figure 4 are equivalent to his geobiontic zone, zones 3 and 4 equivalent to his hydrobiontic zone, and 2 and 3 to his amphibiontic zone.

The amphibiontic zone of Du Rietz is the region spanned by occasional low-water or high-water levels, however caused. The upper section (2 in column *B*, Fig. 5), his geoamphibiontic zone, is one populated by periodically submerged land organisms, and his hydroamphibiontic zone is one of aquatic organisms periodically exposed to air. His eugeobiontic zone we translate as supralittoral, his euhydrobiontic zone as sublittoral. In Figure 5 these latter two zones are consistently aligned.

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Our major interest is in the explanation of what appears between the supralittoral and sublittoral zones.

Shores with a littoral zone.—In a physical sense the essential difference between ocean shores and lake shores is that tides and what we are calling a littoral zone are found only on the former. The scheme presented by Du Rietz, in an effort toward provision of a uniform interpretation of shore zonation of both lake and ocean shores, conflicts with most reports of the zonation on ocean shores in that it lacks this littoral zone. Since Du Rietz's schemes were devised in the light of his studies (1940) of Swedish lakes and the Baltic Sea, neither of which is significantly tidal (Pl. 1), one could not expect, *a priori*, that his scheme would account for features peculiar to the *tidal* ocean shores.

The critical and interesting paper of Du Rietz (1947) was not found in time for thorough digestion and integration in this manuscript. Essentially it expands the earlier paper (1940) and it contains little that contradicts what is said here providing sympathetic interpretation and account of differing definitions are made.

Classically the distinction is had in the terms *lacustrine* and *littoral;* the Romans apparently recognized this difference, although modern ecologists may have overlooked it. The important difference in so far as the biota is concerned is the actual shifting upward and downward of the air-water interface.

The variations in diurnal and semidiurnal tides (Figs. 2, 3) could be expected to induce just such a pattern (*C* or *H* in Fig. 5) as Figure 6 which Stephenson and Stephenson (1949) present as a "universal scheme." Their supralittoral zone is delimited downward in correlation with the Highest High Water (Fig. 2*A*, HHW) level. Their supralittoral fringe appears to be bordered by this level above[4] and below by the Lowest High Waters (Fig. 2*A*, LHW). Their midlittoral zone would be expected then to be distinguished above by a correlation with this same LHW and below at Highest Low Water (Fig. 2*A*, HLW). Their infralittoral fringe would be expected to be limited above the HLW and below at Lowest Lower Water (Fig. 2*A*, LLW). The infralittoral of Stephenson and Stephenson would be expected to be limited upward in correlation with this same LLW. The fringes would appear then to be essentially functions of neap and spring range differences.

Actually the chance correlation of waves, seiches, and such, in co-ordination with the tides and the variations between the ranges of succeeding spring tide (and neap tide) series, would lead us to expect that the zonation patterns would not be sharply delineated as indicated in Figure 5, columns *C* and *H*, unless zonation is independent of the tides and shorter-period waves. Indeed, if this type of zonation, which we can expect along shores where there are diurnal or semidiurnal tides, were clearly present there would without a doubt be a great deal more agreement as to a fundamental zonational scheme and probable causes.

Nevertheless, in recent years the active workers (*e.g.*, Stephenson and Stephenson, 1949; Womersley and Edmonds, 1952; Chapman and Trevarthen, 1953; Guiler,

[4] Many authors have observed that the actual breaks in the biota were displaced upward from the levels of the possibly related tidal features. Stephenson and Stephenson place an "EHWS," presumably "extreme high water springs," quite low in their supralittoral fringe, with little else being given in the way of correlating their levels with tides. Thus one has no way of judging whether the level they mark "EHWS" is intended to represent the functional (effective) level of these tides, the actual level achieved, or some predicted level.

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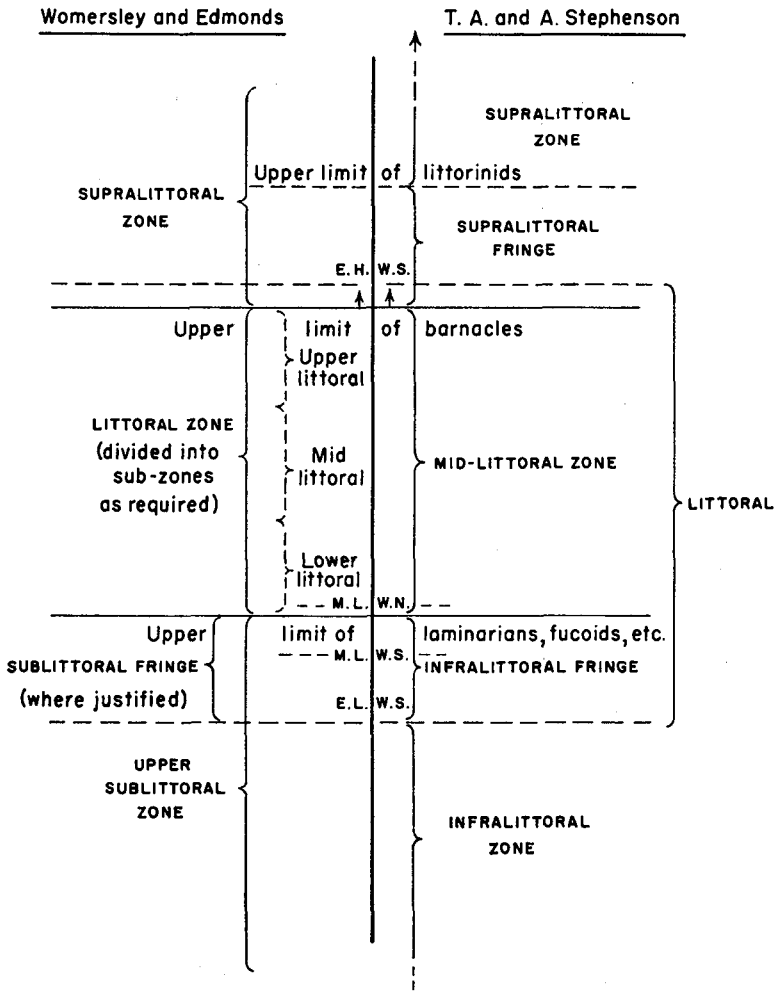

FIGURE 6.—*Universal schemes for zonation, according to the indicated curves*

1951a; 1951b; 1952a; 1952b; 1952c; Lewis, 1953) have rather widely accepted three major zones with two fringes as described above. These two fringes seem to be equivalent to the amphibiontic zone of Du Rietz. The lower part of the supralittoral (lower supralittoral, mangrove zone, white zone of Stephenson and Stephenson) seems to be equivalent to a part of his eugeobiontic zone, the supralittoral fringe to his geoamphibiontic zone, the infralittoral fringe to his hydroamphibiontic zone, and the upper sublittoral to a part of his euhydrobiontic zone. The innovation is the littoral zone which appears (hypothetically, to be sure) regularly between the geoamphibiontic and hydroamphibiontic zones. Again, the regular difference between the relatively, or actually, tideless shores for which Du Rietz proposed his scheme and the ocean shores were this littoral zone is found is the presence of tides on the latter. Waves, humidity, etc., are common to both.

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The authors mentioned in the above paragraphs are concerned with the terminology of these zones. Similarly there are detailed discussions of just where these major zones should be delimited. Passing over these details, we shall discuss first the principal features of the three major zones, and then possible causes.

Supralittoral zone.—The *supralittoral* zone is the lower edge of the maritime terrestrial region. Except for violent storms, tsunami, or under high wind and spray conditions, this area is little affected by movements of the water surface and so is for the most part beyond the scope of the present chapter. The lowest edge of the supralittoral, the *supralittoral fringe*, is the only part affected by the sea in such a way as to be treated with the intertidal region. In many areas (Dellow, 1950, p. 363; Doty, 1948, p. 255) this zone if densely populated is dominated by blue-green algae of the genus *Calothrix*. In the Northern hemisphere *C. scopulorum*, *C. pulvinata*, *C. pilosa*, *C. crustacea*, and *C. vivipara* are the most common. Perhaps *Prasiola meridionalis* of the North Atlantic, *P. mexicana* of the Northeastern Pacific (Doty, 1946, p. 321), and another *Prasiola* in Australia (Womersley, 1948, p. 147) may be used likewise to identify this zone on bird-dung-spattered rocks. Other genera of blue-greens such as *Plectonema* and *Entophysalis* as well as the "marine lichens" are common, though the latter may be more truly elements of levels above the supralittoral fringe. Invertebrates other than the characteristic littorinids are few, but on North American shores most conspicuous are isopods (often *Ligia* (= *Ligyda*) *exotica*, *L. pallasi*, or *L. occidentalis*). The biotic affinities of this region seem to be with the terrestrial fresh water or aerial environment. Edaphic factors are important. This region is the geobiontic zone of Du Rietz.

The so-called supralittoral fringe demands rather careful study. It forms, often, a so-called "black zone" well above the usual levels to which the tide ascends. The isopods of the genus *Ligia*, which Stephenson and Stephenson refer to as "the rapid isopods," appear in this fringe area. Stephenson and Stephenson (1950, p. 367 ff.) find this region divided frequently into three subzones. Their "black zone," the lowest of these three, is accepted as the approximate equivalent of our "supralittoral."

It is observable (Cranwell and Moore, 1938; Dellow, 1950) that during periods of rough seas the littorines (*Melaraphe* and *Littorina*) move upward and browse on the surface or lower edges of the blue-green algal, *Calothrix*-dominated, area. The edge of the latter, as a result of this and perhaps other factors, moves upward. In ti[illegible]m seas these communities move down; the littorines actually move down into the upper [illegible] *Calothrix* dissemules develop at lower levels in such a manner that the *Calothrix* zone ma[illegible] appear as low as the upper limits of the littoral zone.

On Cape Cod, Massachusetts, the *Calothrix* population extends farther down the solid shores in areas protected from wave action, and the species on the rocks around some of the fresh-water ponds near the ocean are similar to those on the maritime rocks. Similarly here the *Calothrix* apparently is eroded or killed upward in correlation with augmenting wave action. It is not surprising to find that the community grows lower on the protected sides of boulders. In most cases at that locality, littorines, although they migrate upward during periods of rough seas, are probably not responsible for the upward delimitation of the *Calothrix* zone.

This region in South Australia is what Womersley calls a *Melaraphe* (littorine) zone or his lower supralittoral zone. Womersley and Edmonds (1952) propose an *upper littoral*, the motile constituents of which may be postulated to move upward during favorable weather or tide periods and to occupy the black subzone of Stephenson and Stephenson (1950, p. 368) or (Fig. 4*B*) extend above it. During periods when environmental conditions are unfavorable for existence at the higher levels, these same organisms may inhabit or even dominate the upper part of the littoral region, and then permit distinction of the upper littoral zone proposed by Womersley and Edmonds. Guiler (1951b, p. 65) discusses what must be this same phenomenon in Tasmania where, sometimes, depending upon surf conditions, *Melaraphe* extends up to the lichens above, or a bare zone[5] (gray subzone) is left between, presumably during calm weather. While we feel that this black zone in semidiurnal tide regions represents the "meeting place" of the marine and fresh-water or aerial communities, Stephenson and Stephenson (1950, p. 367) feel that their white zone should be accorded that distinction.

[5] This gray or barren zone is a useful observation, as one might well expect, *a priori*, that there would be such zones of largely unoccupied surface, dead organisms, and juvenile organisms, as a result of the lagging of biotic development behind the changes in the environment.

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The observations of Stephenson and Stephenson and of Chapman, and their students, are largely from areas of two sorts: (1) those where the tides are largely semidiurnal, or (2) those where the shores between the upper part of the supralittoral fringe and the lower part of the same zone are not exposed to regular differential exposures. Such differential exposure is to be expected where there are significant equatorial and tropic tidal changes. On shores affected by mixed tides such exposures does occur, but it is not found on shores affected by semidiurnal or diurnal tides. Inspection of Figure 2*B* and Figure 3*C*, in reference to mixed tides, reveals that there is not merely a high water of neap tides and a high water of spring tides, but that there is both a higher high water of neap and spring tides and a lower high water of neap and spring tides. Furthermore, successive neap and spring ranges are not the same (Fig. 3*C*), and thus it is advisable to distinguish, in Figures 2*B* and 3*C*, between highest higher high water of neaps (HHHWN) and of springs (HHHWS), and so on. Inspection of these figures reveals the region of the shore between the lowest lower high-tide level (LLHWN) and the highest higher high-tide level (HHHWS) to be divided by two features termed, in Figure 2*B*, LHHW and HLHW. In practice the levels (Fig. 3*D*) of these two probably cannot be distinguished and do not always coincide with neap or spring periods, but they (Fig. 3*D*) may effectively split the region of the semidiurnal shore where one would expect but one zone, the supralittoral fringe. On coasts with a narrow tidal range (*e.g.*, Tasmania), such detail is too cumbersome for practical use.

Does this really have an effect on the distribution of the organisms? It seems reasonable, on the basis of the observations given above, to assume that the *Calothrix* or blue-green algal community is essentially nonmarine and that the littorine community found grazing on it is essentially a marine community. One would be inclined to recognize any limit between these two as the boundary between the supralittoral and the littoral zones. The *Calothrix*-dominated zone, when the two are occasionally distinct, is the uppermost, and we would thus call it the indicator of the supralittoral fringe. As the littorines as lower they indicate the position of an upper littoral fringe. This is perhaps essentially an extension of Womersley and Edmonds' (1952, p. 89) feeling that "the organisms present in the littorinid zone are more closely related to those in the upper part of the littoral, and this region should therefore be called the 'littoral fringe' if it is to be regarded as a fringe zone." Such a segregation of the material in the supralittoral fringe in a semidiurnally controlled zonational pattern might be expected farther along the coast or elsewhere in the world where the tides were mixed and of sufficient range so that the variations in the tide dominated over the chance variations caused by wind. This splitting with change in tide type is illustrated by the change from the zonation "2, 3" in *C* to "2, 3, 4" in *D* in Figure 5.

Littoral zone.—A *littoral* (midlittoral) zone is apparent in midregions. While definitions of this zone differ it is widely recognized. It is recognizable in Japan (Gislén, 1931; 1943; his zone 2) and on the eastern North Pacific Shores (Gislén, 1943; 1944; his zone 2), along the east coast of North America Stephenson and Stephenson, 1950; midlittoral; Johnson and Skutch, 1928a, p. 191, littoral), on South African coasts (Isaac, 1937; Stephenson, 1944), in Australia (Womersley and Edmonds, 1952, littoral), New Zealand (Chapman and Trevarthen, 1953, midlittoral), and elsewhere. The littoral region is, in general, a region of regular alternate exposure to submersion and emersion. Edaphic factors are less important, and the biotic affinities are more truly with the sea-water environment. Du Rietz presumably might have called this a euamphibiontic zone. Biotically it is characterized on the west coast of North America by such species as *Anthopleura elegantissima*, *Pachygrapsus crassipes*, *Pagurus granosimanus*, *Thais emarginata*, and certain algae (Hewatt, 1937; Doty, 1946) This is, in general, the balanoid zone of various authors.

The littoral zone is at time subdivisible near mean sea level. The upper portion, on the west coast of the United States, supports fuci (*Pelvetia* and *Fucus*) and littorines (*e.g.*, *L. scutulata* at Pacific Grove, California), along with *Balanus glandula* and *Tegula funebralis*. The lower portion of the zone on the west coast of North America is characterized by *Mytilus californianus*, *Iridophycus coriaceum*, *I. flaccidum*, *Mitella polymerus*, and *Tegula brunnea*. Johnson and Skutch (1928a, p. 191) describe a perhaps similar subdivision of the littoral zone on the coast of Maine, in North America, and Chapman and Trevarthen (1953) say that a similar situation may be present in some of the localities they have studied in New Zealand. The latter authors and Doty (1946), Womersley (1947), Nasr and Aleem (1949), Stephenson and Stephenson (1952), and Womersley and Edmonds (1952) describe the subdivision of the littoral zone into at least three subzones.

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Such subdivision leads us a step further in our developing hypothetical explanation. The simpler scheme, from top down—supralittoral, supralittoral fringe, littoral, sublittoral fringe, and sublittoral—could be explained, again, on the basis of the presence of either waves or tides of uniform character. This is essentially the pattern displayed in *C* and *H* of Figure 5. Division of the littoral zone into an upper and a lower portion could be ascribed to the variation of waves from zero amplitude to x effective amplitude, where x is the distance between the top of zone 3 and the bottom of zone 4 in column *G* of Figure 5. Similarly it could be ascribed to a semidiurnal tide with low tidal range—so low that the effective levels of the high and low waters are blanked out for example by the diurnal inequality or double tide (an agger or gulder). In a mixed-tide region such as the west coast of the United States the highest low tides and the lowest high tides of the year occur at about the level where this division is recorded. This is not necessarily true of all shores having mixed tides.

Since shores having mixed tides have lowest lower levels of low water (LLLWS) and highest lower low-water (HLLWS) levels both of spring tides and highest higher low water (HHLWN) and lowest higher low water (LHLWN) of neap tides, a set of fringes between the littoral and sublittoral, bordering the (mid-) littoral, might be expected *a priori*, if tides are causes of zonation.

The three subzones of the littoral zone may be these upper and lower littoral fringes, with a (mid-) littoral zone between. Along the west coast of North America in passing upward over the upper limit of the sublittoral fringe one crosses a very sharp break and then comes to a fringelike zone of organisms. Some of these are consistent in appearance, such as *Egregia menziesii*, *Postelsia palmaeformis*, and *Hedophyllum sessile*. Others such as *Gigartina canaliculata* and *Rhodymenia affinis* appear to be less consistent from year to year in the range of levels throughout which they appear.

A few years after publishing (Doty, 1946) a study of the vertical distribution of *Gigartina canaliculata*, done on Hewatt's (1937) transect at Pacific Grove, the distribution of this and related species were restudied. The small, possibly more quickly developing species (pioneer forms of Northcraft, 1948) peculiar to the lower littoral region were spread much more highly than when measured before. The longer-lived species of algae such as *Egregia* and *Hedophyllum*, on a near-by transect at the same levels, were distributed as before. In studies of zonation, long-lived and perennial forms such as these two species have always given more consistent and repeatable results than have the shorter-lived forms.

Kylin (1918) and Gislén (1930, p. 48), as well as others (*e.g.*, Hewatt, 1937, p. 179), have recorded vertical movements of zonal limits or breaks in the intertidal area with the differing of season. Like the overlap or presence in a distinct uppermost littoral subzone of the littorinid, *Melaraphe*, in Anzac regions (Womersley and Edmonds, 1952; Cranwell and Moore, 1938; Dellow, 1950), correlated apparently with roughness of sea, short-lived or quickly developing forms may grow or, if motile, "move" sufficiently fast to cause a shift in elevation corresponding to short-term shifts in critical levels (Northcraft, 1948). When they do not, a bare zone may result, or a zone of hardy forms, such as the perennial forms *Egregia* and *Hedophyllum*, may persist without the more ephemeral or motile indicators or inhabitants. It thus may be wise to keep this lower littoral zone (5 in Fig. 5*D* and *F*) of Womersley's in mind as a candidate for consideration as a *lower littoral fringe* (Fig. 5*E*). Though Hewatt (1937) records no animals restricted to this area, animals such as *Acmaea limatula*, *A. mitra*, *Lottia gigantia*, and *Thais emarginata* range only down to what might be distinguished as the upper level of such a lower littoral fringe.

Organisms appear to settle at random throughout a greater area than that in which they mature, if short-lived forms, or in which they persist, if long-lived forms. This seems particularly true of pioneer species. Many short-lived species thus may appear and mature during a single 7- or 14-day tidal period. These species can be expected to be distributed in conformity with the zoning factors peculiar to their short period of existence. The species already in the region, having been exposed to zoning factors acting previously at different levels, may thus be expected to be zoned differently.

Sublittoral zone.—The sublittoral zone (infralittoral zone of Feldmann and of Stephenson and Stephenson) is characterized in the North Pacific by laminarioid algae and at least in part by the Delesseriaceae (Rhodophyta). The aspect is of a sharp shift from the dull colors of the littoral zone to bright-red forms and the laminarioids below mean lower low-water level. The sublittoral is an area predominantly neritic and benthic. This area, on solid surfaces, is one in which edaphic factors (Gislén, 1930, p. 70) are expected to be relatively unimportant. One would not expect, though, that

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wood-boring cellulose digesters would occur in coral any more than one would expect pholads in glassy basalt. Du Rietz would call this zone the hydrobiontic belt.

Animals characteristic of the sublittoral region in the North Pacific are: nudibranchs, tectibranchs, the large brachyurans, echinoderms, and hydroids. *Zostera* and *Phyllospadix*, two marine flowering plants, are conspicuous here as is *Zostera* in the North Atlantic. *Posidonia* (especially Mediterranean), *Thalassia* (Gulf of Mexico), and *Halophila* (tropical Pacific) are similarly characteristic in more tropical areas. *Halophila* is abundant as far as 15 feet below low-water level in Kaneohe Bay on the Island of Oahu in the Hawaiian chain. The Sargassaceae (Phaeophyta) are characteristic of this region throughout the world, with some specific exceptions. *Halimeda*, which is so largely responsible for the filling in of atoll lagoons, is similarly a widespread indicator.

Various authors (*e.g.*, Lorenz, 1863; Zachs, 1929; Chapman and Trevarthen, 1953) suggest that the sublittoral zone could be subdivided. Feldmann (1937, p. 51 ff.) distinguishes an upper sublittoral (*étage infralittoral supérieur*) and a lower sublittoral zone (*étage infralittoral inférieur*). The latter he redivides into 5- to 10-meter divisions based on elevation. Actually these lower limits and portions of the sublittoral zone are below the scope of this chapter. It is to these areas that Gislén's classical work (1929–30) applies.

The sublittoral fringe, a term suggested by Stephenson (*e.g.*, 1944, p. 301), has been considered the area of the shore between the level of the lowest part ever or only rarely exposed to the air and the lowest levels regularly exposed to the air by, *e.g.*, the spring tides. In regions having mixed tides (Pl. 1) this zone may be expected in relation to lowest lower low water of spring tides (LLLWS) and highest lower low water of spring tides (HLLWS), the latter level (Fig. 3) apparently being approximately the same elevation as mean lower low water. In regions having semidiurnal tides (Pl. 1) this zone may be expected in relation to extreme low water of spring tides (LWS) and extreme low water of neap tides (LWN). Or again as reported in the literature this lower fringe in semidiurnal tide regions of considerable tide range may be more nearly in relation to lower low water of spring tides (LLWS) and highest low water of spring tides (HLWS).

This fringe is recognized on the west coast of North America as the zone dominated by such genera as *Phyllospadix* and the algae *Zanardinula*, *Lessoniopsis*, *Alaria*, and *Gigartina* (*G. corymbifera*, *G. spinosa*, and *G. volans*).

Womersley and Edmonds (1952) feel that the sublittoral fringe is characterized by organisms that so frequently extend down over the lower margin into the upper sublittoral zone that one should not separate this fringe as a separate zone. Thus (Fig. 6) the brackets indicating the extent of the sublittoral zone, as they define it, include the sublittoral fringe as well.

Chapman and Trevarthen (1953) and Stephenson and Stephenson (1949) are inclined to think otherwise. Stephenson and Stephenson (Fig. 6) would include this sublittoral fringe in their littoral zone. Perhaps, since tides are the peculiarities associated with marine shores and, as postulated here, appear with the introduction of a littoral zone, this is a logical classification, but in view of the terminology and classifications that seem to be essential in a scheme expandable to include the most complicated patterns it may be best to continue the term sublittoral fringe and consider it to be an upper border on the sublittoral zone. Certainly the organisms peculiar to it are often characteristic of the sublittoral zone as well.

On Northeastern Pacific shores (Hewatt, 1937; Doty, 1946), the upper level of the sublittoral fringe is the most distinct break between zones. This we would choose as the break between the sublittoral and the littoral.

VARIATION AND INTENSIFICATION OF ZONATION

If tides play a dominant role in establishing the pattern of zonation, the fringes should be most conspicuously developed in regions where there were consistently the greatest periodic *extreme* variations from the *mean* tidal variations. Large tide ranges would tend to favor the more complex patterns, for variations caused by weather would not alter elevational and time features of the tides so greatly on a proportional basis. That is, a 25-mile wind can be expected to raise waves of a

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given size independently of the tide range. Thus a 25-mile wind would have a relatively greater effect on the tides in low-tide-range areas than where the tide range was great. In low-tide regions current weather may obscure the tide through temporary shifts in effective sea level. Small tide ranges and irregular tides (*e.g.*, tides in the lagoons of nearly closed atolls) would be expected to display one of the simpler basic tidal zonation schemes. Such patterns of zonation do occur on the relatively tideless shores of the Baltic and the Mediterranean.

In general, we would expect the zonational patterns to be related to the patterns of tidal variation. This can be tested by studying zonation patterns from ocean shores having different types of tidal variation (Figs. 1, 5; Pl. 1). It will be interesting to expand this study to include more examples for perhaps no valid conclusions can be drawn from so few selected samples. Unfortunately the observations on most shores have been on beaches where tidal zonation was not dominant (Fig. 7), and most reports are so lacking in detail they cannot be used for such a study.

The publications of Stephenson and Stephenson leading to their 1949 study and the experiences of Chapman and of Trevarthen, as shown from their publications, have been with shores having semidiurnal tides. The work of Womersley and Edmonds (1952) might be evaluated in this light for they were working in a region with mixed tides. With modifications the basic scheme of Stephenson and Stephenson (1949) is accepted here as that to be expected on shores having diurnal or semidiurnal tides. This is the scheme illustrated in Figure 5 at *C* and *H*. For shores having what might be called optimumly developed mixed tides the scheme illustrated in Figure 5 at *E* may be the basic pattern. Actually the "basic pattern" is perhaps the whole of Figure 5, representing (hypothetically) the set of responses to the zoning causes that may be present (or absent) along a shore. Very recently Lewis (1953, p. 538 ff.) has taken the same stand—that a simple scheme which can be expanded to fit the more complex situations is best.

In the essentially tideless Mediterranean, Ercegovič (1932; 1934) and Feldmann (1937, p. 40) state that barometric pressure and winds may be important and may act to regulate vertical distribution of intertidal forms through their action on the elevation of the sea's surface. The Black Sea (Caspers, 1951; *see* Chapter 25) is essentially tideless and seems likewise to have the simple zonational pattern in columns *H* or *I* of Figure 5.

As a rule the uppermost breaks between zones are more indefinite, and as one moves downward in the intertidal region the breaks between the zones become more clearly marked. A similar point is to be made in reference to the two sets of fringes. The upper fringes are usually the less regular in their elevational aspects. In summer the lowest tides occur in the morning, and it is during these summer periods when most intertidal observing has been done. At such times wind velocities and probably other related factors that tend to produce anomalous variations in the effective levels of tides are at a minimum. On the other hand, the high tides, probably most effective in the upper-fringe set, occur either during the middle of the day or at other times during which, by chance, greater variations in effective tide level could be expected because of wind and sun. A correspondingly greater irregularity of

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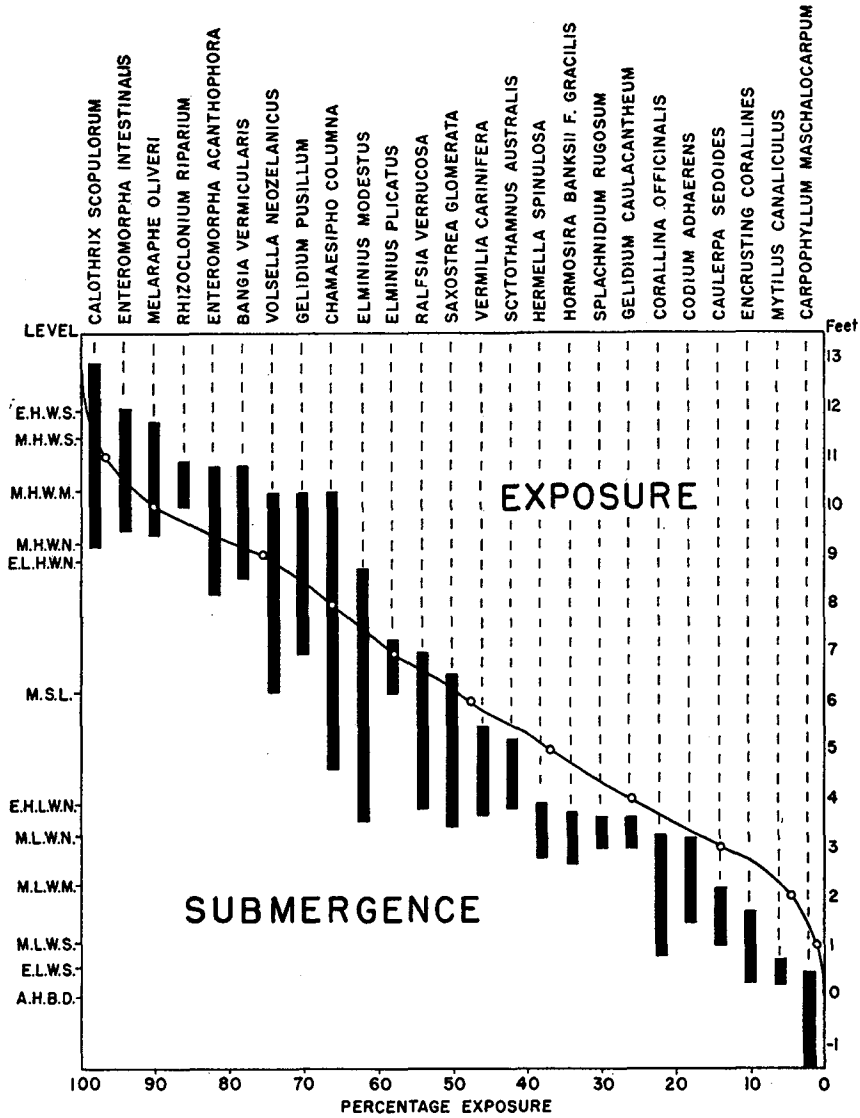

FIGURE 7.—*Vertical distribution of various organisms at Aukland, New Zealand*
From Dellow (1950).

the upper margins of zones has been noted by Chapman (1950, p. 68) and for the present can possibly be best similarly interpreted. Beveridge and Chapman (1950, p. 198) report the reverse in populations growing at high levels.

Intertidal organisms that are not sessile may migrate with the tides. For example *Nerita plicata*, at Raroia in the Tuamotu Archipelago, and *Nerita picea*, on the shores of the Hawaiian Islands, so migrate that they generally remain just above the usual level to which the waves wash. *Littorina rudis* was long ago reported (Batchelder,

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1926) to have similar habits in New Hampshire. Guryanova *et al.* (1930) report extensively on the similar activities of intertidal forms in the subarctic. These authors note the movement downward of this latter species into the water during periods of cold, and a general lowering of vertical distributional limits with an increase in fresh-water content of the medium. In the present chapter we make little attempt to report such distributional behavior displayed by the different motile intertidal organisms on solid surfaces.

HYPOTHETICAL EXPLANATIONS

Along shores the environmental factors which seem likely to be of importance to littoral benthic organisms are factors such as insolation, temperature, wind, wave action, rain, fog, ice, human activity, and tides. All but the last of these do not seem to vary uniformly, as does the zonation. Tides do vary according to the same pattern along great areas of shores, and it has seemed worth while to consider their features and see if these features are correlated with the breaks between zones. Colman (1933) is usually credited[6] with the suggestion that the upward and downward limits of the zones are correlated with certain special features of the tides. That others think otherwise is evidenced by C. M. Yonge's (1949, p. 195) statement "The cause of zonation resides in the varying extent to which different plants and animals are adapted for life on the shore. The more highly adapted and higher do they live upon it."

Stephenson and Stephenson (1949, p. 303) are perhaps the only current active workers who reject the correlations between tides and zonation as indications of probable cause. They say:

> "A mistaken idea, which is commonly held, is that intertidal zonation is a result of tidal action. This is not so. Zonation occurs, both above and below the water level, round static waters such as ponds and lakes, where there is no tidal change. The primary cause of it is the existence of an interface between air and water. Below the surface of the water there is a gradient in light-penetration, and this can be accompanied by other gradients such, for instance, as a change in sedimentation with increasing depth. Zonation results from these gradients. Above the water-surface there is further zonation, controlled by the degrees to which the surrounding rock-surfaces are exposed to influences emanating from the body of water or connected with its presence—such as spray, or moisture formed during evaporation. In a marine area with no tide and no wave-action there would thus be zones corresponding to our supralittoral and infralittoral zones at once, each with its subzones."

In addition to saying that tidal action does not result in intertidal zonation they, in the last sentence, point out only the presence of a supralittoral and an infralittoral zone on marine shores with no tides.[7] The present author (in explanations of Figure 5), likewise, would not expect a littoral zone in a tideless region. This one conclusion has apparently been arrived at by two very different routes. This is

[6] However, far earlier, Lamouroux (1824, p. viii ff.) said in effect that his "Polypiers . . . all suffered from the action of the air" for "at the period of the great equinoctial tide the sea retires from those rocks it covered for many preceding months . . ." and "they perish if uncovered too long . . . " Edmondson (1928) states that most of the reef corals of Hawaii cannot stand exposure to air for an hour. It seems true there that a level never exposed this long is the elevation of the conspciuously plane horizontal general surface of the reef flats. Undoubtedly much of the character of the land of Central Oceania is dependent upon this regulation (and that of wave action) of the upper limits of coral rock.

[7] Possibly the difficulty is more semantic than real; in a comment appended to a paper by Lewis (1955) Stephenson and Stephenson say: "While everyone knows that there is a *relation between* tidal levels and zonal boundaries, this relation is complex, and is not the same (for the same zone) in different circumstances. The fact that there is a relation does not mean that any particular tidal level coincides with any particular zone boundary; this is a thing which can happen but which often does not."

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another instance where experimental work is needed to aid in the selection of alternative explanations. In so far as the author knows Stephenson and Stephenson have done no experimental work to test their hypothesis. Certain applicable experimental work is discussed below.

Stephenson and Stephenson may be credited with recognizing that wave action may intensify zonation. Places exposed to wave action are also places that are less protected by, *e.g.*, the boulders which would introduce the complicating effects of shade and wind as well. In other words, such wave-exposed places have simpler physiographic environments and the same tides; such areas would be expected then to display tidally regulated zonation more clearly.

Many individuals have been concerned with the correlation of the limits of the zones and whatever the tide factors may be. Many have drawn correlations between the distribution of the organisms and average times of exposure or mean levels. (Fig. 2) of the tides. These workers have found their values of use only in description of the observations made. None of these mean features or average values has been fruitful in providing us with experimentally tested explanations of the observed phenomena. Furthermore the distribution of values about a mean or average is a gradient distribution of values and thus hardly likely to be causative of the sharp nongradient limits in the distribution of the populations observable.

Hewatt (1937, p. 7, 171 ff.) was content to use total times (Fig. 8) of emergence or submergence for a period of 6 months in seeking an explanation of the breaks near mean lower low-water level and about mean high-water level at Monterey. He also postulated the frequency of tidal exposure (Fig. 9) as causative of the break near mean sea level and just at the upper limit of *Pelvetia fastigiata* and *Fucus*

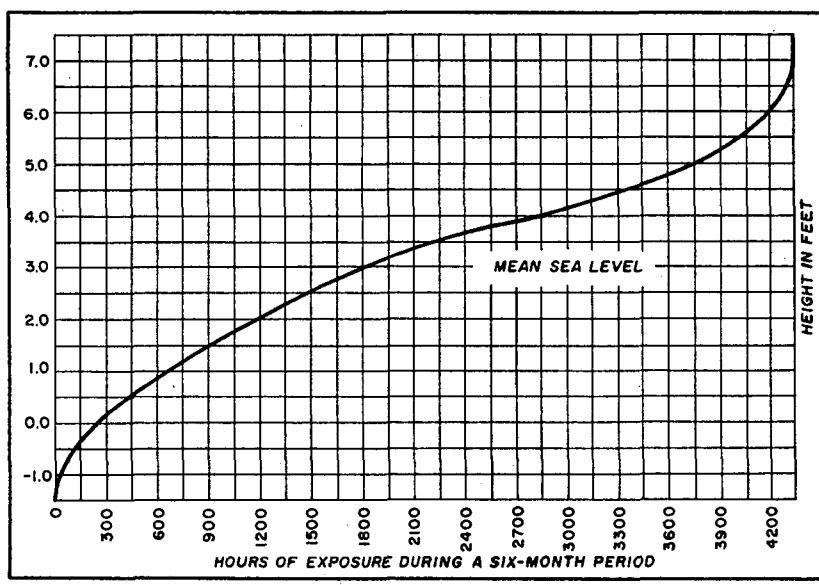

FIGURE 8.—*Exposure curve for San Francisco for 6 months from January 1 to June 30, 1931*
From Ricketts and Calvin (1948).

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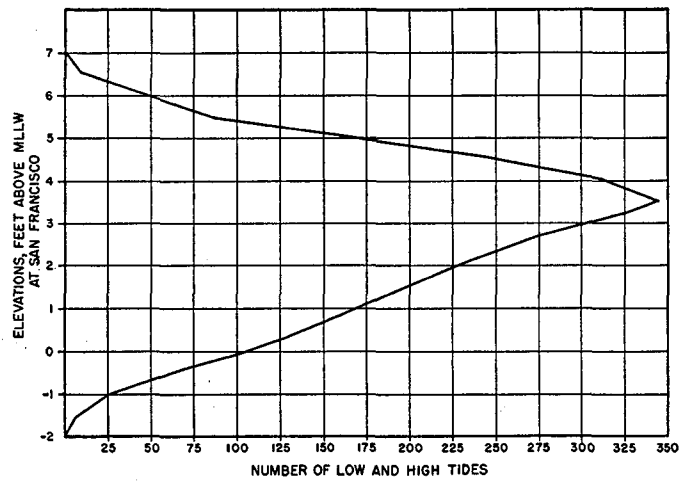

FIGURE 9.—*Number of high and low tides at San Francisco*
From Hewatt (1937).

furcatus. While the latter is a rather sharp break along a distribution curve the former two features are points on a gently changing gradient curve. Thus neither explanation is satisfactory as attested by the nonfruitfulness of the hypothesis as an experimental basis. Some of the latest attempts at correlations between per cent of total time emerged or submerged are those of Guiler (*e.g.*, 1951a, Table I) in reference to the zonation of intertidal organisms in Tasmania, and of Dellow (1950), in a nice study of intertidal zonation near Auckland, New Zealand (Fig. 7). Beveridge and Chapman (1950, p. 201) and Carnahan (1952, p. 43) likewise emphasize total time of exposure and percentage of time exposed with elevation, in explanation of what they term the critical levels (levels where a number of species reach their upper or lower limit).

Moore and Sproston (1940) have supported the idea of Elmhirst (1934) that the greatly increased rate of fall and rise of the tide through the mid range is possibly responsible for the littoral zone. Figure 10 illustrates the functions of this factor. With the change from high tide to low tide, or the reverse change in tidal elevation, during the first third of the time (the tide in falling from high to low level) the level of the water does not change much, during the second third it changes elevation very rapidly, and during the third third the change is again very slight. This middle 2-hour period is the period when tidal currents set hardest. If such a tide feature is active, then in the upper and lower margins of a zone such a feature induced would be expected to fade off with the gradual slackening of the rate of rise or fall near the extreme tide levels. This effect is that obtained when vertical-distribution data are assembled from a nonplane-surfaced transect such as one across a boulder beach. However, clear vertically distinct zones are often detectable and have been reported (*e.g.*, Yendo, 1914, Fig. 1). Grubb (1936) and Moore and Sproston point out, respectively, bare zones and slow seral development in mid-tide regions correlated with the levels through which these tide-level changes are most rapid.

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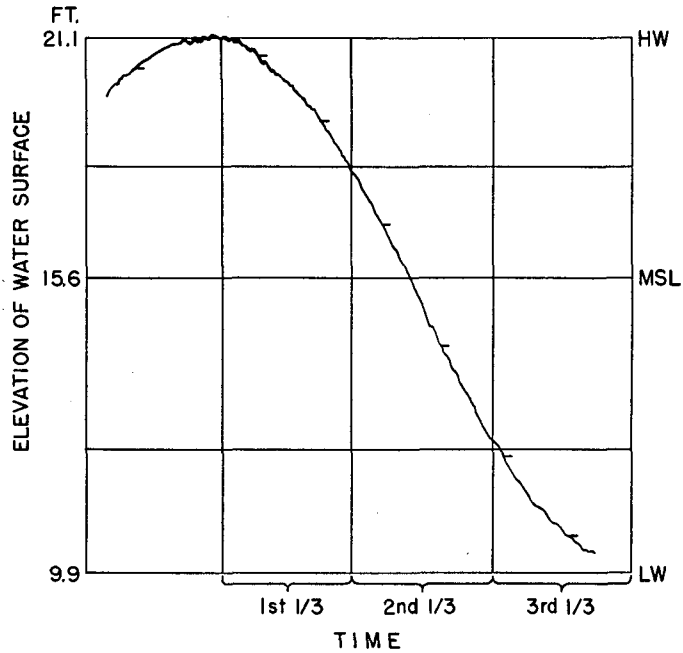

FIGURE 10.—*Actual tide-gauge record (Sitka, Alaska, December 2, 1924)* Showing duration at various stages of the tide.

The treatments of Elmhirst's idea by Yonge (1949) and particularly the precise statements by Wilson (1951, p. 64) relating phases of the rise and fall of the tides to the particular populants affected are well worth consideration.

Gislén (1943, p. 23) credits Ed. Ricketts with having an idea which is different. It apparently originated at the Hopkins Marine Station or the closely associated Pacific Marine Biological Laboratory and was variously credited and generously loaned out to several people. This idea was that, because of the nature of mixed tides during tropic tide periods, the intertidal region is not exposed in a time-height gradient, but between successive heights there may be twofold or threefold differences in time of exposure. Several people working at the Hopkins Marine Station developed this very important idea under the direction of Rolf Bolin, from whom Ricketts may have obtained the idea. One of these, Bruce Roberts, in an unpublished thesis, revealed in a study of tide recordings made at San Francisco the details of the idea for what correspond there to the plus 3.5- and plus 5-foot breaks (or critical levels). At these levels the important discovery was made that the single time of exposure to emergence gradually increased to the 3.5-foot mark, and then suddenly (Fig. 11, at "LLHW") increased to a maximum single exposure time of 10.25 hours. From this level upward the single emergence time gradually increased until it was 23 hours at the 5-foot level, but just above this level it was 144 hours. This idea was elaborated upon by Doty (1946) who pointed out such phenomena (*e.g.*, at "LHLW" and "HLLW" in Fig. 11) at other levels (Fig. 2*B*) and correlated the vertical range limits of many of the perennial and longer-lived

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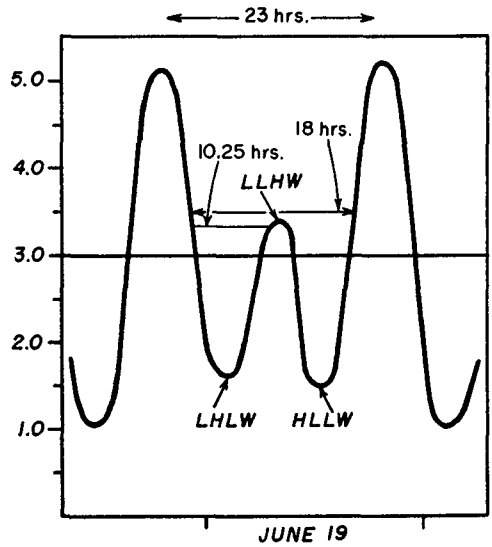

FIGURE 11.—*Time of tide levels, San Francisco, California*

algae (and invertebrates) with these features of the tides. These features of the tides are now referred to as tide factors.

Doty (1946) postulated that these critical tide factors regulated the exposure of organisms to other environmental variables, the tide factors being considered as primary features. Features regulated by the primary factors were considered secondary. The principal secondary factors are considered to be those affecting oxygen or salt concentration and temperature. Of these Doty and Archer (1950) believed temperature to be more important in their studies than desiccation.

Whether the tide factors, or any other, are to be considered "primary" or "secondary" or in yet another rank depends upon the point of view. This question has been a frequent topic of debate between Hilary B. Moore and the author, each of whom has approached this problem from a different immediate direction. Working from the environmental point of view the tides are dominant and perhaps best considered as primary. Working form the point of view of the organism the immediately effective limiting or inhibiting factor, the application of which is being regulated by the tides or other circumstances, is to be considered as primary; in this case the more remote tidal effect can then be considered as secondary.

For testing purposes Doty and Archer distinguished two aspects of the tide-factor hypothesis, the elevational and durational (time) aspects. They exposed intertidal algae to a series of different intervals of submersion in sea water, raise in temperature, change in concentration, or with poisons added. When the time interval was doubled or trebled over that time at which only just significant injury took place, death occurred sufficiently frequently to indicate acceptability of the hypothesis. Thus they felt the tide-factor hypothesis in respect to the durational aspect was acceptable as tested theory.

Since that time Doty and Fahey (Mss.) have been testing the elevational aspects

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of this same tide-factor theory and have obtained results which make them confident the theory is acceptable from the elevational aspect—*i.e.*, it appears that these tide factors in nature can and do restrict a population to the levels at which the forms occurred.

The variations of the tides in this theory are predominantly effective in the elevational phase. Their elevational features regulate the levels at which the secondary factors may cause an effect. The importance of chance correlation of elevational and durational aspects with the intensity of secondary factors is to be emphasized. In other words, it does not necessarily follow because there was an *a priori* favorable tidal variation that there will be a break induced in the biota. Both the vitality or susceptibility of the biotic elements and the intensity of the different secondary factors are important. On a cool or foggy day in some experiments no effect was noticed on a biota of apparently the same sort as one which showed a restriction at the level of the tide factor on a warmer clearer day. Again, on a hot day, with the experimental populations utilized (juvenile *Enteromorpha*), almost all exposed for even an hour and a half were killed. On the Monterey Peninsula many minus 1.5-foot tides have been observed after which there seemed, on subsequent days, to have been no effect on the population. On such tide was observed during the summer of 1943 rather late in the morning on a clear day when the sun rose bright and hot. The next day many of the algae on the sides of the ledges exposed to the sun were dead, apparently the result of the chance correlation of the extremely low tide (primary factor) and the unusually bright sun (secondary factor). The same phenomenon in reference to corals has been observed on the seaward reef flats of Raroia in the Tuamotu Archipelago.

There is a distinct lack of experimental evidence for or against the several other hypotheses concerning vertical distribution. The author can point to several pioneer works such as that of Ferronnière, (1901), who is credited with having shown that worms from higher levels could stand more desiccation than could those from lower levels. Baker (1909) recognized similar probable causation of zones in regard to both the algae and plants of the intertidal region. That euryhaline forms are abundant in higher zones has been noted by Guryanova *et al.* (1930), whose report thus supplements that of these other authors.

Baker and Bohling (1916) apparently came close to the single-exposure idea. It is not clear that it is really this though; as seen from extracts from their discussion: " . . . the factor determining the vertical range of any species appears to be, not the time of immersion per tide, but the number of tides reaching any level. The duration of the long exposure over the neap tides . . . is . . . the most important factor in determining the zonation." Again, however, in their summary they say of zonation where they were working, " . . . the determining factor is not the time of immersion per tide, but the number of tides covering any particular level . . . "

Isaac (1933, 1935) has done experimental work in testing the resistance to desiccation of marine algae such as *Pelvetia canaliculata* and *Laminaria digitata*. Vernon (1899) and Mitsukuri (1901) also experimentally determined limits of environmental factors tolerable by marine organisms. The latter was particularly concerned with light responses in littorines. Broekhuysen (1940) experimentally determined that a

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number of intertidal gastropods resisted desiccation and temperature in order of their abundance at different levels on the shore. He was attempting to explain the distribution of the organisms and not searching for an explanation of zonation in general. It was essentially his experimental techniques that Doty and Archer (1950) used in their work.

Those familiar with the literature of intertidal zonation know that a large number of recent papers report the distribution of intertidal organisms with no explanation and often only a putative attempt to fit the observations into one of the available organizational schemes. Few of these schemes (in relation to vertical distribution) have been formulated from a consideration of the environment.

It is felt that such observations and their classification is worthy only insofar as it yields new ideas that lead to a better understanding of the problem of intertidal zonation. Therefore, a discussion from this point of view seems worth while. Such an approach is taken with the expectation that a fresh viewpoint may be profitable, although ultimately, like all scientifically hypothetical material, it may be expected that it will be rejected or modified beyond recognition.

Disregarding aspects of spatial distribution other than vertical distribution, as well as the aspects of time and numbers, we might expect two sorts of zonation with modifications. The first might be called chance distribution about a mean. Such zonation might be found in the seedlings of different kinds of trees along a transect bisecting a row of the trees, the seeds of which were distributed by random winds. Graphically such a distribution in numbers plotted along an ordinate and distance plotted along the abcissa would appear to be a series of normal distribution curves (Fig. 12*A*) of varying degrees of overlap. Or Figure 12*A* can equally well represent a number of random distributions or larvae or mobile stages across a beach in numbers versus distance from some point. The curves could be entirely overlapping. Northcraft (1948), McDougall (1943), Fahey (1953) and others have

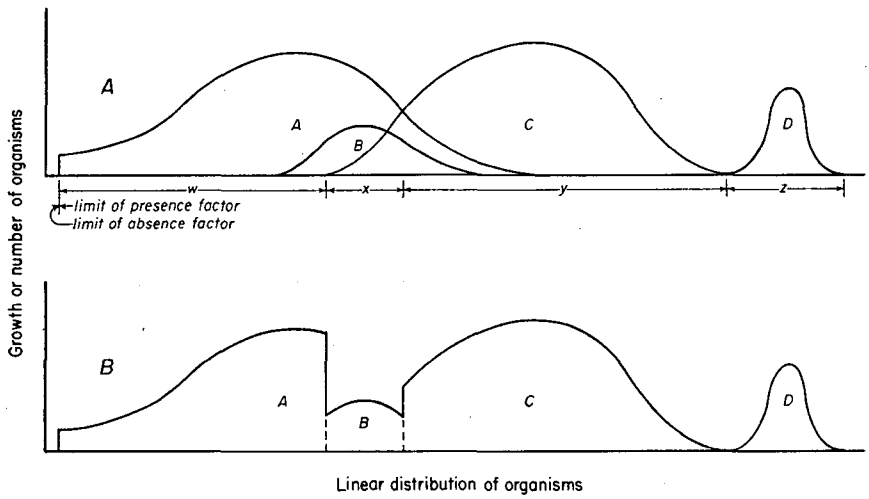

FIGURE 12.—*Zonation due to dominance along a gradient*
For fuller explanation see text.

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found that often marine intertidal organisms arrive by chance and spread through a very broad area as though they were distributed in such a random manner. (*See* references to this topic in the introductory part of this chapter.) On a boat or floating object one might expect motile reproductory bodies to arrive in this manner, but their distribution would be cut off sharply at the surface. An example of this is provided by *A* in Figure 12*A*. In this case the presence or absence factor at the upward extreme might be the water surface. At the lower distributional limit, other things being equal, organism *A* could be expected to taper off (in numbers) to nothing following a normal distribution curve.

If each of the species *A* through *D* can achieve dominance near its optimum—*i.e.*, grow better there than any other of the organisms concerned, as illustrated by Figure 12*A* (growth versus a gradient of factors)—we would expect to find the zonation W–X–Y–Z. This is possibly the type of zonation found around ponds of constant level. It involves the functions of such factors as time of reproduction, rate of growth, temperature, and what is called "ability to compete." To achieve sharp trailside dominance, strongly dominant species would have to be concerned, for codomination would tend to reflect more random distribution than zonation such as that observed in the field. With strong dominance the distribution might come to be as illustrated in Figure 12*B*.

The rather frequent occurrence of zones barren of macroscopic life between these zones of macroscopic forms speaks against the establishment of the intertidal zones according to the "trailside" zonation scheme just outlined. Furthermore if the intertidal zones were so established along a gradient it becomes necessary to explain on some other basis the correlation between the levels at which the tide factors occur and the levels of the breaks between the intertidal zones. This other basis might be "chance correlation" or it might be "the two correlated phenomena have a common cause." The dependable predictability of the tides based upon our current explanations of the action of the gravitational attraction between the water, the earth, and other celestial bodies of the solar system has achieved for these forces rather universal acceptance as causes of the tides. That these same forces could be causes of intertidal zonation independently of the tides might be hard to explain.

Zonation as it develops in the field has been studied by many workers. Northcraft (1948, *e.g.*, Figs. 16–20), working at the Hopkins Marine Station, has demonstrated the whittling down of the vertical range of pioneer colonizers. Fahey and Doty (1947) and Fahey (1953), working at the Marine Biological Laboratory, Woods Hole, Massachusetts, have followed this and another idea of Colman's (1933), that at least pioneer organisms come in over a greater range than they occupy as adults. Fahey (1947) has found this true of many organisms repopulating denuded transects at Woods Hole. It seems clear that even the nonpioneer forms (Northcraft, 1948, Figs. 38–43 in reference to *Egregia*) become restricted in distribution as do the pioneer forms. It appears that the organisms develop in such a manner that in size and numbers they become distributed rather uniformly throughout the zone. This is in contrast to the frequently held concept that the distribution from the upper to lower levels within one of these zones is directly related to chance or a nórmal curve and militates against the trailside zonation type of explanation.

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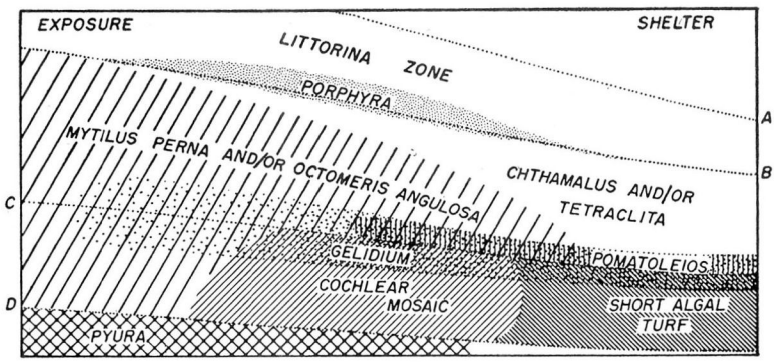

FIGURE 13.—*Zonation related to exposure in South Africa*
From Stephenson (1944).

Lensing (a form of attenuation at lateral margins of the specific biospace) complicates the study of these phenomena, along with shifts in effective (physiological) levels. Data collected in an effort to check further the nature of the establishment of zones must be collected where the upper and lower margins of the zones involved are parallel and sharply defined on a smooth, plane, uniformly exposed surface.

Above are essentially the observations that seem sufficiently uniform, sufficiently correlated with something, or sufficiently simple in apparent nature to encourage attempted explanations. In addition there are many observations that remain as mere heterogeneous facts. Predominant among these are the many descriptions of areas of the shore which show no distinct zonation or show zonation that has not been correlated with anything.

LONGITUDINAL ASPECTS OF DISTRIBUTION

On a grand scale intertidal longitudinal distribution concerns distribution around the world, on the different shores at the same latitudes. On a local scale, longitudinal distribution is often spoken of as onshore-offshore distribution, but this term does not seem adequately descriptive of some of its features. Onshore-offshore distribution is effected on all kinds of lateral boundaries, such as solid or consolidated shores, and estuarine shores.

On both scales the time dimension enters strongly—in the first case in reference to the aspects of paleontology, and in the second in reference to what the "mesophytic" ecologists think should be the series of changes leading to a climax formation. (*See* Chapter 3.)

The aspects of onshore-offshore distribution observed as one proceeds inshore or from a shore exposed to waves toward a shore area of calm water are frequently discussed. From a multitude of observations on as nearly plane surfaces as can be found uniformly exposed at right angles to the shore line, such as jetties (*e.g.*, Hedgpeth, 1953), or favorable coasts (*e.g.*, Stephenson, 1943, p. 226; Stephenson, 1944, Fig. 9; Gislén, 1930, p. 100 ff.), one can expect that the zones will become narrower and their limits lower as one approaches the more calm water (Fig. 13), providing one is concerned with the higher intertidal zones. On the other hand the

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sublittoral zones, though similarly narrowing as the calmer and inshore waters are reached, shift upward. The figures and data given by Evans (1947b, p. 182, 190 ff., Figs. 3, 6, 8), who presents a detailed study of this phase of ecology, illustrate this rather clearly for many species. He did find, however, that some species, such as *Fucus vesiculosus* and *Nucella lapillus*, are relatively independent of changes in wave intensity.

In the paper by Southward and "the late J. H. Orton" (1954) the breakwater sheltering Plymouth harbor, England, is described in so far as topography and wave action and the vertical distribution of organisms on the wave-exposed offshore and the wave-protected inshore sides are concerned. His observations are essentially the same as those above except that he observed a higher frequency of higher and wider zones on the protected side of the breakwater, *e.g.*, for such species as *Fucus spiralis*. The other fucoids were lower and on the wave-exposed side were growing lower down, and most of them had wider distributions. *Ascophylla nodosa* was not present. Southward noted a correlation between the upper limits of crustose coralline algae and the lower limits of the barnacles. *Rhodymenia palmata* and *Himanthalia lorea* seemed little affected by the conditions of wave action observed. *Chthamalus stellatus* was more abundant and frequent on the wave-exposed side. The species of *Patella* and *Littorina* generally extended to the same upper level on both sides of the breakwater but were more abundant, more frequently found lower down, and extended further down the surfaces on the more wave-exposed side.

Hedgpeth's (1953) study of jetties and piling in Texas is one of the first studies taking into account antecedent tidal events combined with observations of distribution on nearly plane surfaces. Figure 14 is taken from his results. Note the lower and narrower range of *Chthamalus* and *Littorina* at successively inshore positions. Although there is apparently interference by the sandy bottom in the intermediate case, note the narrowing and upward shifts in the sublittoral zones.

There seem to be correlated a few significant standard observations that are utilized as the bases for hypothetical explanations of these phenomena. With the greater amplitude of waves on wave-exposed shores the effective tide range is higher and thus the intertidal region is broader vertically with sea level remaining at the same elevation. It may be that the effect is greatest in the fringe areas. Johnson and Skutch (1928b), Orton (1929), Colman (1933), and Moore and Kitching (1939, p. 8), among others, have noted this effect and usually allowed about 2 feet as a correcting figure for shores exposed directly to wave action in contrast to those protected from wave action. Moore (1935) devised a formula based on several factors for predicting the effect of wave action. Guiler (1950, p. 170 ff.) has considerably expanded this, taking into account such factors as bottom topography, wind, distance over which the wind acts on the water, and degree of protection of the coast. Hewatt (1937, p. 179) made no allowance for such exposure through recognizing the effect of wave action as one changing with season and "onshoreness."

There is in general a shift in bottom types from the solid shores and large particles or boulders of eroding shores associated with offshore and turbulent waters to the smaller particles and depositing shores associated with inshore and more calm waters. Such shifts have presence or absence effects on populations and are so fre-

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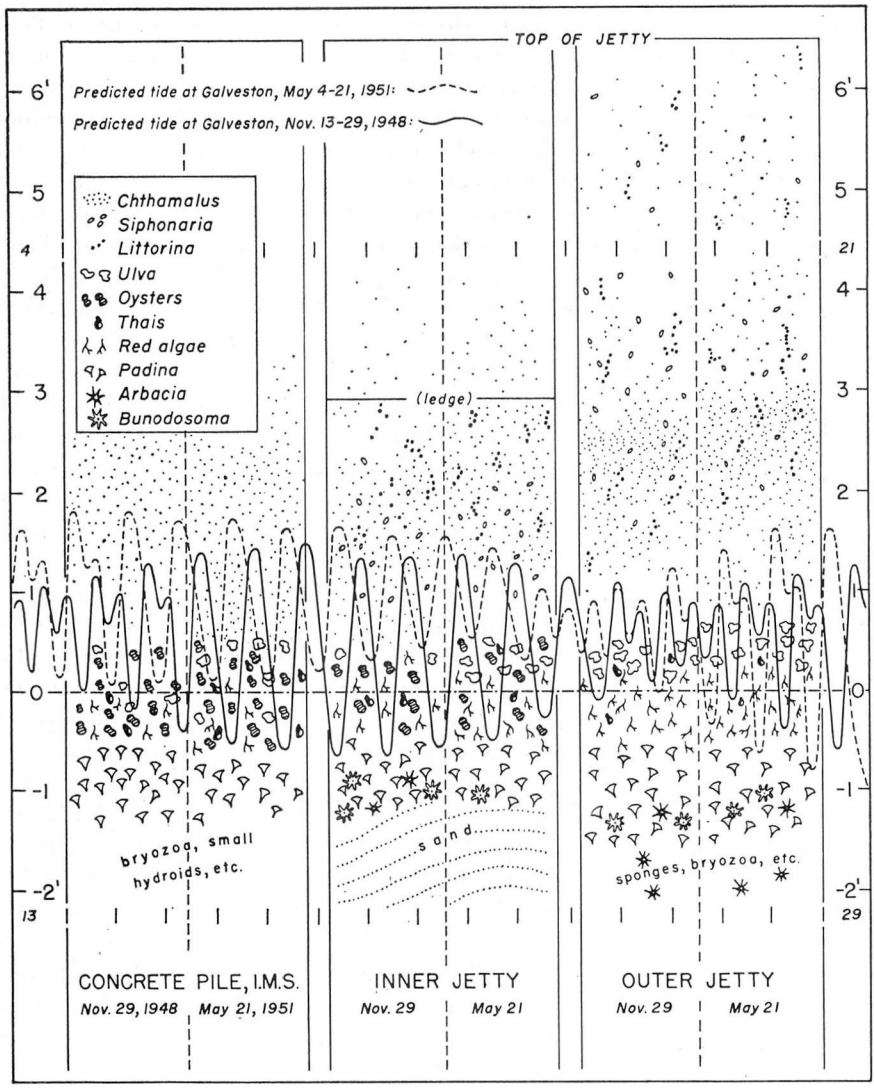

FIGURE 14.—*Zonation at Port Aransas, Texas, as related to season and degree of exposure*
From Hedgpeth (1953).

quent in nature that it is often hard to find ideal natural conditions for study. These changes otherwise are not within the limits of this chapter.

Gislén (1943, p. 40) thought that lower-light intensities correlated with increased turbidities were responsible for the upward shift of the subtidal biota toward the heads of fjords and in shallow water. At Durham, New Hampshire, near the head of Great Bay it was observed (Doty and Newhouse, 1954) that where the salinity was about 7 ‰, a heavy load of waste and silt was borne as a more or less homogeneous suspension that became differentiated farther down the bay where the salinity

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was 14 ‰ into a surface scum and large discrete flocculae beneath the surface. Below where the salinity was about 22 ‰ the water was clear with no surface scum, and what appeared to be the flocculae from upstream were seen aggregated into strands in the otherwise clear water. Where the bay water was of somewhat higher salinity (*e.g.*, 28 ‰) the water became clear and devoid of visible suspended matter. Light penetration and bottom characteristics are closely correlated with these phenomena which are taken to be the sedimentation and the "salting-out" of colloids to be expected in such a strong electrolyte solution as sea water. In the same place there is little in the way of photosynthetic organisms on the bottoms along the upper reaches of the bay, even where the upper shore areas exposed by low tide are heavily populated by marine forms.

That turbidity and decrease in salinity are not uniformly the primary causes of the upward shifts inshore of subtidal forms is suggested by Fritsch (1945, p. 7), who says that the compensation point seems to be reached more quickly by marine algae in water of lowered salinity. In deeper water the pH tends to be lower (*e.g.*, 7.5) than at the surface where it may rise toward the characteristic variation around 8.2 and even go higher with high photosynthesis rates or drop even below 7 as one passes into an extreme brackish or low-oxygen area.

It has been postulated that the changes observed in going from a wave-exposed coast to a protected area are due to variations in oxygen availability. Also the velocity of tidal currents over nearly horizontal beaches cannot be overlooked. Both variables are very likely rather gradually graded over the shores affected, the first in correlation with turbulence of the water, and the second with the tide curve. In an interesting statistical study of sublittoral populations of *Laminaria cloustoni* and *L. saccharina*, Walker (1952) demonstrates a difference in the distribution and development of these two species correlated with differing intensities of tidal current.

Despite the gradient nature of these factors many of the communities dominated by sessile perennial forms are separated rather sharply from one another. Such an example is observable along the west coast of North America where the communities dominated by *Postelsia* and *Mytilus*, characteristic of wave-exposed shores, give way abruptly to the communities that are dominated by different forms, but within the same levels, inshore in more calm water. This type of break is perhaps to be expected between two incompatible dominants whose optima for development are geographically separated (horizontally) as in "trailside" zonation. Barren zones have not been reported between these horizontally distinct zones.

Much measurement of intertidal communities has been concerned with the onshore-offshore width of the intertidal zones. Zones seem to be broadest horizontally when the surface of the substratum is most nearly horizontal and narrowest when the surface is most nearly vertical. In other words here the horizontal breadth is a function of the inclination of the shore. This is not surprising if tide levels are critical.

The effects of substratum inclination have been studied experimentally by Pomerat and Reiner (1942) and by Pomerat and Weiss (1946) on the development of barnacle populations. The economic interest in barnacles has served intertidal biologists well by the demand for more dependable understanding of their biospace. The barnacle

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is one of the very few intertidal organisms of which we have much experimentally derived knowledge. More such work should be encouraged.

The communities on a flat beach can be expected to differ from those on a steep beach. On solid surfaces in New Zealand, Dellow (1950) and others have noted that as one approaches a flatter beach, *Hormosira* replaces the *Corallina* and *Leathesia* characteristic of vertical surfaces at similar levels. Rice (1930), in relating the distribution of barnacles to minor variations in the environment, notes that *Balanus glandula* becomes a more dominant species on rocks of low slope. That this may be due to currents is indicated by her report of the quick change to dominance by *B. cariosus* where there is increased tidal circulation. Rice reports the dominance of *B. cariosus* on the shaded sides of boulders in the same general regions and also that this species is less tolerant of organic decomposition products. This may then be an oxygen-availability phenomenon, for moving water is apt to be cooler, and organic materials in the water are classically associated with low-oxygen tensions. Shade and wind shelter would tend to preserve the water film over the organisms during low tide periods. This would lower their exposure to the desiccation that would arise through increased salt concentrations in an evaporating water film. The amount of water remaining on the organisms and solubility of the oxygen in this water would regulate the rate of gas exchange possible to the particular oganism. Under such circumstances shade at low tide and the greater solubility of oxygen in cooler water might be co-ordinating factors in the distribution of such species as *B. cariosus*.

The interesting thesis of Elmhirst (1934) relating rates of tidal rise (or fall) to vertical zonation has usually been applied (Moore and Sproston, 1940; Hedgpeth *in* Ricketts and Calvin, 1952, p. 397) to vertical distribution in the intertidal area. It can, however, be extended to tidal currents, peak velocities of which occur at about half-tide level, and applied to onshore-offshore distribution especially over very flat shores. It has been shown by F. G. W. Smith (1946) that the various *Balanus* species have optimal (of the order of 1 knot) setting requirements in reference to current and presumably extremes for setting and growth maintenance. There is loss of attachment in some cases where growth rate is subsequently reduced in correlation with changes in current after the preliminary set. In his studies older barnacles appeared to be less sensitive in this regard. Collier and Hedgpeth (1950, p. 170) present evidence which they interpret as indicating that variations in such tidal currents may be not only effective in determining the distribution of the biota, but may seriously affect whole year classes of a species. This work refers actually to bays and passes into bays and thus, other than as an indication of what forces may be active on solid shores, falls outside the scope of this chapter.

Without isolation of each factor and experimentation little can be expected in the way of more sound understandings. Smith (1946; 1947; 1948) has been doing just this in reference to barnacle spat setting. He reviews briefly the earlier work in this field. Pomerat and Weiss (1946) and Weiss (1947) have similarly studied substratum in reference to both texture and inclination.

Allee (1922), studying the benthic organisms in very shallow and intertidal regions at Woods Hole, Massachusetts, found that as one progresses inshore there is in general an increase in temperature range and a decrease in salinity. Guryanova *et*

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al. (1930), also emphasize the importance of salinity in horizontal distribution. In this respect the solid (and unconsolidated shores) shows obvious similarities to the estuarine (fluid) shores studied by Hedgpeth (1951, p. 49–56). The relative constancy of the environment in reference to salinity at the two ends of a transect at right angles to the shore should be emphasized, and the greater variability toward the middle. Toward the marine end of the transect there is a great deal of chemical buffering by the sea-water salts. This is one of the most important of the shore regions economically, for it is here that so many large cities are faced with sanitary and waste-disposal problems, harbor maintenance, and fouling problems, sedimentation problems, and the shellfish and migratory fish problems. (*See* Chapter 23).

Whitten, Rosene, and Hedgpeth (1950), seeking an explanation of the further offshore occurrence of inshore jetty communities along the northern gulf coast of Texas, note that in the northern regions rainfall exceeds evaporation and there is correlated an entry of fresh water that is usually absent along the southern Texas coast. It is perhaps the related further offshore occurrence of the critical salinities in the north that determines the further offshore occurrence of communities there.

Temperatures, especially those caused by insolation and adiabatic cooling, are probably most important. Insolation can be suspected when an effect is consistently observed on surfaces uniformly directed when there is no correlation with wind or sea. On solid or rocky shores the effects may vary sharply, as between one side and the other of a surge channel or pinnacle (Stephenson and Stephenson, 1949, Fig. 4) where often one can only guess from simple observation or the data published as to whether light, wind, tides, temperatures, salinity, or some other factor (or combination of factors) is effective. Frequently the temperatures measured among the organisms just above the surface of the rising tide are approximately 5° higher than the temperature of the water itself. At times of falling tides cooling of the shore just above the water surface is effected by evaporation. Figure 15 presents measurements of temperatures made during part of a tide cycle illustrating this point.

There has been some discussion of treating the distinct intertidal zones as biotic provinces—that is, recognizing them as geographically contiguous areas occupied by different related species. The old classic by Flattely and Walton (1922), and Ellsworth Huntington's *Civilization and climate* (1924) emphasized the importance of the intertidal area as a birthplace of species and that climatic changes are a blessing rather than an affliction. It is in the sea, where the environment has been most nearly constant longest, that we find the largest number of forms that have changed but little during geological time. But the seashore, the intertidal region, is vastly different. Here, the climate is most variable and sharply and frequently so within narrow spatial limits. That this stituation and the peculiar action of the tide factors may be conducive to the evolution of different species zones was postulated recently by Rolf Bolin (1949) in a presentation to the 1948 International Zoological Congress held in Paris. Bolin points out that, since biospaces are often many degrees in horizontal extent and yet are restricted to the shore and often only a few decimeters in vertical height, they have practically only one dimension. This is in contrast to the two and even three dimensional distributions of most standing crops of species on land or in the open ocean. He points out that as a result each

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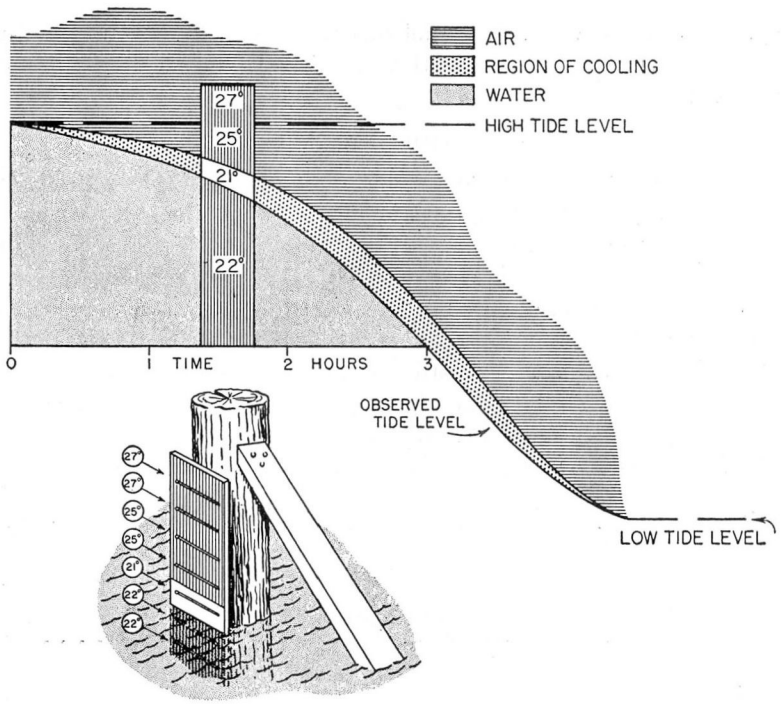

FIGURE 15.—*Temperatures and tidal level relations*

individual in the population is peripheral and "within easy invasion range" of other environments. This situation greatly increases the chances for survival of mutations in new environments, greatly enhances the evolutionary potential, and probably explains in part the magnificant number of intertidal species.

Bolin's hypothesis ties together beautifully the observed occurrences of related species in near-by different zones, their settlement over a wider range than that in which they mature, and the sharp limiting action of the tide factors under extreme conditions. Certainly this will prove of the utmost interest to those ecologists striving toward a theory of uniformity. The algae (Doty, 1946) that might be expected to range throughout this zone are, accepting the taxonomy used by G. M. Smith (1944), often restricted to specific portions of the zone. For example, almost each of the many species of *Porphyra* and *Gigartina* is believed to be restricted to one subdivision of the major zones outlined here. Shotwell (1950a,b) has reported on a similar vertical-range relationship of the limpets, and Hewatt (1937) records the vertical ranges for a series of western United States invertebrates. Northcraft (1948), Fahey (1953), and others have described the setting of organisms over a wider range than that in which they mature. As in most instances ideas in science are usually improvements in older ideas. In this case, Lamouroux, again, is reputed to have said, in a posthumous publication in the 1820's on page xxxvii, Vol. 7 of the Annales des Sciences Naturelles, that algae do not radiate from a center as do land plants, but extend in linear series following the lines of the coast and influenced by a com-

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mon depth of water. The fact that thinkers earlier came up with this idea in crude form and that all the above observations can be readily made adds credulity to Bolin's current thesis.

TIDEPOOLS

Tidepools are essentially anomalous situations in intertidal ecology brought about by shore physiography. Essentially they are pools with continuous rims which hold water in such a manner that the upper surface remains constant at a minimum level for relatively long periods of time, or they are pools with a restricted outlet, the surface level of which changes more slowly than that of the surrounding sea. Around the former of these two general types there is usually a sharp change in the biota just beneath the water surface, and often at that level the standing crop of benthic organisms is the highest. Around the edges of the latter type such a peculiarly-near-the-surface mass of organisms is absent.

Tidepools are handy places in which to make observations. They are often in-

TABLE 2.—*Appearance of the fauna at different salinities*
From Johnsen (1946).

Animal \ Salinity	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
Herpobdella lineata	O																																		Only in fresh water
Hæmopis sanguisuga	O																																		
Daphnia longispina	O																																		
Ceriodaphnia megops	O																																		
Anurophorus laricis	O																																		
Libellula depressa	O																																		
Triturus vulgaris	O																																		
Micropterna sequax	O																																		
Piona sp.	O	×																																	
Cypridopsis aculeata	×	×	×																																
Callicorixa limitata	O	(×	×)																																
Coelambus parallelogrammus	×	(×	×)																																
Glyptotendipes sp.	×	×	×																																
Bufo viridis	O	O	O																																
— *calamita*	O	O	O																																
Heterocypris salina	×	×	×	O																															
Candona compressa	×	×	×	O																															
Hydrometra stagnorum	O	O	O	O																															
Callicorixa fabricii	×	×	×	O																															
Anticorixa linnei	×	×	×	×																															
Callicorixa hieroglyphica	×	×	×	O	×																														
Chironomus thummi-Grp.	×	×	×	O	O	×																													
Rana esculenta	O	O	O	O	O	O																													
Dendrocoelum lacteum	×	×	×	×	×	O	×																												
Limnoporus rufoscutellatus	O	O	O	O	O	O	O																												
Callicorixa producta	×	×	×	O	O	O	×																												
Oecetis ochracea	×	×	×	×	×	×	×																												
Limnophilus rhombicus	×	×	×	×	×	×	×																												
Notonecta maculata	O	O	O	O	O	O	O	O																											
Cloëon dipterum	O	×	×	×	×	×	×	×																											
Macropelopia sp.	×	×	×	×	×	×	×	×																											
Limnotrechus gibbifer	×	O	O	O	O	O	O	O	×																										
Notonecta glauca	O	×	×	×	×	×	×	×	×																										
Callicorixa semistriata	×	×	×	×	×	×	×	×	O																										
Illybius (obscurus)	×	×	×	×	×	×	×	×	×																										
Bufo bufo	O	×	×	×	×	×	×	×	×																										
Aeschna cyanea	O	×	×	×	×	×	×	×	×	×																									
Anopheles maculipennis	×	O	×	×	×	×	×	×	×	×																									
Limnotrechus lacustris	×	×	×	×	×	O	O	O	×	×	×	×																							
Haliplus immaculatus	×	×	×	×	×	×	×	×	×	×	×	×																							
Colymbetes sp.	×	×	×	O	×	×	×	×	×	×	×	×																							
Ischnura elegans	O	O	O	×	×	×	×	×	×	×	×	×	×	×																					
Theodoxus fluviatilis	O	O	O	O	O	O	O	O	×	×	×	×	×	×	×	×																			
Hydrophorus praecox	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	O																		In fresh and brackish water

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TABLE 2.—*Continued*

Animal \ Salinity	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
Limosina humida	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	○																		
Orthocladiinae sp.	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○																
Nepa cinerea	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×																
Nais elinguis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×											
Podura (aquatica?)	○	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×											
Bidessus geminus	×	×	×	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×										
Hydrobia ventrosa	×	×	×	×	×	×	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×										
Asellus aquaticus	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
Trichotanypus sp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
Limnotrechus thoracicus	×	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×									
Radix ovata	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○						
Chironomus halophilus-Grp.	○	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					
Pygosteus pungitius	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				
Dytiscus marginalis	×	×	×	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			
Enchytraeidae	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Tubificidae	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Chydorus sphaericus	×	×	×	×	×	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gammarus duebenii	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
Haliplus lineatocollis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gyrinus natator	×	×	×	×	×	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Helophorus guttulus	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
Enochrus bicolor	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
Culex pipiens	×	○	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Cricotopus sp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Eristalis sp.	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Scatella stagnalis	×	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Hydrobia jenkinsi	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	○	○	○	○	○	○	○	○	○	○	
Anguilla anguilla	×	×	×	×	×	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gasterosteus aculeatus	○	×	×	×	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Pleuronectes flesus	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Idothea baltica**		×	×	×	×	×	×	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Sphaeroma rugicauda		×	×	×	×	×	×	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
Ephydra riparia		○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Hydrobia ulvae		×	×	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
Mytilus edulis		×	×	○	○	○	○	○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Membranipora crustulenta		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Nereis diversicolor			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Idothea viridis**					○	○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Calliopius laeviusculus**					○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
*Praunus inermis**					○	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gobius flavescens					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
— *minutus*					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	

In fresh, brackish and salt water

Only in saline water

○: Personal observations in rock-pools. ×: According to information taken from the literature. *: After the name of the species indicates that the statement of salinity in the right side is not based on a ‰ statement, but it is estimated after a local statement. Species which according to information exist in "brackish" water are stated at 2 ‰ with × in parenthesis.

teresting for the clues they yield as to beach formation and destruction. Yet there has been little extensive study of them. The bibliographies of Davy de Virville (1935), Lindberg (1944), Johnsen (1946), and Maucha (1949) should be consulted, especially their résumés of the work on the higher pools. A few special kinds of tidepools have been studied in considerable detail, far more have been studied cursorily. Well-illustrated discussions of tidepools and their development are those of Henkel (1906) and Yendo (1914).

As in the case of estuarine waters the tidepools are most variable in the mid-regions of the shore and most constant at the lowest (most nearly marine) levels. It is generally accepted that there are at least three general kinds: those found at high, low, and intermediate levels. Gislén (1930, p. 51) has suggested for them the terms supralittoral rock pools, sublittoral rock pools, and littoral rock pools. Essentially this classification is accepted for the present treatment. Others (*e.g.*, Baardseth, 1941) have recognized only two types—our supralittoral pools and a second category for the remainder.

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Supralittoral pools are usually unaffected by the rise and fall of most tides. Depending upon the rate of evaporation and the rate of water addition as a group they approach most closely the constant minimum level tidepool type. If protected from spray or if they occur in rainy areas, depending again on evaporation rate, they tend to become quite brackish. If evaporation is greatly in excess of fresh-water income the tidepool is saline or briny. As a suggestion, the term metahaline, introduced by Hedgpeth (1951) for bay waters having a salinity higher than that of normal sea water, might be applied to such pools.

In isolated places many of these pools are well supplied with bird droppings and as a result support an enormously rich flora of microscopic algae (often Euglenophyta and Volvocaceae). Strongly saline pools are formed under severe desiccation and may contain certain unique forms such as the crustacean, *Tigriopus*, or the "green alga" largely responsible for the red-orange color of salterns, *Dunaliella*. Johnsen (1946) presents a long table of the distribution of animals versus pool salinities. This is reproduced here as Table 2. *See* Doty and Newhouse (1954) for a similar table of algal distributions in reference to salinity.

Superficially these pools seem to vary principally in temperature, salinity, and mineral nutrients In the less saline pools pH changes appear to be significant. The pools here called supralittoral pools were classified by Levander (1900) as: spray pools, brackish pools, seaweed pools, ephemeral rain-water pools, permanent rain-water pools, moss pools (permanent and ephemeral), rock-sphagnum pools (no free water surface), and bogs (*sümpfe*). Perhaps the first three of these categories are treatable as segments of the upper-fringe areas. It seems unwise at present to attempt to draw a line sharply between what would be the supralittoral fringe tidepools and the upper littoral fringe tidepools. Levander's latter five categories apparently belong to the more purely supralittoral region. Certainly a category must be added for the strongly saline brine pools mentioned above. The pools left by dike bursts (Reijne, 1948), with their major accumulating sediments of algal origin, and such anomalous events as the formation of the Salton Sea may be classified as other peculiar pools of supralittoral affinity. (*See* Chapter 23.)

In general the salinities of the supralittoral pools are too low to permit their consideration as being truly marine. Similarly there is a question of whether or not they should even be considered "tide" pools. However, they are considered here for they represent the low end of the salinity gradient so often found when onshore-offshore distribution is studied. Examples of the chemical and physical nature of some of these pools are to be found in the papers of Wood (1952), in reference to certain brackish-water *Chara* species, and of Järnefelt (1940). Järnefelt presents a study of several supralittoral pools in great limnological detail, but with little consideration for the time element that would reveal the variations with day and night or season. Among the pools Järnefelt distinguished three types, essentially on the following chlorinities: (1) 0.06–0.13‰; (2) 0.59–0.72‰; (3) 4.82–10.54‰. He designates (3) as sea-water pools and he calls attention to the relatively high proportion of magnesium by ion-field diagrams (one selected has been reproduced here as Figure 16*A*). Similarly some are relatively high in calcium and sulfate ions. One might expect as the point of distinction between sea-water and rain-water pools the salinity 6.00‰ often used as a dividing point between brackish and fresh water, rather than this salinity of 8.73‰ (chlorinity = 4.82‰). This number was apparently the lowest salinity in the group of measurements with which he was working. Järnefelt distinguishes brackish and truly marine subcategories in his classification of sea-water pools. The other two types of pools he refers to as limnohaline. These are alpha-limnohaline

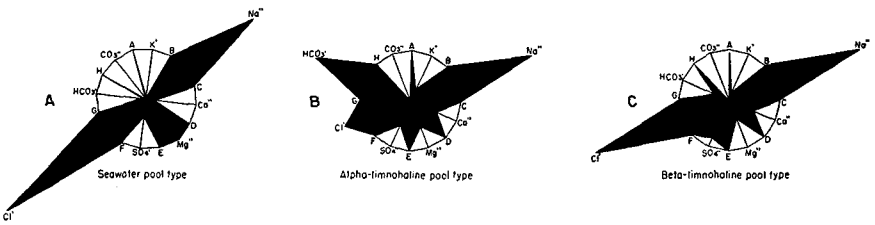

FIGURE 16.—*Relative abundance of ions in different pool types*
From Järnefelt (1940).

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or beta-limnohaline depending upon the distribution of ion fields (Figs. 16*B* and 16*C* respectively). The less saline pools and most of the types distinguished by Levander belong to the alpha-limnohaline group. The limnohaline pools are distinguished by their low chlorinities. The alpha-limnohaline pools are high in bicarbonate, the beta-limnohaline pools are low. Recently Maucha (1949) has modified and extended this system.

In supralittoral pools exposed to rain or fresh-water runoff there frequently develops a halicline below which the temperature may rise considerably. In this situation, high pools, particularly those lined by a blackish layer of algae, adsorb radiation over most at their bottoms and, thus, are warmest there although no distinct thermocline is present. Figure 17, prepared from data collected by T. S. Austin in a supralittoral pool at Rongelap (Marshall islands), illustrates this point. The temperature may rise to such an extent (Feldmann, 1937, p. 93; Nasr and Aleem, 1949, p. 266) that stenothermic algae are killed. Certainly they often harbor very different biota at different times of the year both above and below such thermoclines. Gislén (1930, p. 176) describes the development along Gullmar Fjord of *Enteromorpha intestinalis* communities in the "slightly deeper and considerably warmer and saltier water" peculiar to the bottoms of such pools, the upper layers of which may be putrid and brackish. A similar situation seems to be true on the shores of the Hawaiian Islands where, for example, on Rabbit Island and the south shore of Moku Manu some pools are densely filled only in their bottoms by *Enteromorpha*.

Brown (1915) is among the many who have published the commonly recognized information that *Enteromorpha intestinalis* is a species characteristic of pools into which fresh water seeps. The salinities may so change as to kill or drive out the more truly marine inhabitants or possibly, as Feldmann and Feldmann (1941, p. 291) show experimentally in the case of *Enteromorpha marginata*, may change so as to preserve them.

One factor, which might be called surface-volume ratio, should be taken into account in studies of these pools. It is commonly observed that the larger the pond the more uniform the conditions and, as well, the larger the volume in relation to the surface area the more uniform the conditions within the pond.

Littoral pools are perhaps the most difficult to characterize, but perhaps best are characterized as those that are regularly covered by the sea at high tide and essentially disconnected at low tide. During the times they are covered by the sea they are hydrographically similar to the sea. During the times they are disconnected the conditions with respect to their size and surface-volume ratio vary as the environment about them. The environmental variables that are most important seem to be temperature, fresh water, and sun. The variations in one such tidepool (Fig. 18) have been followed closely (Emery, 1946).

If the benthic marine organisms are stenothermic as commonly believed (*e.g.*, Setchell, 1926, for the algae), it is not surprising that they are less abundant in the smaller higher pools where temperatures mount. However, some species—*e.g.*, *Zanardinula* sp. (red algae)—normally occurring only below normal low-tide levels are found in high, quite warm littoral pools along the west coast of North America. Nowadays a number of eurythermic phenomena are attributed to the littoral forms previously believed to be thorough-going stenothermic organisms.

Temperatures vary daily and widely, from the normal temperatures of the sea to over 40°C. (Feldmann, 1937, p. 92). Through the year populations may vary accordingly. Oxygen concentrations vary from far below saturation at night to as much as between two and three times the saturation point in the bright sunlight of midday. In daytime, these often-algae-crowded pools may experience, in correlation with oxygen increase, pH's of 9 or 10, and at night, with increased carbon dioxide concentrations, pH's as low as 7.5. Atkins (1922) experimentally obtained such high pH's in vitro with *Ulva* under essentially the conditions that might be expected in a deep pool with a small surface area. Emery (1946) measured such relatively low pH's in nature and also reproduced them experimentally.

In studying littoral tidepools at St. Andrews, New Brunswick, Klugh (1924) found fairly distinct though small differences in temperature and salinity between higher and lower pools. The number of pools (six) was too low for a satisfactory comparison. Gersbacher and Denison (1930) made a brief study of four pools in the littoral region and concluded that changes in pH and salinity caused by evaporation are not limiting factors. Like Klugh they consider that depth, wave action, tempera-

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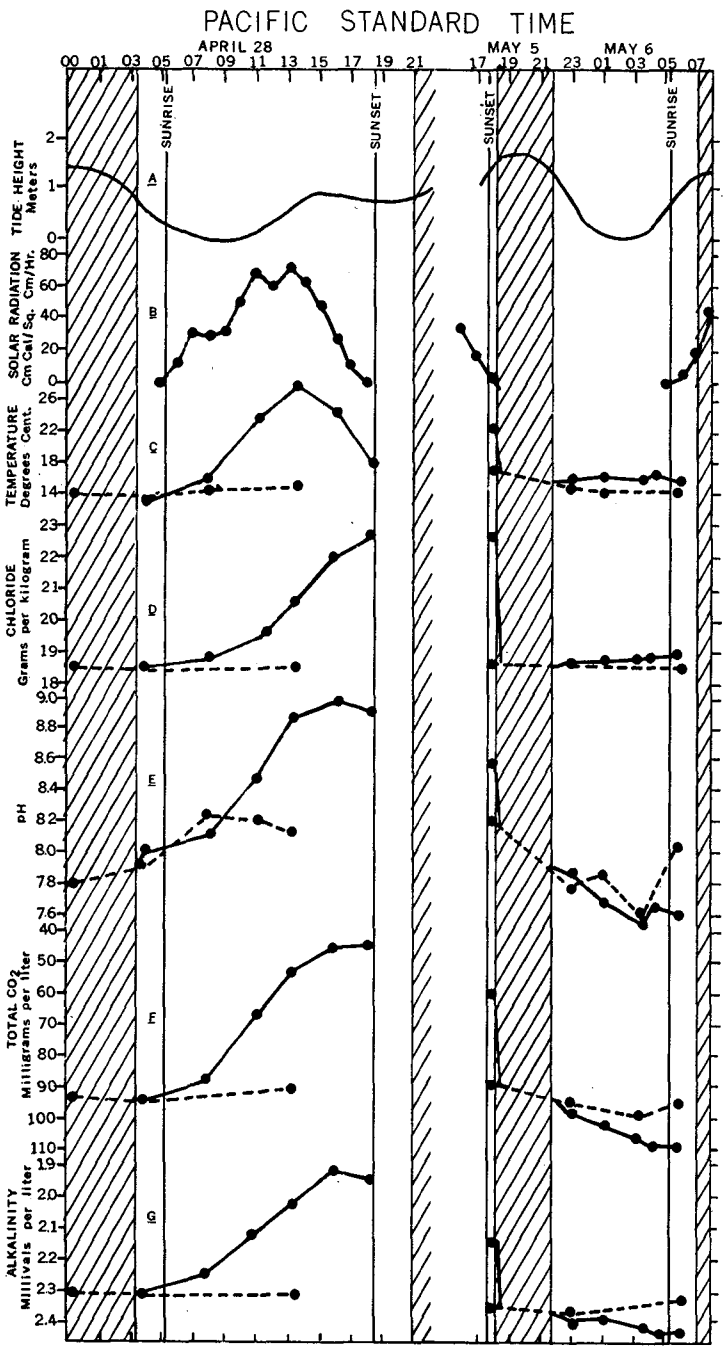

FIGURE 17.—*Diurnal variation of water characteristics of a supralittoral pool*

Dashed line shows variation for ocean water collected near the basin. Cross hatching indicates flooding of basin at high tide. After Emery (1946).

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ture, salinity, light, hydrogen-ion concentration, and particularly the composition of the bottom are important in regulating which animals can be expected to appear.

In tidepools on reef flats Motoda (1939) found that, on rainy days, temperatures, specific gravity, and oxygen content were lower than they were on clear days. However, if there was a heavy rain the pool water might become supersaturated with oxygen. This, he explained, is due to addition of oxygen from the incoming rain water.

There are correlations between pool characteristics and the sizes of the occupants. For example, in Puget Sound, Humphrey and Macy (1930) found that increasing salinities, temperatures, pool elevations, and oxygen content are reflected in a correlated distribution of larger and larger specimens of *Littorina scutulata* and *L. sitchana*. Conversely, the sizes found fell off with rising acidity. The studies of Shotwell (1950a) suggest that for limpets (several species of *Acmaea*) on high intertidal shores, along the Oregon coast, the height of the shell, in proportion to length, decreases for most species with increased elevation and similarly the shells are narrower and the volume smaller. Johnson and Skutch (1928b) report the flora to be correlated with the size of the pool, as well as exposure and shading. Factors such as actual elevation, temperature, and pH they considered secondary or less important.

Hypobiotic forms are common in the littoral pools, but except for their influence on the chemical composition of the pools they are probably of little geological interest. In the pools on limestone reef flats active boring in corals by various invertebrates is important. On the west coast of North America *Pagurus samuelensis* and *P. granosus*, detritus-feeding hermit crabs, are common. As an alga, *Ceramium pacificum* (Rhodophyta) is common in pools at these levels. In Hawaii the blenny *Salarius* (*Istiblennius*) *zebra* and certain gobies (both fishes) are found in the same type of pools as various members of the Cottidae (fishes) occur in along the west coast of the United States. A large propor-

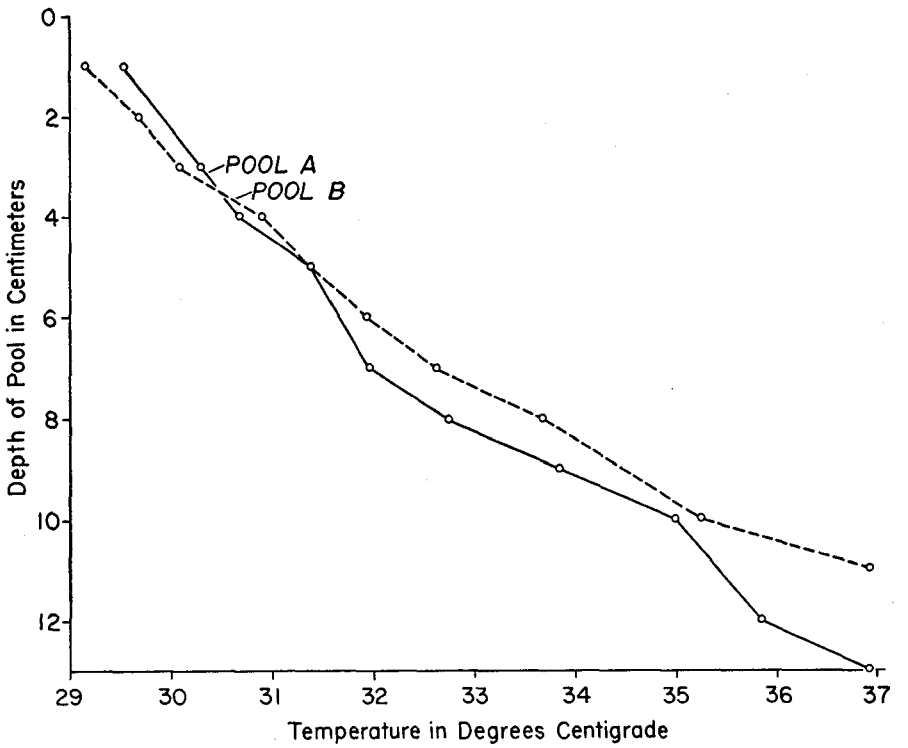

FIGURE 18.—*Variation of temperature with depth in two pools*
From notes of T. S. Austin.

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tion of sand is found in their digestive tracts, but whether or not these organisms actually play a role in beach destruction is unstudied.

Snails are among the best-known positive agents in the corrasive destruction of solid shores. Although the littorines in general retreat to pools and crevices at low tide, they are, probably, most active out of the pools. In pools they and the other algae-eating snails may remove rock fragments and release them as sandy fecal material. In Bermuda Pearse (1932) found in a 15-cm square area an average of over five of the small herbivorous snail *Batillaria minima* per square centimeter of pool surface. Presumably these snails, like *Littorina*, *Tectarius*, and *Nerita*, loosen and remove particles of rock in their pursuit of blue-green algal food, thus contributing to both enlargement of the pools and destruction of the shore in general. Emery has estimated (1946, p. 217) that *Littorina planaxis* may remove on the order of 170 grams of sandstone per square meter per year from the solid shores he had under observation at La Jolla. Considering both species of *Littorina* at La Jolla (*L. planaxis* and *L. scutulata*), North (1954) estimated that their combined erosive activities would deepen the tide pools there at the rate of 1 cm every 16 years. On coral-reef flats, considered here as fluctuating level tidepools the destruction of coralline algae by parrot fish and the probable alteration of particle size by holothurians appears to be important in regulating the nature of these pools.

A subject not touched upon in detail is the effect the blue-green (and other) algae may have in softening calcareous rocks such as the littoral beach conglomerates on atolls. Such information is very much to be desired.

Sublittoral pools are hydrographically characterized by little variation from the sea and are often admitted to the tidepool category though they may never be completely shut off from the ocean. In this latter respect they represent the more purely marine end of the salinity gradient one finds elsewhere in onshore-offshore distribution. While they are the pools most regularly exposed to the influence of waves, one of the principal characteristics, perhaps, is the calm induced by their encircling walls. The sublittoral pools are predominantly of the constantly varying-surface level type. The constant minimum-level pool type is to be found only in sublittoral fringe. Perhaps because of the infrequency of emergence of such pools the near-the-surface biomass is not so conspicuously developed as in the case of otherwise similar higher pools. Sublittoral pools, especially if they are large, tend to become havens of forms upwardly displaced from the deeper sublittoral region.

The reef flats of coral atolls may be considered as specially developed sublittoral fringe pools of the constantly varying surface level type. The role of organisms in the building up of these flats cannot be expanded here. (*See* Chapter 20.) Sargent and Austin (1949) calculate the maximum upward growth rate to be of the order of 1.4 cm per year. The destruction of this upward accumulation by boring urchins, mollusks, and the gnawing of parrot fishes and other organisms is well known but little evaluated. The role of holothurians in the pools on the reef flats in reducing the particle size of sand grains has been variously considered. In similar regions the lagoons of atolls are essentially large sublittoral pools. Again the over-all aspects of their biological activity has received attention by Sargent and Austin and others. Smaller sublittoral pools of an artificial sort are the fish ponds of Hawaii and the holding ponds studied by Tseu (1953), who gives the results of a detailed 2-year study. Detailed aspects of coral reefs and atolls are discussed in Chapters 10 and 20. However, in reference to the anatomy of atolls and their related reef structures as it concerns their "pool-like" nature the papers of Tracey, Ladd, and Hoffmeister (1948) and Cloud (1952) should be consulted.

ADDENDUM

For all the foregoing, the author of this chapter seeks tolerance for all that might have been emphasized. Many readers will feel the lack of specific reference to the different organisms, which after all are the best indicators of the total environment, far better than summaries of the physical and chemical factors. Forebearance is pleaded for having taken this course of emphasizing the nonbiological variations of the different factors over the solid surfaces treated rather than having given the organisms themselves more emphasis in a synecological or autecological manner. Disturbing to some will be the emphasis upon extremes and exceptional conditions rather than upon average conditions —for example, the plane, uniformly exposed surfaces in the vertical distribution discussion and the use of the reef flats of coral atolls as tidepools. This has been done knowingly and with the intent of

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provoking thought and, whenever possible, instigating experimentation in the ecology of the intertidal area.

In closing the writer offers a word of appreciation for Elizabeth M. Fahey, who worked with the author in making many of the observations reported here, and to R. D. Wood, Bryan Womersley, T. A. Stephenson, Joel W. Hedgpeth, V. J. Chapman, Rolf Bolin, Thomas S. Austin, and the many others who, in one way or another, often through strong objections to parts of what appears above, have materially aided the production of this chapter.

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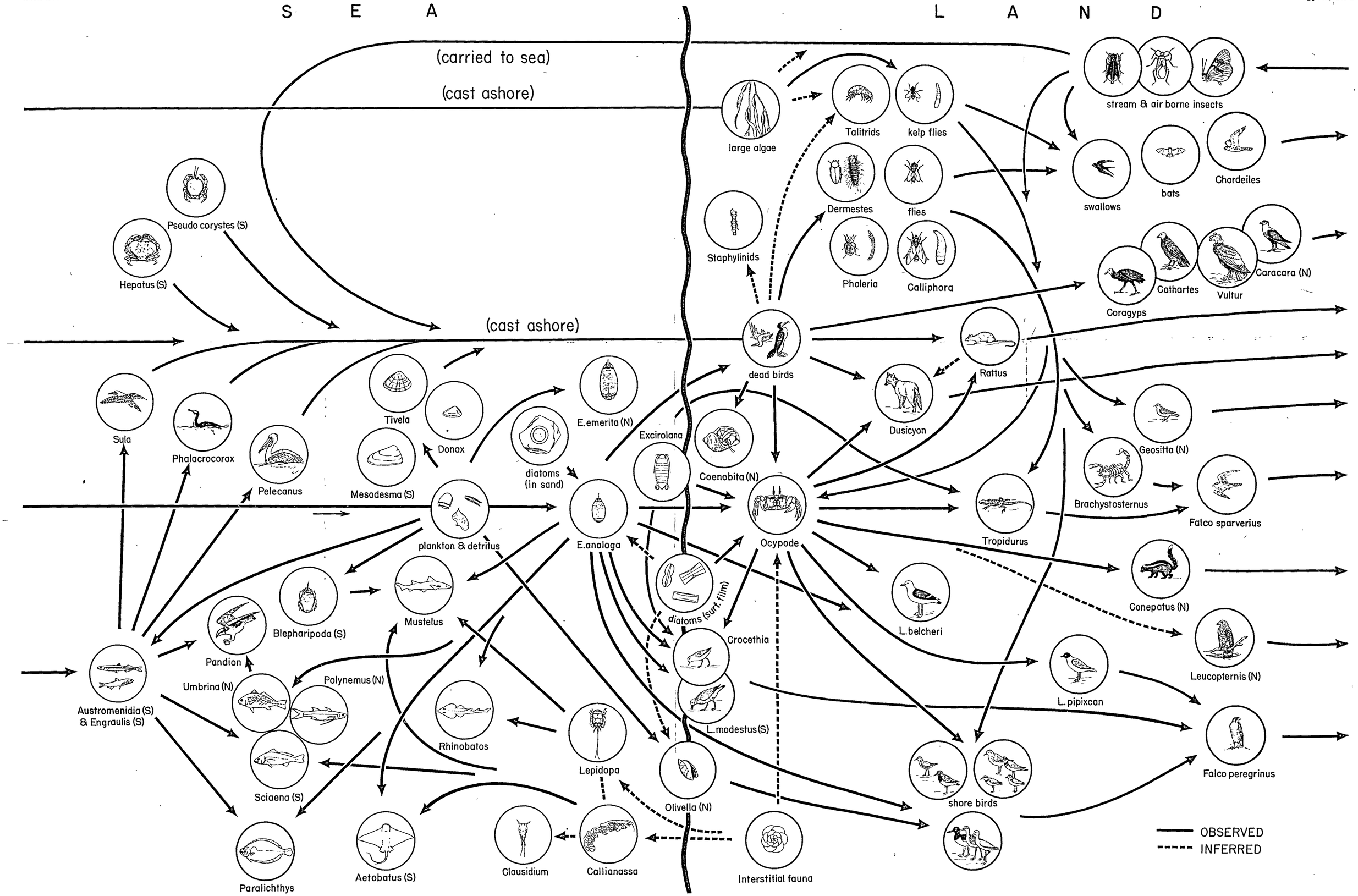

SCHEMATIC FOOD-CHAIN RELATIONSHIPS ON THE PERUVIAN BEACH, WITH SPECIAL REFERENCE TO THE SAND CRAB, OCYPODE GAUDICHAUDI

Those organisms indicated by N occur principally north of 6° S.; those indicated by S, south of that latitude, which is the approximate dividing line between the North Peruvian and Humboldt current regions (Modified from Koepcke and Koepcke, 1952, who kindly supplied the original drawings)

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Chapter 19

Sandy Beaches*

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A great part of the shores of the ocean are bordered by beaches of sand, subject to the full force of the ocean waves. On the open sandy beach physical forces interact to produce an environment which is in many ways less favorable to life than any other part of the ocean shore except gravel or cobble beaches, yet some organisms have been remarkably successful in colonizing it. Few macroscopic plants can survive on the beach, except as epiphytes on the hard substratum provided by an occasional stone or some animal, so the sand beach is essentially an environment occupied by animals and some microscopic plants. The sand flats of shallow bays and estuaries constitute another type of environment. (*See* Chapter 23.)

PHYSICAL CHARACTERISTICS

The phenomena of beaches have been of particular interest to harbor engineers and geologists for generations, and this interest has increased in the last few years as a result of military operations. This has resulted in the accumulation of a large amount of information about the physical processes of the beach which is yet to be correlated with the biological phenomena of sandy shores. In the bibliography by Haferkorn (1929), much of the earlier literature on beach processes and harbor engineering was assembled; since then there has been no similar compilation, although in the last 10 years many papers have been listed in various issues of the Bulletin of the Beach Erosion Board. A further result of this interest in beaches is a reasonably stabilized terminology (Fig. 1).

Many years ago Shaler, in a popular treatise on coastal geomorphology (1894), described the sand beach as a highly organized structure in which the various physical forces are in adjustment. For example, the height of the berm, or nearly level upper part of the beach, is 1.3 times (measured above mean sea level of the time of formation) that of the deep-water height of the waves that formed it, where the waves are not subject to refraction by topographical features (Bagnold, 1940; Bascom, 1954). The beach varies in minor details with the state of the tide, both from day to day and, where the tidal cycle is pronounced, from fortnight to fortnight, and undergoes even more pronounced seasonal changes throughout the year. Such seasonal changes may be spectacular, as at Boomer Beach, La Jolla, where winter conditions, especially increased wave action and change of direction of waves, may remove most of the sand, leaving a beach of large cobblestones, or they may affect the width or slope of a beach to a degree not perceived by a casual visitor. Severe summer storms may also cause temporary changes in slope. Beach sand varies in size and composition, and these variations affect not only the type of life which may

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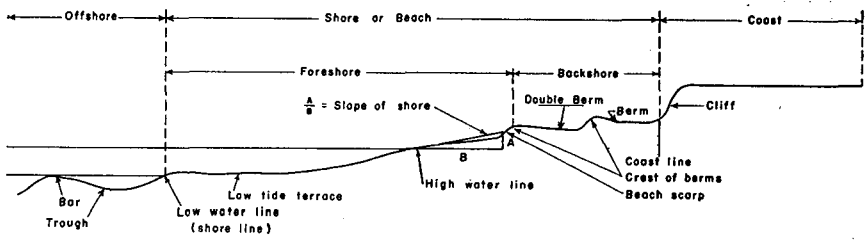

FIGURE 1.—*Terminology of beaches*
From Shepard (1948).

live on—or in—the beach, but to some degree the slope of the beach as well. In general, there is a relationship between the slope of the beach, wave character, and the average particle size: the greater the slope, the larger the particle size (Bascom, 1951). The natural depositional slope of a beach is affected by wave height, so that seasonal changes in slope in the same beach are to some extent independent of the mean particle sizes. During periods of high waves, the beach is flattened, and material is transported away from the beach to deeper water. The slope of the beach steepens markedly with larger particles; a gravel or shingle beach has a depositional slope of about 12°, and a cobble beach may have a slope of 20°. Gravel or cobble beaches are much less hospitable to life than are sand beaches, although they provide the favorite hauling grounds of sea lions and sea elephants.

The size of the sand also governs the amount of water which may be retained in the beach: in graded or sorted sand this is inverse to the size of the grains; in natural ungraded sand the water content is about 20 per cent (Bruce, 1928a). Because of the smaller size of the spaces in fine sand, the capillary rise is more pronounced, and in ungraded sand of the same median diameters it is even greater (Fig. 2).[1] The depth of the water table within a beach varies with both the state of the tide and the composition of the beach; it agrees more closely with tidal heights in a well-sorted sand than in poorly sorted sands (Emery and Foster, 1948). On the landward side of the beach the water table is relatively stable, and a strong tidal effect is noticeable for only a short distance inland. In some Pacific coast beaches, at least, there is no perceptible rise in the water table below the dunes following precipitation, although a rise in the water table occurs in desert sands (Isaacs and Bascom, 1949). In other places, however, the effect of salt-water seepage into the sands is noticeable in wells a mile or more from the coast.

The newly formed, angular sand of volcanic islands is an "inhospitable medium for burrowing animals," as it is easily disturbed by wave action because of its large particle size, and its angularity makes penetration by organisms difficult (Chapman, 1954). The same is probably true of calcareous beaches which are formed of broken shell, echinoid fragments, etc.

Temperatures are lower in the subsurface sand than on the surface of the exposed beach and within a few centimeters may be several degrees lower. Bruce (1928a) found that on the Port Erin beach temperatures at a depth of 20 cm approached sea-

[1] Since wave action is the best agency in sorting, and zone of sorting is narrow in a sheltered beach, some of these references to "ungraded" or "poorly sorted" sand may be based on samples from transitional zones.

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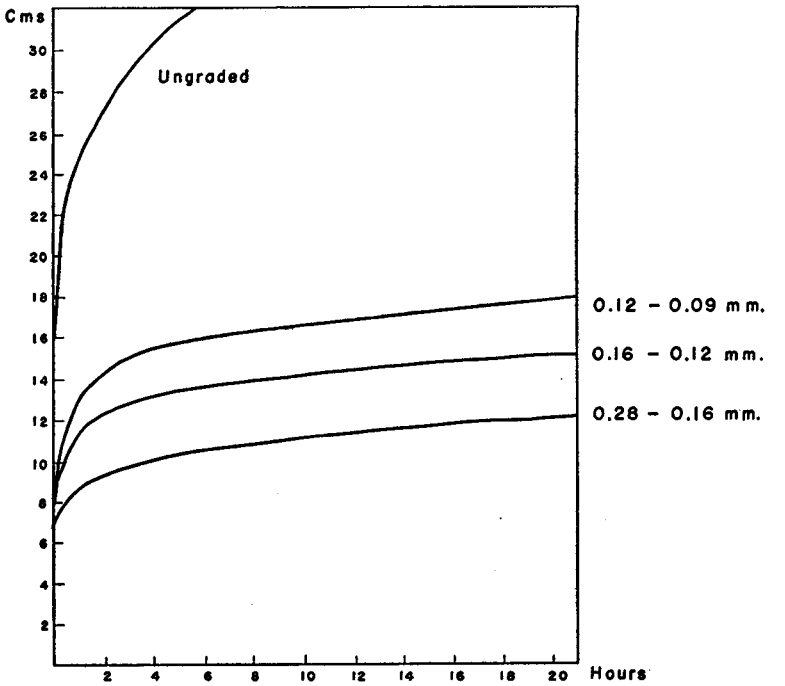

FIGURE 2.—*Effect of sand size upon rate of capillary rise of sea water*
From Bruce (1928a).

water temperatures. These temperature differences are most pronounced during the day in summer. The seasonal temperature regime on a beach coincides with other physical changes, such as beach width, and it is possible to demonstrate an apparent correlation between beach width and temperature which is of course simply the result of coincident changes of these characteristics as a result of changes in wave height (Fig. 3). The development of warm-water organisms on the beach may be favored somewhat during the warm season by the greater expanse of beach available.

One of the most pronounced characteristics of sandy beaches is the formation of bars parallel to the shore. These longshore bars (or offshore bars) are especially well developed along beaches with narrow tidal ranges, where they may extend for miles, as on the Texas coast. Several bars, and their intervening troughs, are developed; their heights and distances from the shore depend on beach slope and wave size. The outermost bar is well marked on most beaches by the first line of breakers on a stormy day. The various hypotheses concerning the origin of these bars and the source of the sand composing them have been reviewed by Keulegan (1948), who demonstrated their formation by wave action in a tank or model and by Shepard (1950). Since these bars modify the shore environment by providing ecological habitats whose stability depends upon seasonal conditions, they are undoubtedly one of the most significant phenomena of the beach insofar as animal populations are concerned. However, little work has been done in relation to this specific problem. During periods of heavy runoff in regions of active deposition, such as the coast of Loui-

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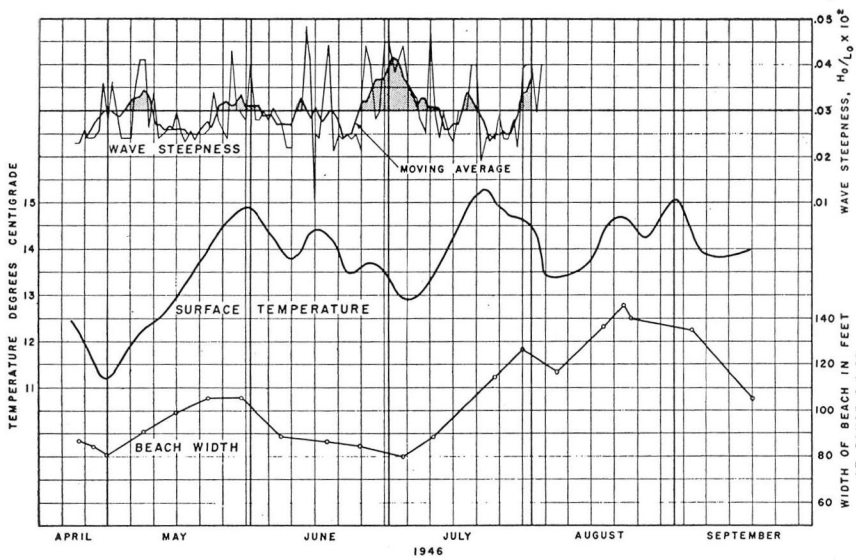

FIGURE 3.—*Comparison of beach width at Carmel, California, with surface temperature and wave steepness*
Courtesy W. N. Bascom.

siana, the troughs serve as temporary silt traps (Kellogg, 1905), and the population of sand-beach forms in this region is apparently much lower than on the Texas coast in regions of reduced runoff.

There are a number of minor geomorphic features of the subtidal part of sandy beaches, the most characteristic of which are ripple marks. On coarse-sand beaches the ripples, in conjunction with the small eddy currents over them, sort out the larger constituents of the sand and move them shoreward. The returning currents are weaker and carry light suspended particles seaward (Figure 4). Similar sorting has been observed in giant ripples as deep as 18 meters (Zenkovich, 1946). As a result of this sorting action, larger particles, including remains of Foraminifera, may be concentrated higher on the beach to form an assemblage which is not the same as that of the living organisms. The effect of this sorting action on a set of clams (*Mya arenaria*) on a Massachusetts beach, segregating small clams on a sandy region and later removing them as they passed the ½ inch size, is described by Turner (1952). A similar action holds on a larger scale with wrecked vessels, stranded whales, and the usual flotsam (Gunter, 1946). Small transitory bars, "swash bars" (King and Williams, 1949), are formed by wave action at the water line, and the shallow swash pools behind such bars are a familiar feature of beaches everywhere. Shrimps, small fish, and mollusks are often trapped in such shallow pools, where they are at the mercy of shore birds. Near the high-tide line on many beaches there occur various minor features, holes, small domes, and miniature craters caused by the action of air in sand, although they may suggest workings by burrowing animals (Emery, 1945).

Cusps are a less conspicuous feature of beaches, at least to an uninitiated observer.

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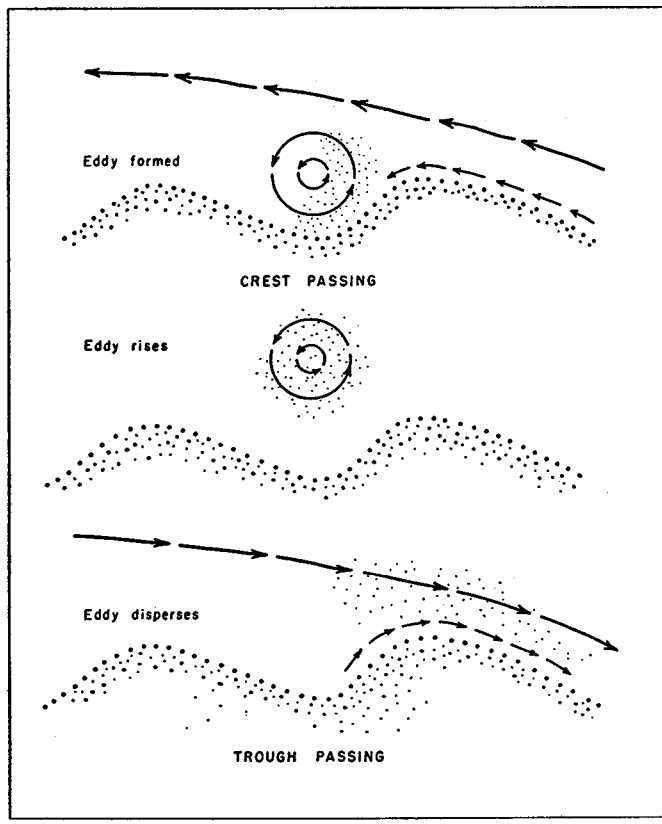

FIGURE 4.—*Transport of particles by wave action*
From Kuelegan (1948).

Their formation is incompletely understood although it is usually considered to be a function of average conditions of tide and wave action. Cusps occur on the tideless shores of the Black Sea, however (Zenkovich, 1948). On some beaches cusps are well developed so that the beach is conspicuously serrate; often the cusps are the immediate result of beach wash along the berm edge, the water carrying sand back down the beach to form the serrations. Such cusps are, in the words of Krumbein (1944), "marginal landforms associated with the berm." Large cusps may be formed by storms and may involve the movement of considerable quantities of sand up and down the beach. Such movements disrupt the environment, covering up colonies of burrowing organisms or washing out other colonies.

There are various types of currents in the environment of the beach. As a result of the mass movement of water against the beach by wave action, longshore or littoral currents moving parallel to the shore line are set up. Other longhsore currents are set up by wind or tidal action. The littoral or longshore currents, set up primarily by wave action, are the principal agency in moving sand along a beach (Shepard and Inman, 1951) and influence to a large extent the movement of detritus and other

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food materials along the shore. There is a regular pattern of near-shore currents, with a net onshore transport outside the surf zone and an offshore component on the bottom nearshore, with cell-like circulatory patterns set up in relation to the bars and the passages between them. Such currents determine the direction of dispersal of pelagic larvae of the animals living in the beach and thus may have some influence on the success of a spawning or the establishment of populations on a beach.

CHEMICAL CHARACTERISTICS OF THE INTERSTITIAL WATER

Few analyses of the chemical character of interstitial water in marine beaches have been made; most of the data come from the work of Bruce (1928b). An almost universal characteristic of sandy beaches is the dark or black layer in the region of stagnation and oxygen deficiency as a result of the formation of ferrous sulfides under reducing or anaerobic conditions. The depth of this layer beneath the surface varies with the location of the beach. In an exposed beach subject to heavy surf the black layer may be 2 feet or more beneath the surface, whereas in sheltered coves and on bay shores it may be only a few centimeters below the surface. To judge from Pennak's (1951) summary, it is as a rule much higher in fresh-water beaches, as might be expected from the absence of tides and reduced wave action on lake shores.

Since the formation of ferrous sulfide in sand is a phenomenon of significance in general problems of sedimentation as well as an important event in the formation of H_2S in such regions as the Black Sea and deep fjords it is unfortunate that it has not been studied in more detail. Inasmuch as the supply of sulfur is dependent on the availability of decomposition products from decaying organic matter (with the active contribution of bacteria) as well as upon inorganic sulfur, it is also an ecological problem. Bruce (1928b) summarized his studies of the sulfur cycle in beaches in a diagram (Figure 5). A review of this subject, with reference to more recent literature, has been made by Perkins (1957).

Other chemical characteristics of the sand beach are even more variable; the free CO_2 content of a beach may vary from 1 to 12.6 ppm at a depth of 8 cm (Pennak, 1942) and sometimes reaches very high values in the presence of active decomposition, and O_2 is correspondingly low. Under such conditions the calcareous matter in the sand acts as a regulatory mechanism in controlling the pH of interstitial water so that the pH of this water is not greatly different from that of the sea water (Bruce, 1928b). Oxygen turnover and utilization is much more rapid in the interstitial water than in the sea, as might be expected.

GENERAL CHARACTERISTICS OF SAND-LIVING ANIMALS

While the variety of animal life inhabiting beach sand is strikingly less than that of the rocky intertidal or shallow tidal flats, the populations of the individual species are often immense. Specialized types, having found a place in a highly specialized environment, make the best of their situation. On a California beach about 4 miles long some 2,000,000 Pismo clams (*Tivela stultorum*, Veneridae), weighing on the average 2 pounds each, were removed by clam diggers in 2½ months, and at least a million undersized individuals were left exposed to die (Fitch, 1950). Fox (1950) has estimated the population at La Jolla, of a beachworm, *Thoracophelia mucronata*

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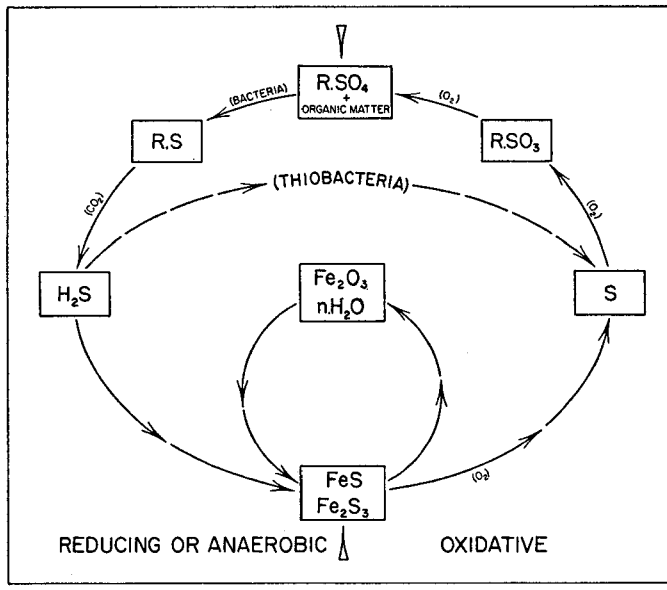

FIGURE 5.—*Sulfur cycle in a marine beach*
After Bruce (1928b).

to be 3000 per cubic foot, and that a worm bed a mile long by 10 feet and a foot deep would contain some 158 million worms. Great droves of beach hoppers and burrowing crabs (*Emerita*) occur in favorable localities. Food supply is apparently not the critical problem on the sandy beach since the organic detritus of the sea is constantly being worked over and into the beach by leaching into the sand and by wave action.

Except for some of the beach hoppers and certain phycophagous insects, the true psammophiles are adapted to feeding upon particulate and suspended organic matter brought to the beach as "peloglea" or "leptopel" (Fox *et al.*, 1952) or resulting from the decomposition of macroscopic algae and animals, and upon microscopic autotrophes in the beach. This dependence upon finely divided material suggests that such substances are more important to the economy of the beach than are the irregular and seasonal strandings of such macroscopic material as detached seaweeds and sargassum. While bacteria are comparatively less abundant in sand than in other types of sediment (ZoBell, 1946), they are still a significant part of the organic cycle; Humm (*in* Pearse *et al.*, 1942) estimated a count of 200,00 bacteria per gram of sand in the Beaufort beaches, which he considered conservative. A number of protophytic autotrophes have met the problem of maintaining themselves on the precarious environment of the beach by migrating to the surface at low tide and exposing themselves to sunlight. At the time of high tide, they retreat into the sand. This migratory rhythm, synchronous with the tide, may persist even when the organism is transferred to a dish in the laboratory (Fauré-Fremiet, 1951). The most famous example of such behavior is that of the flatworm *Convoluta*, host of the symbiotic flagellates *Carteria;* here it is the host which, in a manner of speaking, "farms" its symbionts by carrying them to the surface at low tide and protecting them from wave action by

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retreating downward as the tide rises. (*See* Chapter 15C for a discussion of the nature of this association.)

The animal life of a sandy beach might be classified on the basis of food habits into the active burrowers, which actually pass the substance of the beach through their alimentary tracts—*e.g.*, most of the worms, those animals which scrape their food from the surface of the sand grains, and those which sort or filter the particles of detritus and plankton from the surf waters. On a surf-swept beach there is little chance for an animal to maintain a permanent burrow or any sort of tube, and the tube-building worms are characteristic of sheltered flats. The larger worms of the sandy beach, such as *Thoracophelia*, simply work through the sand, ingesting it and feeding on the colloidal organic film on the sand grains. The scrapers and browsers are principally the smaller metazoans—*e.g.*, copepods, ostracods, and the like. Among the animals feeding on suspended organic material are the various bivalves, some of which are equipped with devices to exclude sand, such as siphonal papillae in *Cardium* (Fig. 6) and *Tivela*, or, as in the case of the Tellinacea (which have divided siphons), the inhalent siphon is developed to pick up detritus and also discharges the waste as pseudofeces (Yonge, 1949). The common tellinid of New Zealand, *Amphidesma ventricosum*, has very long siphons, enabling it to live at depths in the beach below the disturbed upper layer.

Most of the larger arthropods are scavengers or predators, but some, the sand crabs of the genus *Emerita*, have developed a unique method of filter feeding. The long featherlike antennae act as strainers, catching the detritus swept across the beach by the receding waves. The material is cleaned from the antennae by the maxillipeds, and the whole structure of the mouth parts is so arranged that entry of sand grains is hardly possible (Snodgrass, 1952).

Many of these organisms orient themselves according to the slope of the beach and

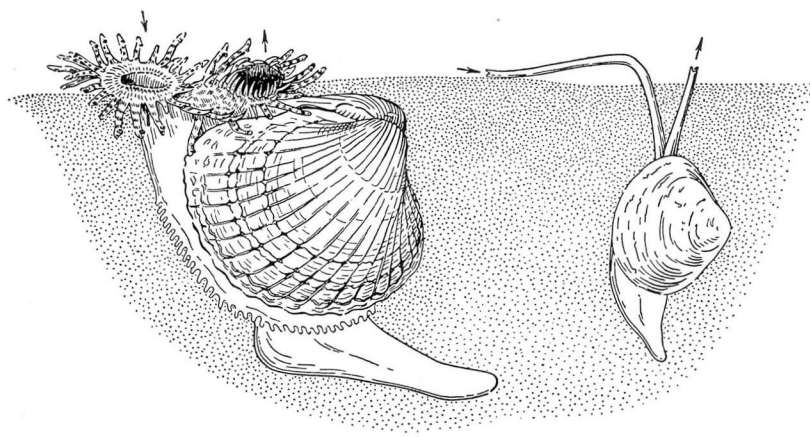

FIGURE 6.—*Sand-burrowing bivalves*

Left, the cockle, *Cardium edule*, a suspension feeder; and right, *Tellina tenuis*, a deposit feeder, showing positions in sand, shape of foot, and inward passage of water through the siphons. Natural size. From Yonge (1949).

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the direction of currents, so that it may be possible to infer the slope and direction of an ancient beach where the organisms may be preserved *in situ* (Seilacher, 1953).

Many of the larger crabs living in sandy bottoms have developed rows of bristles or interlocking arrangements of spurs along the front edge of the carapace and the chelipeds which exclude sand grains (Garstang, 1897). The gastropods of sandy beaches are principally predators (*Polinices*, *Terebra*) upon the bivalves, or specialized detritus feeders (*Olivella*); adaptations for burrowing are either a large muscular foot as in *Polinices* or a stream-lined shape as in *Olivella*. Sand-living bivalves, especially of the open beaches, are smooth-shelled and flattened or at least have reduced ornamentation of ridges (*Cardium*, *Arca*) which do not interfere with progress through the substrate. The tendency toward smooth, solid shells was discussed by Oliver (1923) who noted an exception in New Zealand where a small clam with pronounced concentric ribs, *Antigone spissa*, occurs as abundantly as *Amphidesma* on some beaches.

Many sand-beach animals are blind, and the eyes of various crustaceans are reduced or placed at the ends of slender stalks. The hippids or mole crabs are well adapted fossorial animals, with stream-lined or flattened shapes and strong digging appendages, but the larger portunid crabs frequenting the surf zone simply work their way into the sand by alternate use of the appendages of either side (Pearse *et al.*, 1942).

Among the echinoderms a few forms occur on open beaches, usually just below the tide level. Small ophiurans, asteroids of the genus *Astropecten*, cucumbers, and heart urchins may also be found in such situations. In general, we find a reduction in the structure of the tube feet, as in *Astropecten*, shortening of the spines as in various sand dollars (*Mellita*, *Dendraster*), or the development of a specialized respiratory apparatus (*Echinocardium*). These various echinoderms feed upon detritus or prey upon minute organisms in the sand.

A few hydroids (*e.g.*, *Clytia*) have managed to gain a foothold on the beach, as epizoics on clams or occasionally on gastropods. At least two small species utilize the sand grains as a substrate, *Protohydra leuckarti* in northern Europe and the eastern United States, and *Psammohydra nanna* in the western Baltic (Schulz, 1950a; 1950b). There is also a pasammophilous bryozoan, *Monobryozoon*, reduced to a single zoecium (Remane, 1936; 1938). A few small Turbellaria have been found on Baltic and Mediterranean shores (Ax, 1952; 1953; 1954).

Larger representatives of other groups are meagerly represented. On some sand beaches nemerteans (*Ototyphlonemertes*) may be abundant. Such groups as aspidobranch gastropods, chitons, tunicates, and sponges, adapted to hard substrates and cleaner waters, are not found in beaches, but there are several species of aeolid nudibranchs (*Pseudovermis*) and Acochlidiacea in this environment. (Marcus, E. du B-R., 1953; Marcus, E., 1953; Marcus and Marcus, 1955). Burrowing forms requiring more or less permanent burrows or unable to protect themselves from shifting sand (*e.g.*, sipunculids) are also absent.

Certain small fishes and young of others frequent the surf zone, and one, the grunion (see Chapter 27), uses the beach for a spawning ground. Only one chordate,

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Branchiostoma, might be said to be an indweller of the beach, although flounders, skates, and rays frequently cover themselves with sand.

Macroscopic plants are rare; some green algae live as epiphytes on such clams as *Donax* or on the carapace of *Emerita*.

INTERSTITIAL LIFE OF THE BEACH

There is a large and steadily growing literature on the microscopic fauna and flora of beaches, especially since the discovery of a previously unsuspected order or subclass of Crustacea, the Mystacocarida (Pennak and Zinn, 1943), in New England beaches. Since then species have been found on the Mediterranean coast and in Chile (Dahl, 1952). It had been known for some time that the sand beach harbored many species of harpacticoid copepods (Wilson, 1935). Representatives of several other phyla have been found in this environment, especially by Remane and his students at Kiel, and instruments have been designed to sample it (Delamare, 1954; Karling, 1937). Since the summary papers by Pennak (1951) and Remane (1952) there has been a veritable avalanche of papers on this interstitial or mesopsammon fauna, especially in France (Angelier, 1953; 1954; Chappuis and Delamare, 1954; Delamare, 1954 numerous papers).

The animals of the interstitial fauna are elongated, usually with such irregularities as setae, spines, and tubercles greatly reduced as compared with their free-living relatives. Gonad size and number of eggs produced are reduced, and 98 per cent of the species do not have pelagic larval stages (Remane, 1952).

In some temperate-zone beaches this interstitial life is well developed and seems to be especially rich in more sheltered beaches composed of larger grains or mixed sands, especially small pocket beaches, but is best developed in the intertidal. On the open beach it is seasonal in character and attains its maximum development during the summer months. It has been suggested (Fauré-Fremiet, 1951) that the organic films and slimes produced by bacteria, Protozoa, worms, etc., stabilize the sand to a certain degree and are, therefore, an important factor in this environment. Microscopic algae, bacteria, and detritus constitute the food base for the animal life of the beach, which consists principally of small copepods, nematodes, ostracods, and gastrotrichs (Fig. 7). Some of the same groups constitute the populations of lake beaches (Table 1). As yet there are no detailed reports of interstitial life in tropical beaches.

ECOLOGICAL CONSIDERATIONS

Unfortunately most of the ecological literature on sand-beach life is concerned with problems of life in sand in rather general terms, with few references to the surf-swept beach proper. In the rather comprehensive paper on the Beaufort beaches by Pearse *et al.* (1942) a number of very different environments were studied in which the principal substrate is sand. The same criticism may be made of Newcombe's (1935) paper on the beach at St. Andrews' and of most of the European work. Exceptions to this are the work of Mortensen (1921), Schulz (1937; 1938), Caspers (1951), Pirrie *et al.* (1932), H. W. and M. Koepcke (1952), and Dahl (1953).

Perhaps the most significant aspect of the intertidal populations of sandy beaches, at least in temperate latitudes, is its fluctuation. In an environment subject to pro-

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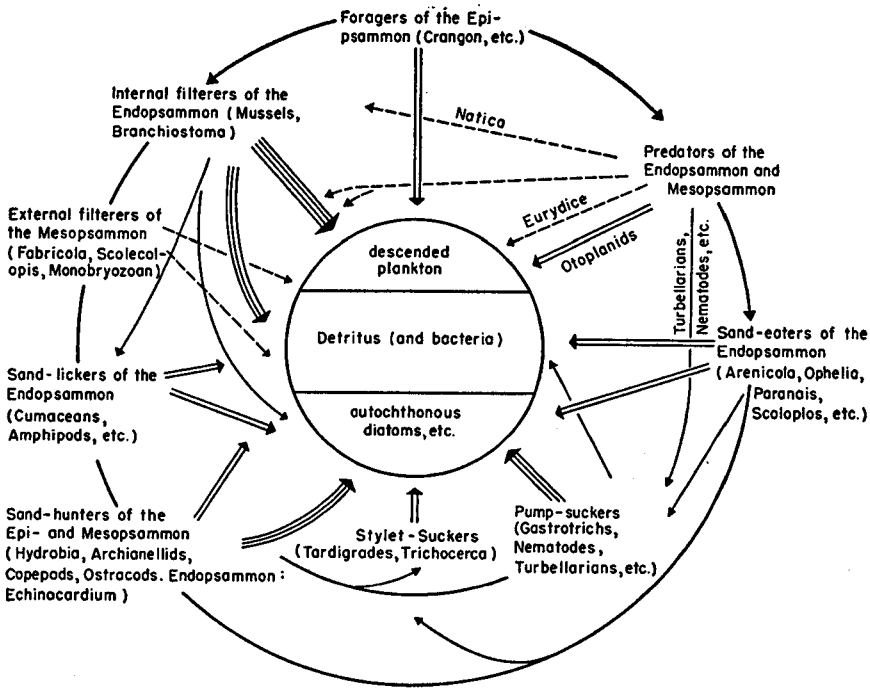

FIGURE 7.—*Feeding relationships of the sand fauna*
After Remane (1952).

nounced seasonal changes in its physical extent most of the organisms are annuals; only on large open beaches are such perennials as the Pismo clam (*Tivela stultorum*) found. In addition to the annual variations, there are irregular fluctuations or pulses in the populations. In some years, for example, *Donax* may be abundant on a beach, followed by periods of extreme rarity (Coe, 1953; 1955; also *see* Chapter 28). A particularly interesting example of population fluctuation is found on New Zealand beaches, where the toheroa (*Amphidesma ventricosum*) may be replaced in some years by another species of the same genus, the tuatua, (*A. subtriangulatum*). While shells of both species may be mingled in natural beach deposits, the two species seem to be mutually intolerant in life (Rapson, 1954). The most important cause of mortality on New Zealand beaches seems to be protracted exposure to high temperatures during periods of low tides; this suggests that such large populations of surf clams as those of the toheroa and Pismo clam may flourish best on temperate beaches in regions of summer fogs.

Recruitment of beach populations depends on long-shore and near-shore currents, and since the larvae are at the mercy of such currents larval life must be of sufficient duration to enable the organism to find new territory. Johnson (1939) suggested that the larval life of *Emerita analoga* may be as long as 4 months.

As compared with studies of zonation on rocky beaches (Chapter 18), very little attention has been paid to the zonation of animals in sandy beaches, yet it is almost

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TABLE 1.—*Comparison of microfaunal groups occurring in marine and fresh-water sandy beaches*
Modified from Pennak (1951)

	Lake beaches	Intertidal marine beaches
Protozoa	Common, sometimes very abundant	Fewer present; seldom abundant
Hydrozoa	Absent	At least two true psammophiles; others epizoic on larger animals
Turbellaria	Few species and few individuals	Several species; Baltic and Mediterranean coasts
Nemertea	?	A few species; sometimes abundant
Nematoda	Numbers of individuals variable; many species present; a regular element of the beach fauna	
Rotatoria	Extremely abundant; about 40 species regular inhabitants of beaches	Rare; several species
Gastrotricha	Not usually abundant; more species in marine beaches than in fresh-water beaches	
Tardigrada	Numbers of individuals highly variable; sometimes abundant in fresh-water beaches; few in marine beaches	
Oligochaeta (Naididae)	Small numbers	Small to medium numbers
Copepoda	Common to abundant; only three species	Common; several hundred species
Mystacocarida	Absent	Probably widely distributed; reported from New England, Europe, Chile
Ostracoda	Absent	Small species sometimes common; true interstitial forms (?)
Isopoda	Rare, more common in caves	Probably common in pocket beaches; several spp. in Med. beaches
Acari	Absent	Several species; uncommon; poorly known; true interstitial forms (?)
Pycnogonida	Absent	One interstitial species known; pocket beach in northern Calif.
Insecta	Apparently micr. insects rare; some brackish water spp.	Sev. spp. Collembola in Med. beaches
Bryozoa	Absent	One interstitial species known, from No. Europe; rare
Mollusca	Absent?	A few small opisthobranchs; sometimes abundant. Species have been found on coasts of North Sea, Black Sea, Mediterranean and Brazil

as pronounced as on more stable substrates. Mortensen (1921) recognized two environmental regions:

The fauna of sandy beaches may be naturally divided into two main regions, the foreshore zone and the tidal zone. The marine species inhabiting the foreshore are adapted to living on dry land

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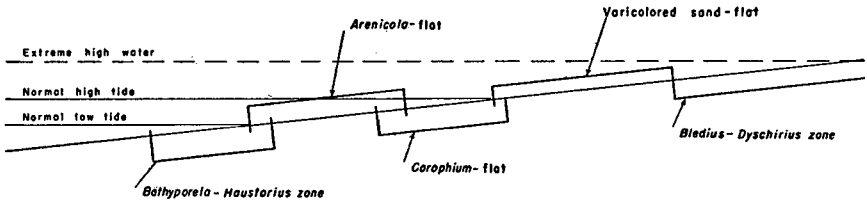

FIGURE 8.—*Zonation in the sand beach at Amrum, North Friesians*
From Schulz (1937).

but can stand being washed over by the sea; those of the tidal zone remain true marine animals but can stand lying dry during ebb tide. The foreshore forms partly follow the water outward with the ebb tide and retreat for the rising flood, always keeping above the water; they are mostly fast-moving animals, which makes it possible for them as a rule to avoid being washed over by the waves. The free-swimming forms of the tidal zone keep below the water; if left by the retreating waves they will quickly burrow themselves into the sand and remain here until the water rises and sets them free again. The sedentary forms simply retreat into the sand during ebb tide.

Davenport (1903) divided the beach of the Cold Spring Harbor sand spit into three zones: (1) the submerged beach, below low tide; (2) the lower beach (intertidal); and (3) the upper beach. Within the intertidal region may be found several regions of concentration of various animals. Schulz (1937) identified at least four intertidal zones (Fig. 8) including a comparatively barren area between normal high tide and the lower limit of insects and subterrestrial amphipods. Dahl (1953) recognizes three zones on the basis of the larger crustaceans, comparable with the tripartite division of rocky shores proposed by Stephenson and Stephenson (Chapter 18). The uppermost zone, or subterrestrial fringe, is occupied by talitrid amphipods in temperate latitudes and ocypodid crabs in the tropics; the midlittoral zone is usually occupied by cirolanid isopods, and the sublittoral fringe may be characterized by various burrowing amphipods in the arctic and temperate regions and by hippid crabs (especially *Emerita*) in the tropics. Even on the shore of the tideless Black Sea there is a well-marked zonation of organisms, especially when studied on a quantitative basis (Mokievskii, 1949). In the splash, or pseudolittoral, zone of the Crimean coast the upper zone (down to the region of mean wave splash) supports first a region of amphipods, *Ponotogammarus*, then massive colonies of *Ophelia* near the middle region. The lower zone, down to the beach slope, is occupied by a small mactracean, *Donacilla*. Much more study is necessary before we can decide which of these schemes is closest to describing a universal zonation. Dahl's scheme, for example, does not apply to the temperate coast of California, where *Emerita* is the most abundant crustacean of the *middle* zone. Many of these organisms move up and down with the tides, and it is therefore difficult to decide where to place them in a zonation scheme. Thus Davenport found the upper limit of Collembola at Cold Spring Harbor near the high-tide line but observed that the lower limit moved downward with the receding tide. The movement of *Emerita* up and down the beach with tide has been observed by MacGinitie (1938) and Pearse, Humm, and Wharton (1942).

Such movements associated with the rise and fall of the tide have been studied for the beach clam *Donax semigranosus* (Mori, 1938; 1950 [as *Donax semignosus*]) on

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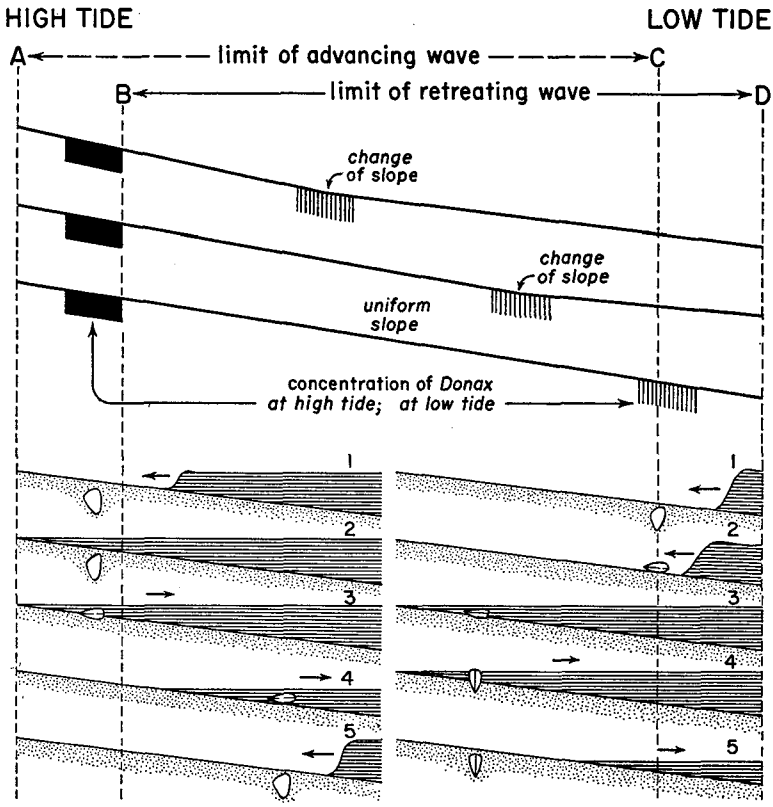

FIGURE 9.—*Donax*

Above: relations to beach slope; Below: their method of migrating with the tide; left, on a falling tide, right, on a rising tide. Compiled from Mori (1938).

the coast of Japan. According to these observations, the clams react to the vibrations caused by the incoming waves on the flood tide by emerging from the sand and are then carried shoreward. As the wave loses force, they dig into the sand at the new level in a few seconds. On the outgoing tide, the clams do not emerge until they feel the outgoing current of water and are then carried down the beach to a lower level (Fig. 9). As a result of these migrations the maximum density is found slightly higher than mean sea level at ebb tide, and slightly lower than mean sea level at the flood. Mori believes that this difference in reaction, which results in a delicate balance of the populations in the intertidal zone, must be the reflection of an internal physiological rhythm. A similar behavior is exhibited by species of *Donax* on the Gulf coast of the United States (Hedgpeth, 1953), and *Donax fossor* on the Atlantic coast (Jacobson, 1955), but other species, such as *Donax gouldi* on the California coast, are more sedentary and remain near mid-tide level, lying exposed for some hours at low tides. The habit of migrating with the tides may be associated with coasts where exposure to sunlight at low tide is severe. On the other hand, such migrations are associated with feeding, and the semisedentary behavior of *Donax* on a cold but rich

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shore may mean that it does not have to feed as continuously as do species on warmer coasts.

In addition to such movements of populations, there are segregations by age and sex of various sand-living organisms in relation to tidal levels. MacGinitie (1938) found that the males of *Emerita analoga* were concentrated somewhat higher up the beach than the ripe females. There is a general distribution of Pismo clams according to size, ranging from the smallest to the largest, up the beach, except that the largest, adult individuals occur at the lowest part of the beach; this, however, may be an effect of human predation (Weymouth, 1923). A similar size distribution, with some tendency toward separation into discrete beds according to size, is noted for the toheroa in New Zealand (Rapson, 1952). According to Dales (1952), the larger individuals of *Thoracophelia mucronata* are higher up the beach than the smaller ones. A similar distribution is noted for *Tellina tenuis* in Kames Bay (Scotland), whereas the larger individuals of *Cardium edule* occur near low water (Stephen, 1953). The amphipods of the beach (*Orchestia, Talorchestia*) are concentrated near the region of detritus accumulation on the beach. Mokievskii (1953) has studied the biomass distribution of beach hoppers in the Sea of Okhotsk in some detail, with diagrams showing the population distribution of *Orchestia ochotensis* associated with fresh and dry flotsam during the monthly tidal cycle. In general, the various sand-beach organisms are arranged in zones according to the state of the tide which enables them to obtain the most food, as Corrêa (1949) has indicated for sand-living nemerteans (*Ototyphlonemertes*) near Santos, Brazil. The complexities of the food chains and cycles of organic transfer in such an apparently simple environment as the sand beach are demonstrated in the diagram by Koepcke (Pl. 1) for a Peruvian beach.

The interstitial life also shows well-defined zonation; Pennak (1942) found a pronounced horizontal distribution of various species of harpacticoid copepods in New England beaches. On wide beaches the horizontal distribution was correspondingly greater (Fig. 10). Although this distribution corresponded for the most part with the amount of water in the sand, the overlapping of species suggests that other factors are also significant.

Little is known of the distribution of organisms in the beach just below the low-

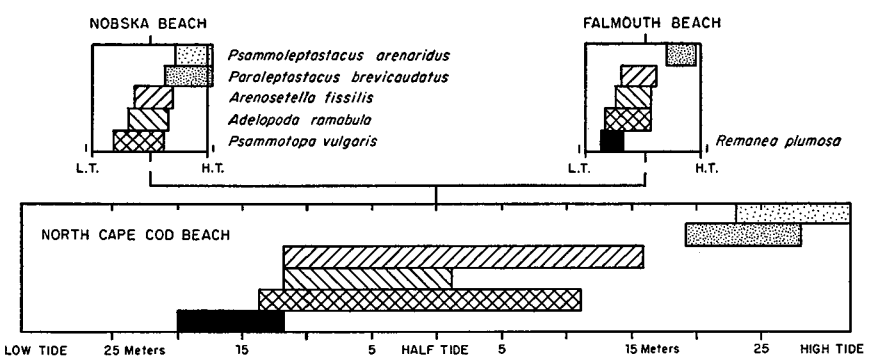

FIGURE 10.—*Distribution of various interstitial copepods on New England beaches* Showing increase of horizontal range with increased width of beach. From Pennak (1942).

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tide level in relation to the bars and troughs. When conditions are established for several months, as on the Gulf Coast of the United States, the troughs may become favorable locations for detritus feeders; Hedgpeth (1953) has noted a concentration of sand dollars (*Mellita quinquesperforata*) in the outermost trough on the Texas coast. Such preliminary suggestions indicate the need for thorough ecological investigations of the life of marine beaches; Neel (1948) found that the microscopic life in lake beaches was much denser where ridges and bars were developed.

THE BEACH AS AN EMIGRATION ROUTE

Although the open beach seems at first glance an unlikely avenue for landward migration, it has nevertheless proved to be such a route in tropical and subtropical parts of the world where high relative humidities have protected organisms from excessive water loss. A number of crustaceans have almost succeeded in making the transition although they must still return to the sea to spawn. These include the ghost crab *Ocypode*, various burrowing land crabs (*Cardisoma*, *Gecarcinus*, and the like), and the land hermits or coconut crabs (*Coenobita*). In all these semiterrestrial crabs, the lining of the gill chambers is enlarged, with increased respiratory surfaces and blood vessels, and functions like a lung. In those crustaceans possessing brood pouches, the transition to land across the open beach has been complete, and there are several amphipods (*Talitrus*) and various isopods which have successfully escaped the limitations of marine life.

Perhaps the most characteristic animal of the sand beaches of middle latitudes is the ghost crab, *Ocypode* (Fig. 11). This fleet-footed crab spends most of its life well above the high tide line, although it must occasionally return to the wave line to dampen its gill chamber. Population densities of *Ocypode* are greatest just behind the berm, as indicated by Koepcke and Koepcke (1953) in their study of the Peruvian species. Cowles (1908) found that *Ocypode* might survive as long as 48 hours without contact with water. During daylight hours the crab usually retires to its burrow but is active at night and on cloudy days. It is apparently an omnivorous scavenger, since it will eat all sorts of luncheon refuse, and droves of them will assemble around dead fish or whales, actively burrowing under the carcass and thus speeding the burial of such objects in the sand. According to M. D. Burkenroad (personal observation) the ghost crabs feed readily upon the tentacles of stranded *Physalia*, and Cowles reported them feeding on jellyfish. Dahl (1953) suggests that they occupy

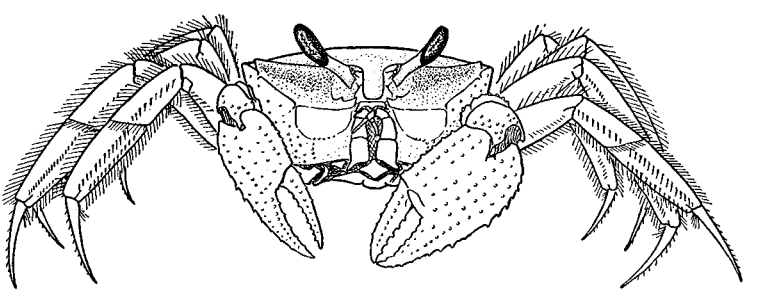

FIGURE 11.—Ocypode albicans, *the ghost crab of the Atlantic and Caribbean coasts of America* (original)

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the same ecological niche in the tropics as that occupied by large beach hoppers in temperate latitudes, and in a general way, according to his Figure 6, the two groups have a separate distribution around the world. Cott (1930) considered the biological position of *Ocypode* to be analogous to that of the rabbit—*i.e.*, an alert, swift animal that burrows for shelter and feeds by rapid forays. This contrasts with the gallery-forming habit of certain mole crickets which sometimes occur in the same part of the beach with *Ocypode* (Sawaya, 1939).

There are some differences in the ecology of the various species of *Ocypode*. According to Crane (1941), *O. gaudichaudi* is the only member of the genus that feeds on microscopic organic matter in the sand as adults, producing small balls of sand in the process. Koepcke and Koepcke have estimated that an *Ocypode* could thus obtain 2 grams of diatoms from the sand in 12 hours. This feeding method is confined to immature individuals in *O. ceratophthalma* in Formosa (Takahasi, 1935), and has not been observed at all for the other American species, *O. occidentalis* and *O. albicans* (Crane, 1941; Milne and Milne, 1946). According to Crane, *O. gaudichaudi* is less of a predator and scavenger as an adult, although the young stages are predacious, than its relatives, which would suggest that this species at least occupies a somewhat different niche than the amphipods of the upper beach, and certainly requires a different environment than *O. occidentalis*, which has a similar range. *Ocypode occidentalis* on the west, and *O. albicans* on the east coast of America, are frequenters of dry, open beaches and are colored to blend with the sand, whereas the brightly hued *O. gaudichaudi* prefers moist, sheltered beaches. Since the eggs of *Ocypode* hatch as free-swimming zoea, the crabs must return to the surf to spawn; the return to land is made during the megalops stage.

Marine turtles, on the contrary, must return to the shore to lay their eggs, which they deposit in holes—or nests—dug in the sand above the high-tide line, sometimes at the base of the dunes. Some species make their excavations in the shelter of bushes or near the beach grasses. The chance of a successful hatch is poor if the eggs are laid where salt water may penetrate the nest, since salt water coagulates the yolk.

On the sheltered shores of estuaries, especially where plant growth is heavy and tidal action may be damped, aquatic organisms are most likely to make the landward transition, and Gislén (1947) considers the estuarine mangrove swamp to be the most favorable environment for transition to land. Nevertheless, some ecologists (MacGinitie, 1935; Pearse, 1950) have been of the opinion that the open, surf-swept beach is the most favorable route for landward migration. This may be true in the region studied by MacGinitie (central California) where humidity is high during the summer months (at least during periods of morning fog), and plant cover on the shores of estuaries is comparatively sparse as compared with the tropics, but the sand beach remains a formidable barrier to most soft-bodied organisms, and it seems unlikely that it has been an important avenue in terms of geologic time on a world-wide basis.

PALEOECOLOGICAL CONSIDERATIONS

The activities of such mass species of active burrowers as *Donax*, *Emerita*, and *Thoracophelia* disrupt bedding, layering, and the orientation of beach deposits, yet may leave few remains of their activities at the site, since winds and waves will re-

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move the shells and carapaces and pile them up in deposits without clear relation to their positions in life. There may, however, be conditions under which a beach population may be preserved *in situ*. Under such conditions it may be possible to infer the original orientation of the beach (Seilacher, 1953). Few paleontologists seem to have studied beaches, with the exception of Krejci-Graf (1935), who published an excellently illustrated series of papers on tracks and living and dead assemblages. Takahasi (1932; 1935) made gypsum molds of crab burrows, including *Ocypode*, and Hayasaki (1935) noted the resemblance of such molds to Tertiary and Cretaceous pipe rocks and certain problematical fossils.

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Chapter 20

Coral Reefs

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"... wo jedes Thier zur Blume wird." (Haeckel)

GENERAL CONSIDERATIONS

The beauty of color and form and the overwhelming variety of life on coral reefs are both legendary and real. Nowhere else in the seas is there such a bewildering range of living things, and perhaps nowhere else is the physical and biological pattern so uniform, characteristic, and widespread as in the coral reef. Reefs are scattered over an area of 190,000,000 square kilometers (68,000,000 square miles) wherever a suitable substratum lies within the lighted waters of the tropics beyond the influence of continental sediments, and away from the cool upwellings of the sea in the eastern parts of the ocean basins.

Coral reefs are deterministic phenomena of sedentary organisms with high metabolism living in warm marine waters within the zone of strong illumination. They are constructional physiographic features of tropical seas consisting fundamentally of a rigid calcareous framework made up mainly of the interlocked and encrusted skeletons of reef-building (hermatypic) corals and calcareous red algae. The framework controls the accumulation of sediments on, in, and around itself. These sediments are derived from organic and physical degradation of the frame and organism associated with the reef constructors and have a bulk ten or more times as great as the frame itself. They are best developed where the mean annual water temperatures are approximately 23–25°C. No significant reefs occur where temperatures during the year fall below about 18°C, except for very short periods, although a few hermatypic corals and calcareous algae can maintain themselves in temperatures considerably below this. Coral reefs are thus confined to the tropical and near-tropical regions (Pl. 9). The coral-reef biotope is a facies of the marine tropical biochore, and its "essential fauna and flora" consists of corals and calcareous algae, which dominate in numbers and volume and provide the ecologic niches essential to the existence of all other reef-dwelling animals and plants. In addition there is an "associated fauna and flora" of other sedentary organisms, which may be represented by relatively few species, and there is also the "epifauna and epiflora" of associated commensals, symbionts, and parasites living on and within the essential and associated organisms, and, finally, the "mobile fauna" of nektonic species.

Corals play a major role on most living reefs, although they have not always done so in the geological past. They are closely followed in importance by encrusting calcareous algae. Sometimes the latter cement the corals, sometimes they smother them. The existence and potentials of reefs are largely conditioned by the ecologic requirements of hermatypic corals and calcareous algae. The close correlation among

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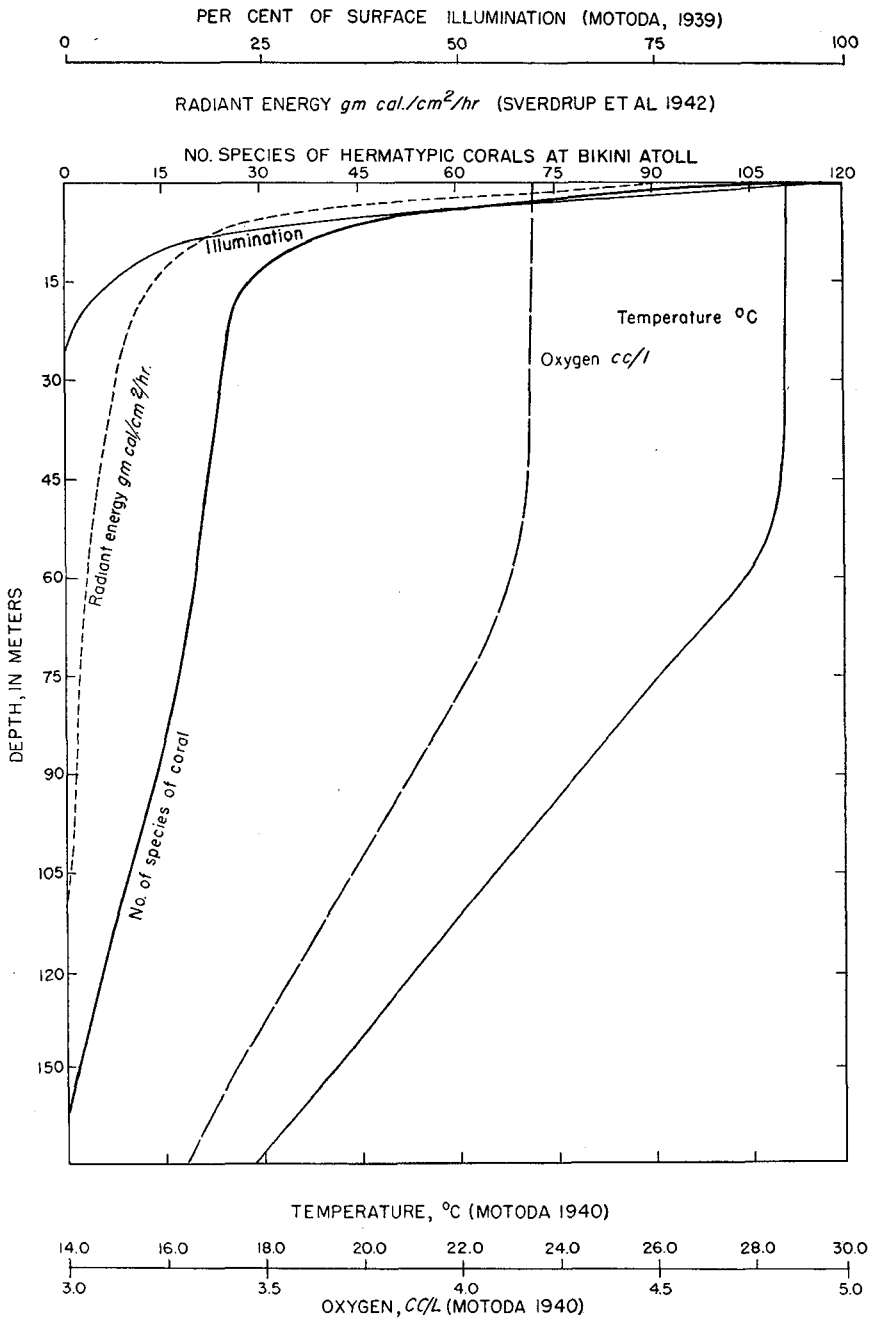

FIGURE 1.—*Graphic analysis of reef-coral distribution according to depth, oxygen, temperature, illumination, and radiant energy.*

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some, but not all, of the physico-chemical conditions and species of hermatypic corals is suggested in Figure 1. From this it appears that the number of species of reef corals is controlled by light intensity and radiant energy rather than by oxygen supply or temperature. Even where oxygen supply and temperatures are favorable, reef corals will not flourish except in relatively shallow depths where radiation and light values are high. This is, of course, a result of the restrictive effect of the symbiotic zooxanthellae in the tissues of hermatypic corals (Chapter 15C), and the same restrictions apply to other reef organisms with associated zooxanthellae and to the crustose algae. Another light factor, not brought out by the diagram, is the length of the "day" at various depths, which diminishes exponentially the total amount of radiant energy receivable each day at increasing depth. For example, at Funchal the "day" is 11 hours at 20 meters, 5 hours at 30 meters, and only 15 minutes at 40 meters (Hesse, Allee, and Schmidt, 1937, p. 160).

Reefs do not flourish at sites where circulation does not maintain equable temperatures and provide fresh supplies of nutrients. Temperature variation is a partial factor in determining the distribution of corals over reef flats. At Maer Island, Torres Straits, Mayer (1918) found that corals were almost absent in the inner reef flat where the daily range of water temperature was as much as 12.5°C. but were abundant near the seaward edge where the range was 3°C. or less. Wells (1952) found much the same thing at Arno Atoll, Marshall Islands, where a leeward reef showed a range of 7.5°C. near shore and only 1°C. near the outer margin. Water movement is perhaps less essential in providing for the large amount of oxygen required than it is for removal of biogenous carbon dioxide, where this is produced in excess of the capacity of the zooxanthellae to utilize it. On the reef flat at Low Isles, Great Barrier Reef, Orr and Moorhouse (1933) found that CO_2 contained in the water is depleted by photosynthesis during hours of sunlight, while the O_2 content rises to as much as 250 per cent or more of saturation, and the pH rises to 8.9. At night photosynthesis ceases, O_2 may fall to as low as 18 per cent saturation, and the pH drops to 7.8. These are extremes found in shallow, poorly circulating water, and where corals flourish in circulating water the range is much less. Availability of $CaCO_3$ in solution does not seem significant in coral distribution, for sea water of normal salinity, between 30 and 40‰, to which corals are restricted, is normally supersaturated in $CaCO_3$.

How are the planktonic food supply and the population of isolated insular reef communities maintained, lying, as most of them do, in the paths of great currents? Most of the benthonic animals of reef associations are pelagic during their larval stages, and this has long been accepted as explaining the cosmotropical aspect of most reef communities, but how is the benthos as well as the nekton of a reef conserved, as it must be, against this dispersal? Bearing on this are the investigations of Johnson at Bikini (1949) and Boden (1952), and Boden and Kampa (1953) at Bermuda. Measurements of water circulation over and immediately around the islands showed a relatively closed local circulation controlled by local temperature and density variations. Although it varies from winter to summer, this circulation pattern appears to act as a conserving mechanism. Similar local systems probably occur around other tropical islands.

Thus large organic reefs in oceanic areas, where the nutrient supply is low, are not

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dependent on materials from the open ocean for their maintenance and growth. They are favored, of course, by the lack of seasonal fluctuations in quantities of nutrients, in contrast to the communities of cooler seas and upwellings. The few measurements that have been made of plankton populations on reefs and in the waters surrounding them indicate that, although plankton is abundant in lagoons and elsewhere within reefs, it is much sparser in the sea around reefs (Motoda, 1940; Johnson, 1949; 1954). But corals and other animals flourish as well on seaward slopes as behind reefs where the supposed food supply is much larger.

On the assumption that oxygen production and consumption on a reef tract is a measure of organic productivity, Sargent and Austin (1954) found that productivity from unit areas on reefs is higher than in the waters of the open sea around them, and that reefs appear to be self-sustaining organic structures. They suggest that this is due in large part to the greater efficiency of the zooxanthellae and other fixed algae compared to planktonic algae. The general significance of algae in organic-reef economy is also emphasized by Doty (1954), and their primary importance in the reef ecosystem has been confirmed recently by Odum and Odum (1955) who measured the primary production and total respiration of the estimated biomass of a windward seaward reef on Eniwetok Atoll. They made the striking discovery that, whereas the average coral colony contained three times as much plant as animal tissue, only about 6 per cent of the plant material consisted of zooxanthellae; the rest was filamentous green algae in the skeleton. Hence it would seem that the role of zooxanthellae as food has previously been much overrated. (For more detailed discussion *see* Chapter 15C.) The corals are scarcely the dominant part of the whole reef metabolism when viewed from this aspect, but each colony is "almost a whole ecological unit in itself with producer, herbivore, and carnivore aspects." They conclude that this particular reef community, and doubtless many others, is an ecological climax system (*see* Chapter 3), and that the reef does not derive its net gain from the plankton in water crossing the reef from the open sea.

Among the factors that enable scleractinian corals to dominate reef communities are their remarkable adaptability to a wide range of ecologic conditions, their edificatory growth, and their near immunity from predators. Living coral polyps are not a direct food supply for any other organism, plant or animal, except for certain fish. The plasticity of form of coral colonies with respect to water movement and sedimentation is too well known to be enlarged on here.

Little is known about the competition for *Lebensraum* among the coral dominants of reef associations. According to Gravier (1910), those with foliaceous, ramose, or encrusting growth forms tend to displace massive or nodular forms growing in close proximity, possibly because of their more rapid growth rate, and ramose forms such as *Acropora* are least displaceable. A certain niche on a reef may be occupied by colonies of a single species to complete exclusion of other species and genera, but an immediately adjacent niche, apparently with exactly the same physical environment may be completely occupied by another species or genus. Such dominants are always species with ramose or foliaceous growth form and rapid rate of growth, which provides some support for Gravier's generalization. Competition of a sort seems to exist between scleractinian corals and alcyonarian corals on some reefs; the latter fre-

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quently take over a niche when the normally dominant scleractinians have been wiped out by some such disaster as devastation by hurricane waves, floods of fresh water, or "black water". In such cases, scleractinians only slowly replace the temporarily dominant alcyonarians, and the reef may not grow at all or may be reduced in size.

Competitive relations between corals and algae are also difficult to assess. Areas where coral has been killed off by "black water" may be quickly repopulated by filamentous green algae before the slower-growing corals can regain their position, and, according to Wood-Jones (1910; 1912), resultant entrapment of sand reduces the possibility of coral regrowth. Wood-Jones also points out that flourishing coral patches in shallow pools during periods of low tides and hot weather may suddenly become invaded by a green filamentous alga beginning at first on injured or necrotic parts of corals, then spreading over the healthy portions, obliterating much of the coral growth. Such algal bloom goes as suddenly as it comes, and the coral colonies, never completely killed, quickly re-assert themselves.

Both physically and organically, reefs are complicated structures and are the result of a near balance of constructive and destructive forces. The constructive forces are largely organic—the accumulation of the calcareous skeletons of corals, calcareous algae, Foraminifera, mollusks, etc., roughly in that order of importance. Physical constructional forces are mainly those that tend to consolidate the accumulated debris by cementation with calcium carbonate precipitated from sea water, as in beach rock, and secondary filling of cavities in coral and algae, and by entrapment of particles by plants. Destructive and degradational forces tending to break down the stout framework of reefs are exemplified in the ceaseless breakdown of coral, algal, and molluscan skeletons and reef rock by the normal life activities of a wide variety of perforating, boring, and dissolving algae, sponges, mollusks, worms and echinoids. Some fish nibble on coral and calcareous algae. The activity of organisms provides large amounts of loosened material of all sizes for transport and redistribution by water movements, and more is loosened by the abrasive action of the transported material, although eventually this is nearly all more or less permanently deposited as chinking in the crevices of coral rock, as talus on seaward and lagoon slopes, and as sandy deposits on the floors of lagoons. It is true that such deposits are constructional, but only at the expense of destruction of other parts of the reef, for no new material is added thereby. A more obvious, but no more important, destructive agency is wave action, both by wind-driven waves, which during hurricanes strike prodigious hammer blows on reefs, and by swells. Waves and swell break and wrench coral colonies and pieces of organically weakened coral rock from reef margins and carry them over reefs onto boulder tracts or into lagoons, or drop them down the seaward talus slope. In places this action undermines the edge of the reef and is followed by collapse of large sections. Coral colonies not torn loose by hurricane waves may be killed by the abrasive effect on the polyps of such violent water movements. Solution of calcareous material also occurs, but the amount lost in this way is small in comparison to the amount ultimately extracted from the sea. On any reef tract these forces are constantly acting, but to different degrees at any one place, here extending the reef laterally or upwards, there breaking it down, and elsewhere more or less in uneasy equilibrium.

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The reefs most closely approaching the "ideal" are those of Indo-Pacific atolls (Pl. 1, fig. 1), which may be regarded as a "pure" biotope because they are rarely associated with land other than that developed as a transient effect of reef development. Atolls, with few exceptions, are oceanic and hence insulated from the modifying effects of terrigenous sediments and influxes of fresh water except from local rains. The other classic types of coral reefs—barrier, fringing, and platform (patch)— are convenient geomorphic terms expressive of some degree of physiographic control in their development, but they are similar ecologically to the atoll type. In the ensuing discussion the atoll reef is taken as typical of the coral-reef biotope and the distribution of its coral constructors as representative of the essential fauna, with less emphasis on the associated and secondary organisms. The generalizations are based principally on the typical atolls of the Marshall Islands with which the writer is most familiar, supplemented by other zonal analyses made of atoll reefs elsewhere.

ATOLL REEFS

Figure 2 shows a cross section of part of an ideal Indo-Pacific atoll. Physiographically, several regions are clearly defined: (1) seaward slope, (2) reef margin, (3) reef flat, (4) island (when developed), (5) lagoon reef, (6) lagoon slope and floor, and (7) knolls. Reef margin, flat, lagoon reef, and probably the cores of knolls (Nesteroff, 1955) are primary constructional forms developed by the rigid calcareous framework. The rest are secondary constructional features. Below about 30 feet the seaward slope is formed largely by talus derived from wave and organic degradation of the reef flat and margin. The lagoon is floored with organic skeletal debris derived partly *in situ* and partly from material transported across the reefs by waves and currents. The exposed-reef rock frame forms an ideal substrate for attachment of reef corals, algae, and other adherent organisms, whereas the loose sediments of the seaward slope and lagoon slope and floor are largely unsuited for such reef-frame constructors, although they are the home of many psammophiles. Thus, the physical environment of the reef is determined by marine hydrography and sea climate, whereas the local-reef environments are functions of the geomorphic forms resulting from aggradational and degradational agencies. The reef margin, reef flat, lagoon reef, and knolls support associations of the coral-reef community which resemble each other more than they do those of the lagoon slope, lagoon floor, and seaward slope. Within these two broad types, however, the separate divisions are ecologically quite different, and each of these is zoned according to the varying degrees in which species of corals and other organisms are adapted to varying local physical conditions.

SEAWARD REEFS

These include two intergrading ecologic sites: to windward and to leeward. These are distinct and separable, particularly in regions of dominantly unidirectional winds such as the trades. Windward reefs are characterized by the development on their margins of a ridge (Pl. 1, fig. 2) formed by growing red calcareous algae (algal ridge, *Lithothamnion* ridge, coralline ridge), which extends actively into the surf as a low, scraggy, red-purplish ridge rising a few feet above low tide level and above the reef flat that extends between ridge and shore or lagoon. Reefs to leeward, or in regions

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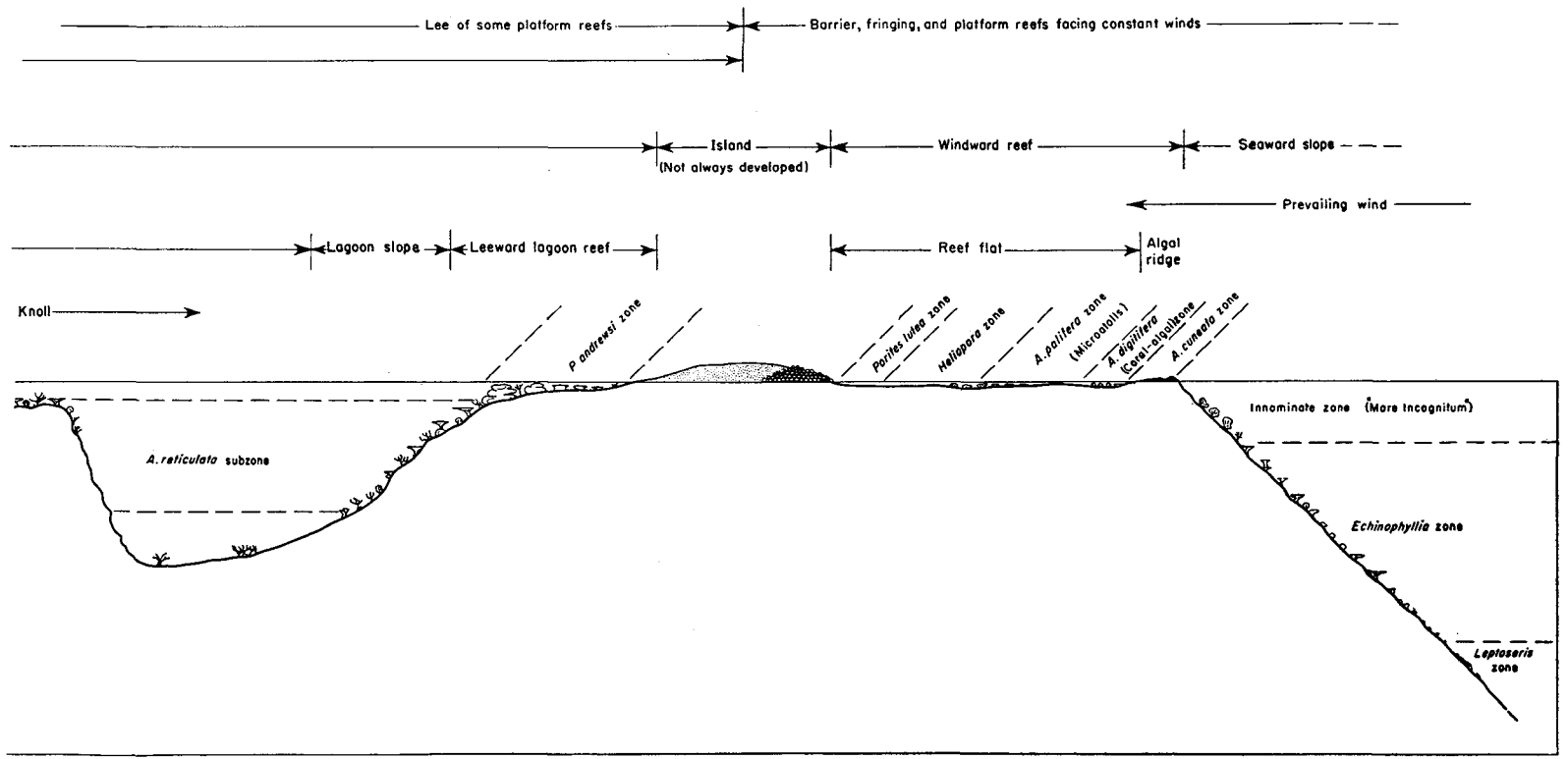

FIGURE 2.—*Cross section of an atoll*

At top are indicated approximate equivalent ecologic sites on other reef types. (Highly schematic; vertical exaggeration 6 times).

ability of a few hermatypic corals to exist but not flourish—in places as much as 500 feet—may be termed the *Leptoseris* zone. Several species of this delicate vasiform to branching coral must be common here, for dredges almost always bring them up. The depth of 500 feet is the extreme lower limit of the reef environment, but the reef biocoenosis below 150 feet is highly attenuated and is only a fraction of what it is in the well-illuminated upper 25 feet.

Reef flat.—A windward reef flat extends inward from the algal ridge toward shore or lagoon for a few tens or a few thousands of feet (Pl. 2, fig. 2). It is a more accessible environment and therefore better known than that of the seaward slope. Although the flat is a reef-rock surface more or less at low-tide level, gentle slopes from the shore and from the algal ridge, scattered hollows and pools, and "boat channels" provide a number of environments with considerable diurnal ranges of physical conditions such as temperature, exposure to air, oxygenation, pH, agitation, turbidity, and so on. Only a general description of these environments can be attempted here, and these are more in the nature of suggestions rather than certainties for any particular reef tract.

Coral-algal (Acropora digitifera) *zone.*—On most reefs the back slope of the algal ridge slopes rapidly down to a zone, from 25 to several hundred feet wide, of rich coral growth covered by only a few inches of water at lowest tide. Parts are often exposed to the air during such tides, but occasional large waves or swells keep the coral colonies wet. This region has been termed the "coral-algal zone" by Tracey *et al.* (1948) and the "red alga zone" by Cloud (1952). It may be the place of greatest coral growth on the reef flat, with the surface as much as half covered by colonies. Crustose algae surround the corals and pave the spaces between them, and there are innumerable pockets occupied by burrowing echinoids, especially *Echinometra* and the chiton *Acanthozostera*. Among corals, species of *Acropora* predominate, especially squat, corymbose colonies of the closely related *A. humilis* and *A. digitifera*, although the spreading, thickly ramose *A. rotumana* characterizes the zone on some flats where the water is deeper, and spreading, slender-stemmed, corymbose *A. corymbosa*, *A. surculosa*, *A. squamosa*, and similar species commonly cover large areas. All coral colonies are of modest size, rarely more than 1–2 feet across, firmly cemented and encrusting, nodular, stunted ramose, or corymbose in form. Other important genera are *Pocillopora* (Pl. 2, fig. 3), *Favia*, *Favites*, *Porites*, *Leptastrea*, *Platygyra*, *Cyphastrea*, and *Goniastrea*. Less common are: *Lobophyllia*, *Stylophora*, *Coscinaraea*, *Pavona*, *Montipora*, *Leptoria*, *Galaxea*, *Hydnophora*, and *Tubipora*. This is about the only place on windward reefs where there is an abundance of colonial zoanthids (Pl. 2, fig. 4), which may pre-empt areas up to several hundred square feet, and where there are occasional large anemones such as *Discosoma* and *Stoichactis*. The brilliant blue starfish *Linckia* is characteristic. Green algae such as *Caulerpa* and *Halimeda* are common on the undersides or overhangs of coral colonies. On some reefs there is an inner subzone with the articulate red coralline alga *Jania* and with scattered coral boulders which in places may constitute a boulder zone or even a low rampart. Such Foraminifera as *Calcarina* and *Marginopora* (Pl. 3, fig. 1) are locally abundant in this subzone. Much of the life on surface reefs in this and other zones lies hidden during the day. A reef seethes with activity at night: the polyps of reef corals, mostly contracted during the day, are fully expanded; crustaceans, worms, mollusks, and fish come out from burrows, crevices, and the shelter of coral colonies and loose blocks, seeking food. The apparent paucity of life on many reefs is an erroneous impression gained from daytime observations.

Microatoll (Acropora palifera) *zone.*—As the water deepens inward from the coral-algal zone to a low-tide depth of 2–3 feet, the coral facies changes through scattered, small, low microatolls of *Favia*, *Favites*, *Platygyra*, *Cyphastrea*, *Goniastrea*, and *Porites*, to larger, less compact microatolls consisting mostly of the thickly and stoutly branching *Acropora palifera* (*A. brueggemanni* on some reefs). These Acroporas are 2–3 feet high and up to 10 or more feet across; their lower parts are rotten and crumbling from the assaults of burrowing algae, sponges, and mollusks. They shelter many encrusting or delicately branching corals: *Seriatopora*, *Stylophora*, *Stylocoeniella*, *Porites* (*Synaraea*). *Psammocora*, and other species of *Acropora*. The solitary coral, *Fungia*, lies loose on the tops and on the bottom where microatolls are closely spaced. The shelter and constant cover of more or less steadily moving water makes this perhaps the richest life zone of the reef flat. Fish are more abundant, crustaceans are common, and most of the branching pocilloporid corals—*Pocillopora*, *Seriatopora*, and *Stylophora*—bear the galls of hapalocarcinid crabs. (*See* Chapter 15A.) The burrowing species of *Tridacna*, *T. crocea*, is common, especially in the "lagoons" and lower parts of microatolls;

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of seasonally alternating winds, show little or no development of algal ridges, and the reef margin is only partially exposed at low tide.

Algal ridge.—The algal-ridge environment is dominated by globular, spongelike red calcareous algae of the "crustose" type, such as *Archaeolithothamnion, Lithophyllum, Lithothamnion, Goniolithon,* and especially *Porolithon,* flourishing in the teeth of thundering breakers. Other organisms are almost excluded, for few are adapted, either basically or secondarily, to this most turbulent of reef zones. The ridge is generally not continuous along the whole length of a reef margin but is more or less regularly notched by surge channels ("chutes") normal to the edge, a few feet wide, extending from just behind the ridge outward and downward to as much as 50 feet, widening outward and extending down the seaward slope as grooves. Much of the water that is poured onto the reef drains back through these channels, often carrying detached fragments down to the talus slope below. The floors and sides of surge channels are nearly smooth, with a veneer of calcareous algae, and their upper edges commonly have overhanging eaves of growing algae and a few corals. On some reefs the surge channels are partially or completely roofed over by continued growth and extend back under the reef flat (Pl. 1, fig. 3), with cross channels or tunnels like the room-and-pillar distribution of a mine. Where the roof openings are large enough to permit some illumination, these passages support a good growth of encrusting, massive, ramose, and foliate corals stout enough to resist the constant surging of the water, such as *Coscinaraea, Turbinaria* (Pl. 1, fig. 2), *Pocillopora, Acropora, Millepora,* and *Heliopora.* Occasional colonies of such sciarophilous ahermatypic corals as *Culicia, Balanophyllia, Tubastrea,* and the hydrocoral *Distichopora* grow in the darker parts. On the ridge, *Millepora, Pocillopora, Porites,* and a few other corals grow precariously in sheltered nooks among algal heads, together with a few mollusks such as *Turbo* and *Trochus,* rugged clinging echinoids such as *Heterocentrotus* (Pl. 2, fig. 1), and barnacles (*Lithotrya*). On the gentle backslope of the ridge the spongelike colonies of algae give way to low botryoidal crusts of "pavement" species that are somewhat lighter in color. Other algae are uncommon; *Halimeda,* for example, is represented by only occasional patches in protected crevices. The characteristic corals of this zone are *Acropora cuneata* and *Pocillopora meandrina, P. danae, P. elegans,* and *P. verrucosa,* a few other species of *Acropora,* and *Platygyra,* encrusting *Montipora, Millepora platyphylla,* and other corals with adaptive growth forms. All are low-growing, spreading forms but generally cover less than a quarter of the surface.

Seaward slope.—Three zones conditioned by relation to wave base and illumination may be distinguished down the seaward slope from the algal ridge. The uppermost is a region of alternating grooves and buttresses or spurs. Some of the grooves are extensions that notch the reef margin and continue downward to depths of about 50 feet. The upper part is more or less barren except for crusts and nodules of algae, but as the wave base is approached more and more corals appear, apparently growing in great profusion and to immense sizes, judging from what can be seen from brief glimpses, refracted in breakers, on relatively calm days, or from loose pieces (negroheads) torn loose by storm waves and hurled over the algal ridge onto the flat. Unfortunately, little is known about this upper innominate zone ("*mare incognitum*"), which probably should be divided into two subzones—an upper, nearly barren zone and a lower reef-coral subzone. This zone is quite different on leeward reef slopes and gives few clues to the corresponding zone on the weather reefs.

Below the upper zone, beginning at about 50 feet, in the moderately illuminated waters below normal wave base, is a zone characterized in many places by abundant foliate growths of *Echinophyllia* and its close allies *Oxypora* and *Mycedium.* Some dredgings have been made from this zone at a few sites (Hawaii, Funafuti, Bikini, and the Maldives), which show that it is transitional between the surface-reef coral fauna and the deepest reef-coral zone, and that it extends down to about 150 feet. Besides a few wide-ranging forms such as *Stylocoeniella* and certain species of *Montipora, Porites* (*Synaraea*), *Heliopora, Fungia, Pocillopora,* and *Distichopora,* there are a number of special forms, mostly delicately foliate or branching, of *Acropora, Montipora, Pavona, Madracis, Cycloseris,* and *Millepora.* Conditions in this zone are much the same as in the equivalent bathymetric zones on seaward slopes to leeward, in deeper atoll lagoons, in lagoons behind barrier reefs, and on coral banks (Tizard and Macclesfield Banks, among others). The *Echinophyllia* fauna resembles that of the *Acropora rayneri* subzone of lagoons, but it is as yet only superficially explored.

The third zone, beginning at about 150 feet and reaching down to depths determined by the

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it slowly rocks its way deeper into the coral skeletons as it grows. Cypraeid, conid, and nudibranch gastropods crawl about or reside under the microatolls, and *Lima* swims erratically here and there. The loose, apparently barren, sandy, or gravelly bottom between the microatolls has its own fauna of worms, holothurians, echinoids, and mollusks.

On many windward reefs, however, where the surface of the flat does not deepen away from the coral-algal or *Calcarina* zones, this zone is replaced by a green-algal zone, where such forms as *Cladophora, Cladophoropsis,* and *Dictyosphaeria* form mats on the surface, with some patches of the hardy nodular *Porites lutea* (Pl. 3, fig. 2) and *Leptastrea purpurea* (Green alga—*Porites lutea* zone). On other reefs this zone may be simply a barren, red-brown, rocky surface with a few pools of water at low tide and occasional boulders which shelter small gastropods, holothurians, crustaceans, ascidians, ophiuroids, and small fish, especially blennies.

Heliopora *zone.*—At still other places on reef flats, where the surface of the flat does not shoal inwardly to a green alga—*Porites lutea* zone or a barren zone, the *A. palifera* zone may grade into another distinct zone of huge microatolls of the blue alcyonarian *Heliopora coerulea.* These microatolls (Pl. 3, fig. 3) are generally dead and flat on top, solider than those formed by *A. palifera. Heliopora* is apparently less vulnerable to riddling organisms and commonly coalesces to form more or less continuous flats at low-tide level. Between the flats, the bottom is veneered with coarse sand on which few corals can grow, except for scattered tufts of delicately ramose *Acropora, Seriatopora,* and *Stylophora.* Most of the tufts are infested with small crabs and are surrounded by a cloud of small blue fish, *Hoplochromis coeruleus,* of mixed ages, which constantly wheel about in unison, now and then vanishing into the coral and reappearing. In places where *Helioporas* lie in quiet water a considerable distance in from the reef margin, the channels between them may be 5–10 feet deep and may support an extraordinarily rich growth of corals—thickets of such species as the ramose *Porites andrewsi, Acropora acuminata* (Pl. 3, fig. 4), many species of *Fungia,* large colonial fungiids such as *Herpolitha, Podabacia,* and *Parahalomitra,* large numbers of fish, and such mollusks as *Tridacna "gigas"* (lying loose on the bottom) (pl. 4, fig. 1), *Hippopus* (Pl. 3, fig. 4), and *Lambis.*

LEEWARD REEFS

Algal ridges, so characteristic of windward reefs, are much less well developed or even absent on leeward reefs. The lack of steady, wind-driven waves is not compensated by the frequently heavy swells. A richer growth of reef corals on the margins and upper seaward slopes of reefs is characteristic of this situation. Leeward reef flats are generally narrower than those to windward, and the slope from the shore, if there is an island, or from the lagoon reef flat, toward the outer margin is relatively uniform. The environments are like those of windward flats, with an *Acropora cuneata* zone if a low algal ridge is developed, grading laterally into a zone dominated by low-growing species of *Pocillopora* where the algal ridge is very weak, or into a zone of *Acropora humilis-digitifera* where it is lacking. Inward from these marginal zones the flat is nearly barren of corals and is either a green alga-*Calcarina-Chama* zone or a nearly barren rock platform. The seaward slope is generally much steeper than on windward reefs, with well-developed surge channels (Pl. 4, fig. 2).

The seaward slope downward from the margin is zoned in general like that of the windward slope, but where it is protected from heavy swells there is a zone marked by great brackets formed by anastomosing, spreading branches of *Acropora* (*A. reticulata-hyacinthus-cytherea*) (Pl. 4, fig. 3) beginning at about 10 feet and extending well down into the upper part of the *Echinophyllia* zone. Other corals growing here are such massive types as *Favia, Favites, Platygyra, Leptoria, Astreopora, Hydnophora, Porites, Symphyllia,* and others, together with less surge-resistant ramose and foliate species of *Montipora, Porites, Alveopora, Stylaster,* and *Millepora.* Unattached forms, such as *Fungia* and its allies, lie on shelves, and crinoids, antipatharians, gorgonians,

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alcyonids (*Lobophyton, Sarcophyton, Sinularia, Alcyonium, Xenia*, etc.), *Trochus, Pinctada*, and holothurians are abundant. Fish, especially sharks (Pl. 4, fig. 4) range back and forth and show a bathymetric zonation. The fauna of this zone extends into the deep, sand-floored recesses that break the edge of the steep slope. The steepness of the reef face where this zone is developed best, in places even vertical and clifflike down to several hundred feet, may be ascribed to the wonderfully profuse growth of corals that extend the reef margin outward rapidly with the production and accumulation of relatively little talus. This may decrease the stability of the outer part of the reef, and hurricane waves may undermine it, causing large blocks to slump; this breaks and scallops the general contour of the margin. The flat above such cliffed edges commonly has no algal ridge; the water at the edge is several feet deep, and the margin is uncovered only briefly during lowest tides (Pl. 5, fig. 1). The corals on the upper edge are either stunted colonies of species growing in deeper, quieter water in the recesses or down the slope, or are adaptive forms, especially of *Millepora* (*M. platyphylla*), *Acropora* (*A. humilis, A. conigera, A. rotumana, A. corymbosa, A. surculosa*), *Favia, Favites, Goniastrea, Plesiastrea, Leptastrea, Pavona, Coscinaraea, Montipora* (*M. socialis, M. venosa, M. foveolata*), *Porites* (*P. lobata, P. lutea, P. lichen*), and *Pocillopora* (*P. elegans, P. danae, P. meandrina, P. verrucosa*). *Acropora* again easily dominates, and the zone may be termed the *A. corymbosa* zone, for low corymbose colonies of this species may cover the reef, affording shelter for more delicate forms. In a single area of a few acres at Arno Atoll, Marshall Islands, the writer collected about 80 species of scleractinian corals, representing some 30 genera, from this zone, which is probably the region of richest coral growth on any type of seaward reef in the open ocean. In general this zone is ecologically the same as the inner part of the coral-algal (*A. digitifera*) zone of windward reefs, but it is much more extensively carpeted by corals. Toward shore the variety decreases rapidly, and the inner part of the flat tends to be dominated by one or two species in exclusive patches. Thus loosely branching, bushy *Acropora hebes* (Pl. 5, fig. 2) may form patches of an acre or so, wedging into equally large patches of ramose *Montipora* (Pl. 5, fig. 3) or stretches

PLATE 1.—ATOLL REEFS

FIGURE 1.—An atoll: air view including about one-fifth (5 miles) of the circumference. At left is open ocean; at right the lagoon; the reef is about 2000 feet wide, with a few small islets (Ailinginae Atoll, Marshall Is.).

FIGURE 2.—Algal ridge: seaward side to right; reef flat to left (Bikini Atoll, Marshall Is.).

FIGURE 3.—Pool behind algal ridge, connecting below with surge channel, margined with calcareous algae (Bikini Atoll, Marshall Is.).

FIGURE 4.—Corals at about 8 feet in the pool shown in preceding figure (*Turbinaria* at left and center; *Coscinaraea* upper right) (Bikini Atoll, Marshall Is.).

PLATE 2.—ATOLL REEFS

FIGURE 1.—Slate-pencil sea urchins (*Heterocentrotus*, about 12 inches across) on back slope of algal ridge (Bikini Atoll, Marshall Is.).

FIGURE 2.—Windward reef flat, about 1500 feet wide, at low tide (Bikini Atoll, Marshall Is.).

FIGURE 3.—*Acropora digitifera* zone, just behind algal ridge: stunted *Millepora platyphylla* at left; rest mostly low, compact, colonies of *Pocillopora* (Bikini Atoll, Marshall Is.).

FIGURE 4.—*A. digitifera* zone: area dominated by colonial zoanthids (Bikini Atoll, Marshall Is.).

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FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4

ATOLL REEFS

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FIGURE 1

FIGURE 2

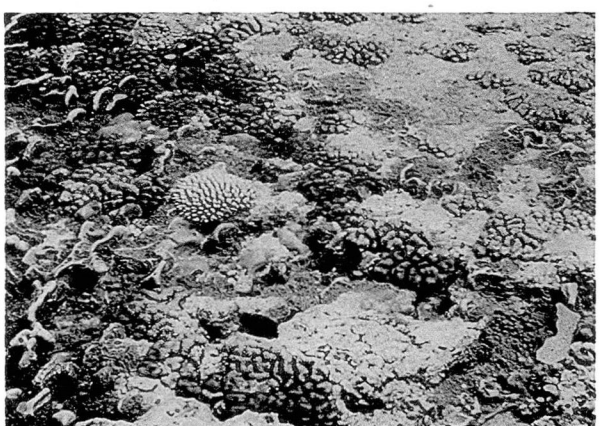

FIGURE 3

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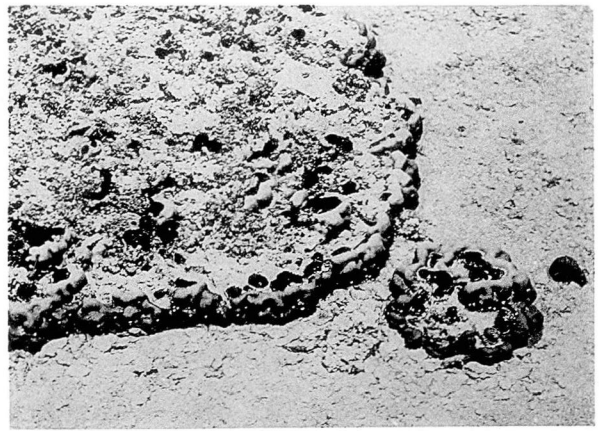

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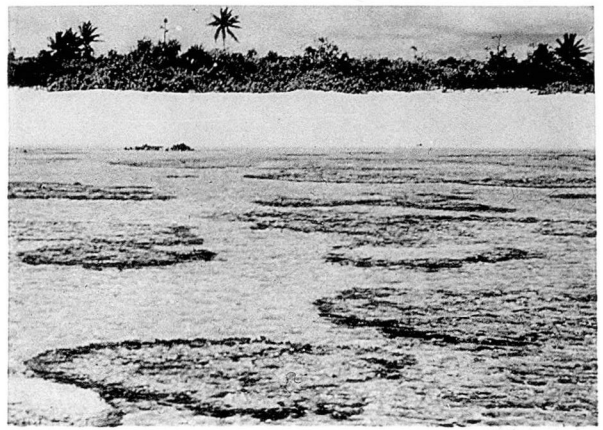

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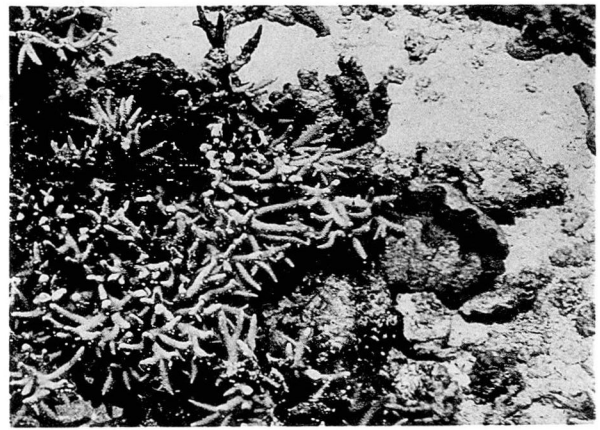

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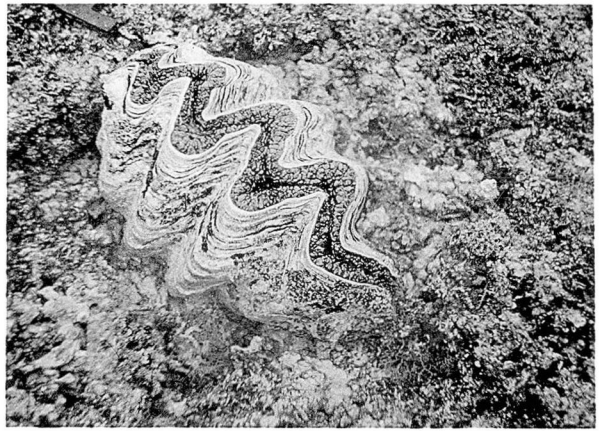


FIGURE 1

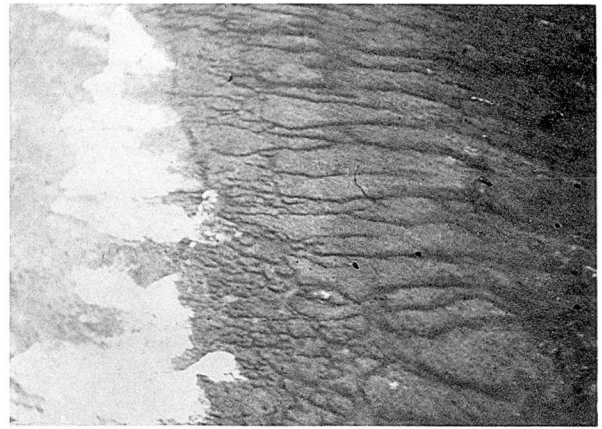
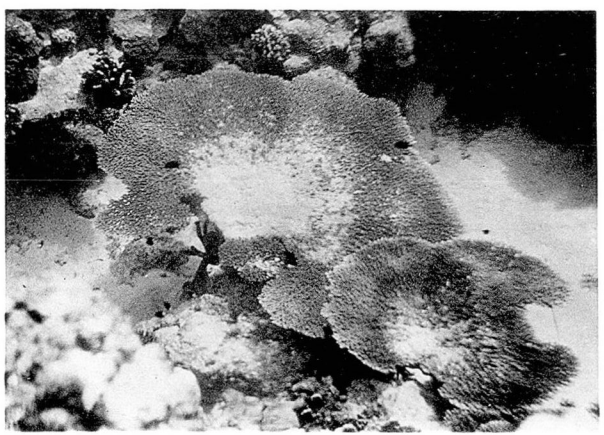


FIGURE 2



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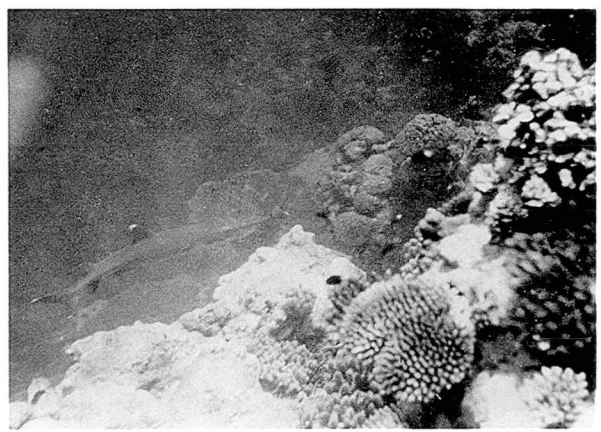

FIGURE 4

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of soft alcyonarian corals (Pl. 5, fig. 4). Close to the shore or boulder tract where the flat is exposed and nearly dry even at ordinary low tides, only an occasional *Porites lutea*, the characteristic euryoecic coral of the same environment on windward reefs, struggles to survive. Where islands are not developed between seaward and lagoonal parts of an atoll reef, the inner *P. lutea* zone generally grades into a boulder zone separating the two reef tracts.

LAGOON REEFS

The relatively quiet waters of the lagoon enclosed by an atoll reef include two principal environments: (1) lagoon reefs, patch reefs, knolls, and sand flats; and (2) lagoon slope and floor. Lagoon reefs border the margins of the lagoon, patch reefs are scattered in shallow parts of the lagoon, while knolls rise from the lagoon floor. The slope to the lagoon floor may be gentle or precipitous, and the lagoon floor generally lies at depths between 75 and 150 feet, rarely as much or more than 200 feet. Water circulation is sufficient in most places to provide near-optimum conditions for the growth of corals and other reef organisms except the red calcareous algae, which require constant, strong wave action. In some large lagoons where there is sufficient fetch for the wind to generate strong waves the algae occur in abundance on the downwind lagoon reef. Sedimentation exerts a greater control on reef development here than on seaward reefs. Much of the sediment of gravel to silt size, derived by the degradation of outer reefs, is shifted over lagoon reefs into the lagoon, and many parts of lagoons otherwise suitable for coral growth are practically barren because this shifting substrate prevents their establishment. The principal sites for lagoon-reef development then are obviously those places protected from mass shifting of sediment, as in the lee of weather islands and on the leeward margin of the lagoon.

PLATE 3.—ATOLL AND PLATFORM REEFS

FIGURE 1.—Large Foraminifera (*Marginopora sp.*, 0.25–0.5 in.), growing on sea grass and dead coral fragments in shallow pool in equivalent of *A. digitifera* zone at Low Isles, a platform reef (Great Barrier Reef, Queensland).

FIGURE 2.—*Porites lutea* zone: microatolls, 4–8 inches high, of this characteristic euryoecic species (Bikini Atoll, Marshall Is.).

FIGURE 3.—*Heliopora* zone: microatolls of *H. coerulea*, 1–2 feet high and up to 10 feet across, on inner part of reef flat (Bikini Atoll, Marshall Is.).

FIGURE 4.—*Heliopora* zone: *Acropora acuminata* (*Hippopus maculatus* at right) in channel between microatolls: depth 3 feet at low tide (Bikini Atoll, Marshall Is.).

PLATE 4.—ATOLL AND PLATFORM REEFS

FIGURE 1.—*Tridacna "gigas"*, about 30 inches in length, lying in a reef-flat pool about 2 feet deep at low tide (Low Isles, Great Barrier Reef, Queensland).

FIGURE 2.—Leeward reef lacking algal ridge, but with well-developed surge channels or chutes and incipient room-and-pillar structure (Ailinginae Atoll, Marshall Is.).

FIGURE 3.—*Acropora reticulata* zone: colonies of the characteristic species, 2–3 feet across, on sand-floored recess near leeward reef margin; depth about 10 feet at low tide (Arno Atoll, Marshall Is.).

FIGURE 4.—Cliffed margin of leeward reef, from near surface (at right = *A. corymbosa* zone) to about 20 feet (at left = *A. reticulata* zone). Note white-tipped shark (*Triaenodon obesus*) (Arno Atoll, Marshall Is.).

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Leeward lagoon reefs (Porites andrewsi *zone*).—Although the situation of reefs in lagoons is broadly similar to that of seaward reefs in the lee which lack algal ridges, there are differences. The lagoon reef (Pl. 6, fig. 1) is narrow and discontinuous in many places, with a scarcely developed low-tide level rock platform or flat between the margin and shore and a rich growth of corals extending practically to the beach. The slope of the bottom from the shore outward is rapid, and depths of a fathom or more may be reached less than 100 feet out. The coral patches tend to be elongated normal, rather than parallel, to the shore, with irregular sand-floored stretches between. Massive and ramose corals grow luxuriantly and freely in the reef patches, and single colonies may attain great size—up to 20 feet across and 10 or more feet high. Such reef patches are truly coral "gardens", with many characteristic species, especially *Porites andrewsi* (Pl. 6, fig. 2), a ramose form which is taken as indicative of this environment, along with *Montipora verrucosa* and foliate or ramose *Montipora*, *Acropora acuminata*, *A. nasuta*, and "bottle-brush" species as *A. exilis*, *A. echinata*, *A. striata*, and *A. rosaria*, *Pocillopora eydouxi* and *P. damicornis*, *Seriatopora hystrix*, *Hydnophora exesa*, and *Millepora tenera*. Many species common on seaward reefs are also found. These include *Acropora humilis* (long-stemmed "*samoensis*" facies), *A. palifera*, *Porites lutea*, *Pavona clavus*, *Stylophora mordax*, *S. pistillata*, *Millepora platyphylla*, and species of *Favia*, *Favites*, *Platygyra*, *Echinopora*, *Astreopora*, *Goniopora*, *Symphyllia*, *Lobophyllia*, *Fungia* (Pl. 6, fig. 3), *Halomitra*, *Herpolitha*, *Podabacia*, *Pectinia*, and others. Near the shore or in very shallow water, *Acropora corymbosa* and similar species, or ramose *Montipora*, predominate. Where the water deepens to 5 or 6 feet, the *P. andrewsi* association begins to merge into an *Acropora hyacinthus-reticulata* zone on the upper part of the lagoon slope.

Corals are the dominant organisms on lagoon reefs, and in and under the coral colonies there is a rich variety of crustaceans, echinoids, gastropods (*Lambis*, *Cypraea*, *Conus*, nudibranchs), pelecypods (less abundant, but *Tridacna*, *Hippopus*, and *Spondylus* are common), a few soft alcyonarians (*Sarcophytum*, *Sinularia*), and actiniarians (especially *Stoichactis* with commensal fish, such as *Amphiprion bicinctus* and *Actinicola percula* (*see* Chapter 15A) and the crustaceans *Bithynis* and *Periclimenes*). Many specialized algae (*Gomontia* and *Ostreobium*), sponges, mollusks, cirripedes, sipunculids, and polychaetes burrow in the corals (Otter, 1937). The alga *Halimeda*, an important contributor to the calcareous detritus of lagoons, is abundant over wide areas, forming rich green tufts. The sandy areas between coral patches support innumerable holothurians and various mollusks, including species of *Strombus*, *Polinices*, *Voluta*, *Tellina*, *Mactra*, *Codakia*, *Pinna*, *Terebra*, *Oliva*, and *Melo*, asteroids such as *Acanthaster*, *Nardoa*, *Echinaster*, *Culcita* (commonly with its commensal fish [*Carapus*] and hippolytine crustacean), and occasional *Oreaster*. *Centrechinus setosus*, the freely moving echinoid, each with its group of centriscid fish, *Aeoliscus strigatus*, occurs here. The fish are one of the most remarkable features of this community with their astonishing polychromy, variety, and oddness of form; they exhibit not only bathymetric zonation but also local restrictions to types of bottom, and certain kinds of corals and algae have their own little circles of fish. "The fish . . . are often laterally flattened and sometimes have elongated filaments in front of the dorsal fin or on the sides of the tail. Their skin is usually thick and their scales strong. The color may be in the skin below the scales, or in the scales, or both, and the scales are often sculptured so as to give complex reflecting surfaces" (Gardiner, 1931, p. 95). For a particularly good analysis of the fish-algal-coral associations of similar reef sites, *see* Catala (1950); for an analysis of similar associations for an atoll in the Taumotus, see Morrison (1954), and Doty and Morrison (1954).

Flourishing reefs, however, are not always found in such a protected leeward position, for in places swells refracted into the lagoon through passes from the open sea often make the water turbid and shift debris back and forth. Such sites may have scattered patches, mostly of ramose types of *Millepora*, *Helipora*, *Pocillopora*, and *Acropora*. Often these corals are moribund and coated with green and brown algae.

Windward lagoon reefs.—In lagoons broad enough to provide sufficient fetch for the generation of more or less constant waves several feet high, red calcareous algae are able to grow to some extent, paving reef flats and developing low algal ridges comparable to those of seaward reefs. In general, however, lagoon-reef flats in the wind are rather wide; cemented platforms slope at first from shore to depths of 2–3 feet at low tide, then upward gently to a margin that may be awash at low tide, with a fairly steep talus slope down to the lagoon floor. Reef-coral distribution follows a roughly parallel zonation with respect to the margin, but the zones are less well defined than on seaward

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reefs, and coral growth is patchy because of the uneven, thin veneer of sand and silt. At high tide waves move across the flat and keep the water fairly turbid, inhibiting coral growth. Near shore, in water a few inches deep, the ubiquitous *Porites lutea* is the only common species, associated with *Pocillopora damicornis* and green algae with holdfasts deep in the sand, holothurians, and psammophilic mollusks and crustaceans. Around and under microatolls, cypraeid and conid gastropods in some variety are common, as are also *Hippopus* and *Tridacna squamosus*. As the water deepens outward, the *P. lutea* association gives way to a vaguely defined zone of large but widely spaced colonies of *Astreopora, Acropora palifera, A. humilis* ("*samoensis*" facies), *Pocillopora eydouxi*, and *Porites andrewsi*, with occasional large thickets of ramose *Montipora*. The margin is usually swept clear of sand and coated with calcareous algae. No coral appears to dominate the margin, but many species of *Acropora* and soft alcyonarians are common. Over the margin the water deepens, and the *Acropora hyacinthus-reticulata* association comes in. *Trochus* is generally abundant and large in this area.

Other lagoon reef structures.—Patch reefs are, in effect, detached outliers of the leeward lagoon-reef environment, dominated by a mixture of species of the *Porites andrewsi* association, or of only one or two species. They frequently represent successful colonization of sandy bottoms by reef corals and are similar in this respect to the patch reefs on the shallow, muddy bottom of the Bay of Batavia (Umbgrove, 1939), although in most atoll lagoons they are generally not awash at low tide. They are usually best developed where large marine deltalike structures have been built out into the lagoon opposite low parts of the encircling reef.

Knolls are reef-rock masses rising from the floor of the lagoon (Pl. 6, fig. 4), with steep, talus-covered sides, with tops covered by a profuse growth of corals. They vary from pinnaclelike structures to broad, more or less flat-topped mounds; their tops may lie at any depth. Those within a few feet above normal wave base are covered by the *Acropora corymbosa* association, those just below wave base by the *Porites andrewsi* association, while the *Acropora reticulata* (Pl. 7, fig. 1) association extends from about 10 feet down to about 50 feet, merging below into the lagoon deeper-water *Acropora formosa* zone. Where the tops of the knolls are 15–40 feet below the surface, there is a near-optimum environment for reef-coral growth in the sediment-free, gently oscillating, well-illuminated water. The most delicate corals can grow freely, and many forms attain gigantic proportions. Fragile vasiform colonies of *A. reticulata* expand upward and outward 10 to 20 feet, limited only by the inherent strength of the skeleton, and *A. palifera* forms huge tree-like colonies that a man can climb about on. Other ramose species of *Acropora* form great bushes, *Pocillopora eydouxi* big clumps, and species represented on surface reefs by small colonies here show their powers of almost unlimited growth. Soft alcyonarians reach great sizes, *Halimeda* is common, and Tridacnas 2–3 feet long are not scarce.

Sand flats develop in lagoons where there are areas of flat sheltered by angles in the encircling reef or where the lagoon is narrow. Waves and tidal currents spread a veneer of sand and some coarse debris over the uneven, creviced surface of the rock flat, smothering or greatly inhibiting the growth of corals. Conditions vary considerably in this environment: parts are awash or almost dry at low tide, water temperatures rise to extremes, and the sands are moved back and forth several times a day with some scouring action. The flat may appear barren or more or less covered by "pastures" of algae such as *Caulerpa, Laurencia, Boodlea, Dictyosphaeria*, and *Avrainvillea*, and *Sargassum* and the vascular plants, *Thalassia, Cymodacea*, and *Halophila*. At high water there is a large fish population, especially rays. On some flats the crustacean *Thalamita* is abundant, on others there is a wide variety of sponges, including the striking chalciform *Phyllospongia foliascens*. *Actinodendron* is not uncommon, with its column deeply buried in the sand, which it rapidly withdraws into when disturbed. Exposed rock surfaces are covered by small, nodular Chamas, while the sand supports a large population of mollusks, especially pelecypods, as *Spondylus, Lima, Pinctada, Pinna, Arca, Hippopus, Corbis, Loripes, Codakia, Tellina, Mactra*, and *Cardium*. Ophiurans (*Ophiothrix*), and holothurians (*Stichopus, Holothuria*); *Edwardsia* and *Balanoglossus* also occur. Some idea of the abundance of organisms even in such an unfavorable site for coral growth is given by Stephenson *et al.* (1931, p. 90), who surveyed in detail the surface population of an area of scanty coral growth 2 meters square between such a sand flat and the margin of a platform reef (Batt Reef) on the Great Barrier Reef:

Corals: 70 colonies, representing 9 genera

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Algae: 42 stems of *Turbinaria*, more than 69 tufts of *Amphiroa*, abundant melobesians, and small numbers of 7 other forms

Other animals: Xenia (85 colonies), abundant *Diplosoma* and *Marginopora*, one or two each of *Euspongia*, *Aplysia*, nudibranch indet., *Tridacna*, *Echinometra*, and a polychaete.

Mangrove swamps are found on some mature atoll reefs, where islands or boulder ramparts provide a lee over adjacent flats, which may be colonized by the halophilous mangroves, *Rhizophora*, *Avicenna*, *Ceriops*, and *Bruguiera* (Chapter 23). These swamps, like islands, cays, and ramparts, are not a part of a coral reef but represent the intrusion of a quasiterrestrial niche on the marine environment of a reef. They support a small association of special marine organisms such as the gastropods *Pyrazus* and *Telescopium*, the arthropods *Scylla* and *Clibanarius*, and the fish *Periophthalmus*, and relics of the displaced normal-reef community growing on mangrove roots above the slowly encroaching reducing environment of silt and organic mud, including euryoecic species of *Porites*, *Leptastrea*, and *Cyphastrea* and even other corals, and *Stoichactis*, zoanthids, *Hippopus*, *Tridacna*, and holothurians.

Lagoon slope and floor (Acropora formosa *zone*).—The slope from the lagoon reefs to the lagoon floor and the floor itself are generally covered with a thick veneer of coral, foraminiferal, and *Halimeda* debris. This unstable substratum is unsuitable for most corals, and except on the tops of coral knolls only a few are able to maintain themselves. *Halimeda* is usually the most abundant organism, with here and there patches of branching acroporans, of which the commonest and most characteristic is *A. formosa*. This is a rare species on seaward reef slopes, but it appears in the *A. reticulata* zone on the deeper parts of surface-lagoon reefs and occurs at depths of as much as 180 feet in the deeper parts of some lagoons. It forms bramblelike thickets (Pl. 7, fig. 2) that afford sites for a few other corals, such as *A. echinata*, *A. arbuscula*, *A. nobilis*, *A. teres*, *Anacropora*, *Montipora*, and *Seriatopora angulata*, only a few of which are found on surface reefs or in shallow water. A few solitary, unattached corals, especially *Cycloseris*, live on the sandy bottom, which also supports or includes a distinctive association of psammophilic crustaceans, mollusks, and echinoids. In contrast to the generally strongly colored corals of surface reefs, corals in this poorly lighted zone are nearly uniformly a very pale tan with pale-lavender or violet shades.

Two bathymetric subzones may be recognized within the *A. formosa* zone, one characterized by *A. reticulata* and the other by *A. rayneri*. The former corresponds broadly to the same bathymetric zone on the seaward slope and the deeper *Echinophyllia* zone and extends wherever exposed-reef rock affords footholds from about 10 feet down to about 75 feet. Many surface-reef species live in this zone, especially in the upper part, along with a few restricted species such as *Acropora implicata*, *Montipora composita*, and related species with foliaceous growth forms, and laminar species of *Goniopora*. In some reef areas gorgonians such as *Melitodes*, the "Red King Coral", are abundant. The *A. rayneri* subzone lies in the deeper parts of lagoons below about 75 feet and is characterized not only by the special species from which it is named, and its close relative *A. rambleri*, but also by other species of the seaward slope: *Seriatopora angulata*, *Stylaster asper*, and species of *Leptoseris*, *Anacropora*, *Mycedium*, *Oxypora*, and *Cycloseris*.

BARRIER, FRINGING AND PLATFORM REEFS

Barrier reefs, classically exemplified by such great structures as the Great Barrier Reef of Australia and the Great Sea Reef northwest of Fiji, are almost continuous chains of elongate "ribbon" reefs (Pl. 7, fig. 3) roughly parallel to and some distance from islands or coasts. They may be separated from the land by lagoons with depths comparable to those of atoll lagoons and with widths from a few thousand feet to 50 miles or more. Barrier reefs grade into or merge with fringing reefs, which are immediately adjacent to the shores of "high" islands and coasts of mainlands (Pl. 7, fig. 4) conditioned by the climate, vegetation, and rock structure of the associated land. Conditions near shore are often less than optimum, because of excessive sedimentation and reduction of salinity by fresh water from the land, but fringing reefs are developed to some degree everywhere in the tropical Indo-Pacific, including

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the Red Sea and Persian Gulf, and in the Atlantic, at sites where physical conditions are suitable.

Platform (table) reefs rise from the shallower parts of continental shelves, in the lagoons behind barrier reefs, in archipelagoes, and occasionally from stable oceanic shelves among atolls. They are flat on top, without lagoons, and commonly ovate, with the longer axis parallel to the prevailing wind if in barrier reef lagoons or otherwise relatively protected situations, or athwart the wind if they lie in or toward the open ocean. Some rest on pre-existing rocky substrates, the topography of which may exert some control on their shape. Others, as in the Bay of Batavia, rest on muddy bottoms. They present all gradations, depending on their stage of development, ranging from small patches comparable to the reef knolls of atoll lagoons to great tracts as much as 15 miles across, from banks below wave base to reef flats awash at low tide with their monotonous sand-flat surfaces "drying" extensively. Mature platform reefs with drying sand flats may develop sand cays toward their lee ends, and the cays may become covered with vegetation. Boulder ramparts may be developed on the weather side, with mangrove swamps developing behind them. Only on the margins is there an appreciable growth of corals and other active reef builders.

Geomorphically, barrier, fringing, platform, and atoll reefs are not distinct and heterogenetic entities but a syngenetic series of forms having a single origin. Wherever suitable ecologic conditions exist or develop, organic-reef communities build reefs whose shape and situation are guided by hydrologic, meteorologic, and pre-existent geomorphic controls. The different "types" provide no ecologic niches and support no organic associations significantly different from those previously analyzed for atoll reefs. Sections of atoll reefs may be compared with equivalent sections of other reefs (Fig. 2). Reef margins with algal ridges are characteristic of the rough-water reefs of barrier and fringing reefs facing strong waves and swells the year round. Sections and environments across platform reefs are homologous with those across atoll reefs from seaward to lagoon. Their calm-water reefs (Pl. 8, figs. 1, 2) away from the weather side correspond either to atoll lagoon reefs in the lee of windward reefs or seaward reefs on the lee side of atolls, and most of their weather reefs correspond closely to atoll lagoon reefs facing the prevailing wind across a considerable fetch of lagoon waters. The sand-flat surfaces of platform reefs are ecologically similar to sand flats found around the ends of some atoll lagoons. The bathymetric coral associations of atoll lagoons are found in practically the same depths off barrier, fringing, and platform reefs.

BIOGEOGRAPHICAL CONSIDERATIONS

INDO-PACIFIC

The coral-reef communities remain remarkably constant in their composition, even to species, within the limits of the tropical Indo-Pacific from the Red Sea and east coast of Africa and Madagascar eastward across the Indian Ocean, through the East Indies and on to the Tuamotu archipelago, an equatorial distance of some 14,000 miles, and are at least recognizable as far east as Panama, 3000 miles farther on.

The number of species, from protozoans to fish, inhabiting any large reef tract has never been determined with any degree of completeness, but it would reach well

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in excess of 3000 in such areas as the northern Great Barrier Reef, the Celebes area, Palau, or the Marshall Islands. The most notable faunal changes are not from east to west but develop in regions peripheral to that area of optimum temperature conditions which lies between the East Indies and the central Pacific. In all directions from this region there is a faunal attenuation, with little or no substitution, correlated with the minimum temperature gradient. Away from the central region to about the 18°C. isocryme, the organic-reef community as a whole and in its parts is fully developed, except for the attenuating effects of geographic isolation. The atoll reefs of the Tuamotus, far to the east of the central area, but within the 25°C. isocryme, with only 18 hermatypic coral genera (Newell, 1954), exhibit the attenuating effects of distance.

Beyond the 18°C. isocryme the reef fauna undergoes little change, but simply becomes reduced as species, genera, and families disappear, with few, if any, new forms replacing them. For example, on the Great Barrier Reef, from its northern limit at about 9°S. Lat., off southern New Guinea, where it lies well within the optimum, about 60 genera of hermatypic corals are found southward to about 21°S., a distance of about 900 miles. From this point on, where winter temperatures fall below 18°C., the number of genera falls rapidly to about 20 in the next 250 miles to 25°S., where minimum temperatures are about 15°C. A similar attenuation is found northward from the Philippines, whence the Kuroshio extends the tropical-reef environment as far north as Honshu (Tokyo Bay).

Thus, there appears to be a direct relation between geographic distribution and temperature, but, as pointed out by Yonge (1940), it is not attributable to the effect of temperature on the individual but to its effect on reproduction: "horizontal distribution depends in the first place on the temperature range within which [corals] can spawn."

PLATE 5.—ATOLL REEFS

FIGURE 1.—*Acropora corymbosa* zone: cliffed margin, with recesses, to seaward but in sheltered lee situation, at low spring tide (Arno Atoll, Marshall Is.).

FIGURE 2.—Area near shore of reef shown in preceding figure, dominated by *Acropora hebes*. Colonies are 1–2 feet across (Arno Atoll, Marshall Is.).

FIGURE 3.—Another part of same reef flat, dominated by *Montipora gaimardi*. Colonies are 1–1½ feet high (Arno Atoll, Marshall Is.).

FIGURE 4.—Still another part of the same reef flat, dominated by colonies of the fleshy alcyonarian, *Sinularia*, about 6 inches high, exposed at low tide (Arno Atoll, Marshall Is.).

PLATE 6.—ATOLL LAGOON REEFS

FIGURE 1.—Lagoon reef in the lee: inner part of seaward reef flat at right; sand-boulder zone diagonally through middle to islet at upper right; lagoon reef at left with coral patches best developed in lee of islet (Kwajalein Atoll, Marshall Is.).

FIGURE 2.—*Porites andrewsi* zone: characteristic species on lagoon reef at depth of about 6 feet (Bikini Atoll, Marshall Is.).

FIGURE 3.—Patch of *Fungia fungites*, with individuals up to 6 inches in diameter, in very quiet water about 1 foot deep on lagoon reef in lee of an islet (Arno Atoll, Marshall Is.).

FIGURE 4.—Coral knolls (white spots) rising from lagoon floor at 10 fathoms. Lagoon is about 1 mile across ("North horn" of Arno Atoll, Marshall Is.).

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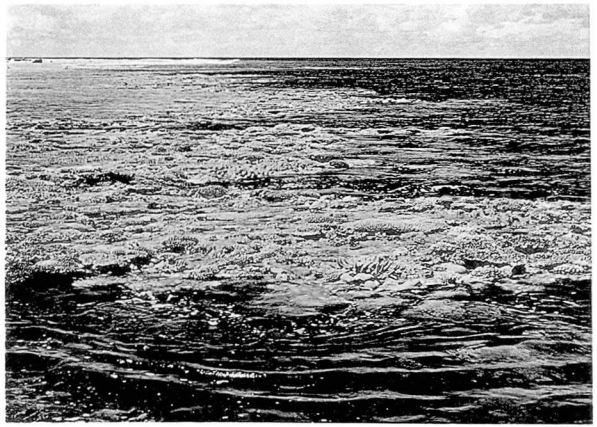

FIGURE 1

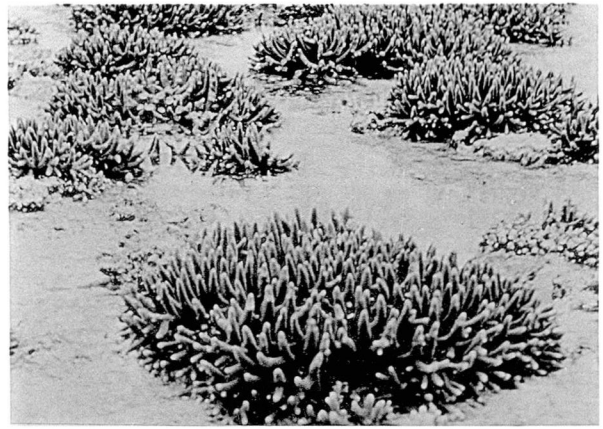

FIGURE 2

FIGURE 3

FIGURE 4

ATOLL REEFS

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FIGURE 1

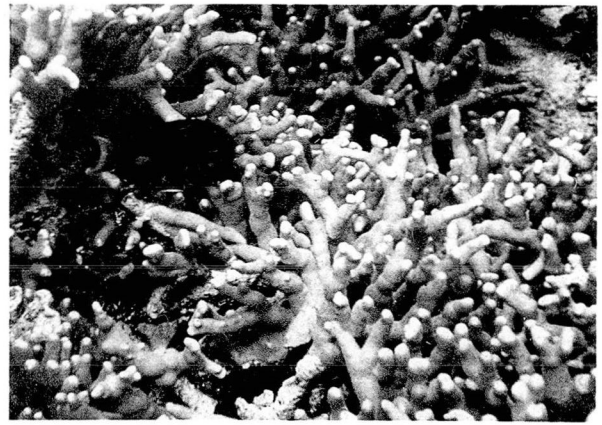

FIGURE 2

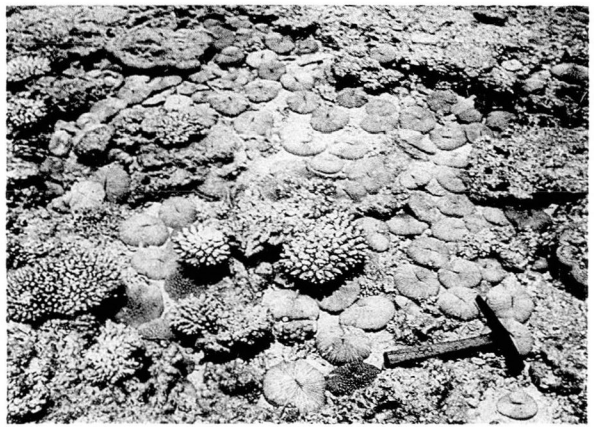

FIGURE 3

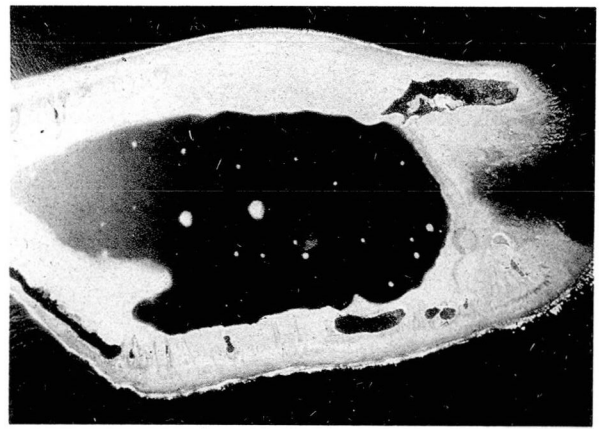

FIGURE 4

ATOLL LAGOON REEFS

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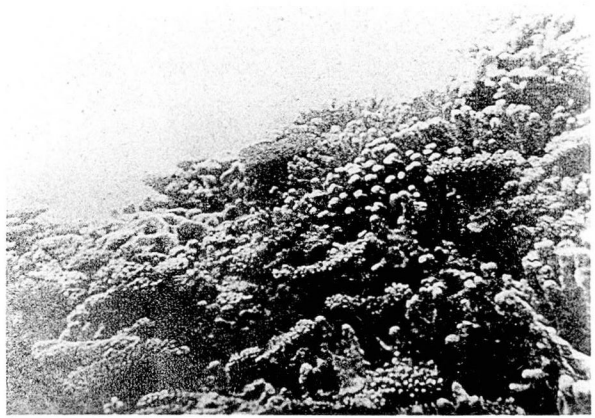

FIGURE 1

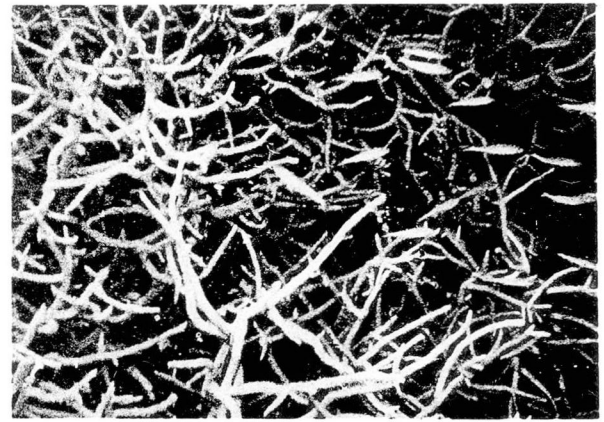

FIGURE 2

FIGURE 3

FIGURE 4

ATOLL LAGOONS; BARRIER AND FRINGING REEFS

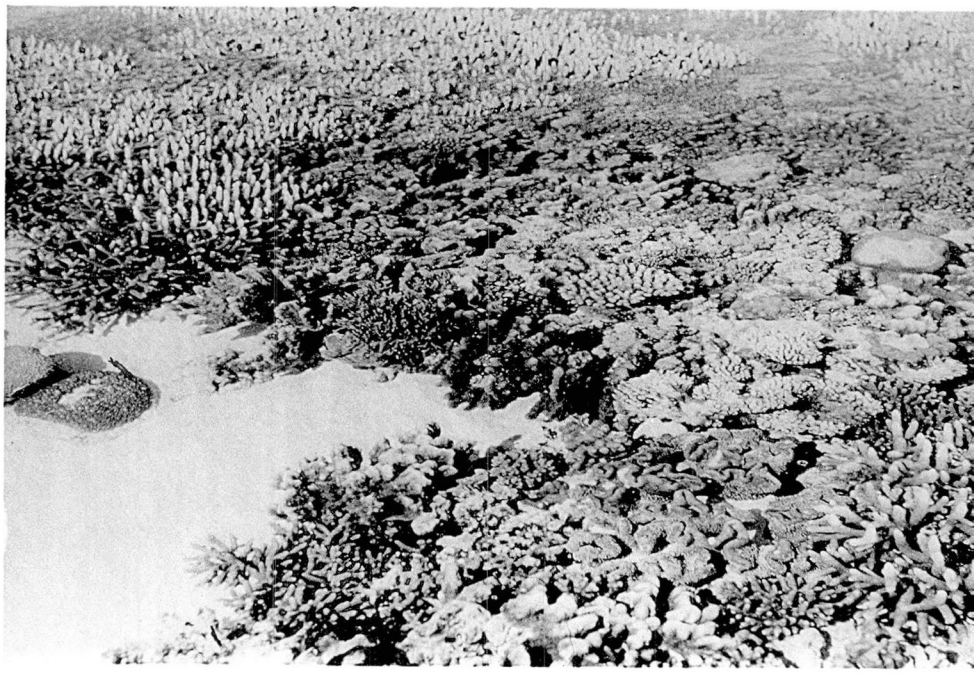

FIGURE 1

FIGURE 2

PLATFORM REEF

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As a natural corollary, there is a diminution of reef development with the attenuation of composition of the reef community. Beyond the 16°–17°C. isocrymes reefs are less well developed as geomorphic features. They are mostly sporadic fringes or patches, growing in depths near or below wave base and rarely uncovered at lowest tides.

TROPICAL ATLANTIC

The coral-reef communities of this region include those of the Caribbean and West Indies, the northern and eastern coast of South America south to about Rio de Janeiro, and the Gulf of Guinea off tropical west Africa. While sea temperatures throughout are about the same as in the central Indo-Pacific, comparable reefs are developed, and then relatively weakly, only in the Caribbean and West Indies, parts of southern Florida, the Bahamas, Bermuda, Brazil, and the Gulf of Guinea, West Africa. Elsewhere, as well as along the north and west coasts of the Gulf of Mexico, influxes of fresh water and sediment from adjacent lands greatly reduce possibilities of significant coral growth. The same distributional controls operate as in the Indo-Pacific, but reef structures are almost wholly of the fringing type. Constructional activity is less, and algal ridges are never developed, even where waves and swells are comparable to those of the Indo-Pacific. The absence of an algal ridge and algal pavements may account for the fact that none of the reefs is exposed at or during low tide except the parts on which sedimentary debris has been piled.

The reef-coral fauna includes only 26 genera and some 35 species, compared with 80 genera and about 700 species in the Indo-Pacific. *Acropora* and *Porites*, as in the latter region, are the two most important coral genera, but in the Atlantic each is represented by only 3 species contrasted with more than 150 and 30, respectively, in

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PLATE 7.—ATOLL LAGOONS, BARRIER AND FRINGING REEFS

FIGURE 1.—Side of coral knoll in atoll lagoon, at 10 fathoms (*Acropora reticulata* subzone) (Bikini Atoll, Marshall Is.). [Emery, 1948, pl. 5, fig. 1].

FIGURE 2.—Lagoon slope (*Acropora formosa* zone): thicket of *A. formosa* at 10 fathoms. Scope of photograph is about 4 feet (Bikini Atoll, Marshall Is.). [Emery, 1948, pl. 5, fig. 2].

FIGURE 3.—Barrier Reef: ribbon (platform) reefs of Outer Barrier, Great Barrier Reef, off Cape Direction, Queensland, Lat. 12 45′ S. (Channel between the two reefs is Captain Bligh's 1789 longboat passage).

FIGURE 4.—Fringing reef: south coast of Viti Levu, Fiji.

PLATE 8.—PLATFORM REEF

FIGURE 1.—Reef flat on leeward side of islet, homologous with atoll lagoon reef in the lee. Depth at low tide about 2½ feet (Heron Island, Capricorn Group, Great Barrier Reef, Queensland).

FIGURE 2.—Orientation sketch of reef area shown in preceding figure:

A. *Acropora hebes*
B. *Acropora brueggemanni*
C. *Acropora squamosa*
D. *Acropora corymbosa*
E. *Seriatopora hystrix*
F. *Pocillopora damicornis*
G. *Platygyra lamellina*
H. *Goniastrea pectinata*
I. *Porites annae* (*P. lichen*)
J. *Pocillopora verrucosa*
K. *Porites lutea*
L. *Favia speciosa*
M. *Sarcophytum sp.*

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the Indo-Pacific. Some Indo-Pacific genera, not represented specifically in the Atlantic, may be said to have generic ecologic equivalents.

Ecologic Equivalents of Reef Coral Genera

Indo-Pacific	Atlantic
Plesiastrea	*Montastrea*
Symphyllia	*Isophyllia, Mycetophyllia*
Lobophyllia	*Mussa*
Platygyra	*Diploria*
Euphyllia, Caulastrea	*Eusmilia*
Pavona, Leptoseris	*Agaricia*
Scapophyllia	*Dendrogyra*
Leptastrea	*Siderastrea*
Trachyphyllia	*Manicina*
Acrhelia	*Oculina*
Pectinia, Oulophyllia	*Colpophyllia*

Many important Indo-Pacific genera are not represented by such equivalents: *Pocillopora*, *Stylophora*, *Seriatopora*, *Montipora*, *Goniopora*, *Goniastrea*, *Hydnophora*, and *Astreopora*, although all occur in the Tertiary faunas of both regions. The Atlantic reef-coral fauna as a whole seems to be a weakening relic of that of the mid-Tertiary Tethyan seas.

Many characteristic reef-coral associates are either absent or greatly reduced in variety in the Atlantic. Calcareous algae play a minor role on the reefs. There are no such great pelecypods as *Tridacna* and *Hippopus*, no coral gall crabs, no giant anemones with commensal fish and crustaceans, and only a few species of cypraeids and conids; other Mollusca present in wonderful variety in the Indo-Pacific are similarly diminished. One of the most striking differences is found in the alcyonarian corals: *Heliopora* and *Tubipora* do not occur in the Atlantic; gorgonians are very abundant on reefs in the Atlantic Ocean but relatively insignificant in the Indo-Pacific; and the soft corals so common in the latter region are a minor element in the Atlantic. These differences from the Indo-Pacific reef associations, however, are actually minor, for there are many genera and even species common to both regions, aside from the common coral genera. The faunal and ecological similarities have recently been analyzed in some detail by Stephenson and Stephenson (1950, p. 300–384). The habitats and sedimentary environments of the reefs off the eastern side of Andros Island, regarded as the most extensive in the Atlantic, have been described by Newell *et al.* (1951, p. 17–26).

CORAL-REEF PROBLEM

It has already been pointed out that reefs develop in the tropics wherever the ecologic conditions necessary for the growth of hermatypic corals and calcareous algae exist. A most important condition is a substrate at or above the maximum depth in which these reef builders can flourish. It would seem as if coral reefs, once the broad concept of their construction as a by-product of the vital activities of tropical shallow-water organic associations was understood, present no "problem". And indeed coral reefs present no special geomorphic problem in those shoal parts of the tropical seas

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marginal to continents and high islands which they fringe or where they develop as barriers or patches. But there are many oceanic reefs independent of such ready-made substrates connected with near-by land, especially in the central Pacific and Indian oceans, and most of these reefs have the form of atolls—rings of reef enclosing relatively shalllow lagoons, in many places 20 or more miles across. Lagoons may be as much as 200 feet deep and studded with hundreds of coral knolls or may be very shallow or even filled. It is here that the real coral-reef problem (or rather problems) emerges: (1) the problem of the origin of the platforms on which the reefs have grown, and (2) the problem of the origin of the characteristic ring shape of atoll reefs. It is around these questions that the "coral reef controversy" has raged ever since Darwin (1837) suggested his now-venerable but enduring hypothesis of subsidence. A recent paper by Ladd and Tracey (1949) summarizes the many contributions and hypotheses advanced since Darwin's time and their current status, with references to pertinent literature; to this the reader is referred for an introduction to the "problem".

Darwin postulated the development of a fringing reef around a foundation such as a volcanic island, with the fringing reef becoming a barrier reef and finally an atoll by organic growth of the reef and slow subsidence of the island. Many subsequent investigations either supported Darwin's hypothesis or suggested others such as the development of atoll lagoons from platform reefs by solution in areas of elevation. One of the most popular alternate hypotheses was the glacial-control theory elaborated by Daly—the upward growth of reefs from the margins of platforms as sea level rose following the melting of the Pleistocene continental ice sheets. Attempts have been made to integrate these, especially the subsidence and glacial-control hypotheses, but at the present time there is no generally accepted unified hypothesis for (1) the origin of the ring form of atolls or (2) the origin of the foundations of existing atoll reefs.

Deep borings have long been regarded as an important source of direct information on atoll problems. They have been made on atolls at three sites in the Pacific: Funafuti (Ellice Islands), Kita-Daito-Zima (Borodino Islands), and Bikini and Eniwetok (Marshall Islands). Although penetrating to depths of as much as 4500 feet, only one, at Eniwetok (Ladd *et al.*, 1953), has reached the foundation on which reef and reef-associated sediments were laid. In this case the ultimate foundation was basic igneous rock of volcanic origin of great age, for overlying it is a succession of relatively shallow-water calcareous reef and reef-controlled rocks of Eocene, Miocene, Pliocene, Pleistocene, and Recent age. The foundations of some atolls are apparently old, and at least in these cases subsidence of reef structures has been an affair of long standing. The coral reefs of the Pacific have long been a factor in its geologic history.

Much remains to be learned of the effects of physical and chemical processes on the denudation of reef tracts, of the nature of the sediments, floors, and knolls of atoll lagoons, of the role of seamounts, and of the foundations of existing reefs. One of the many obstacles to the understanding of atoll reefs, and other reefs, is the broad scope of the facts, physical and organic, to be analyzed. Few observers are without preconceived concepts and endowed with sufficient objectivity even to agree on the status of a given reef, whether flourishing, static, or decadent.

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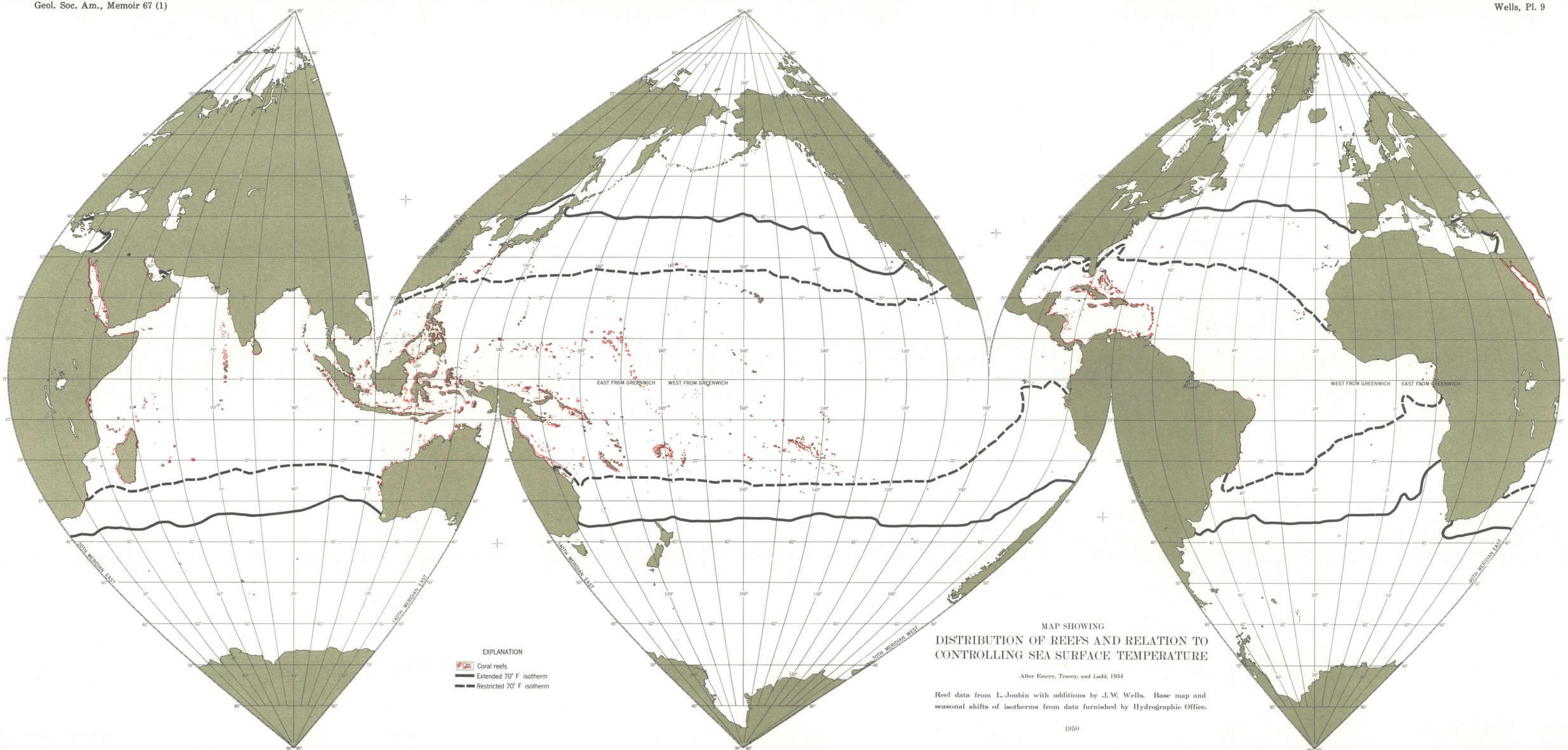

EXPLANATION

Coral reefs

Extended 70° F isotherm

Restricted 70° F isotherm

MAP SHOWING

DISTRIBUTION OF REEFS AND RELATION TO CONTROLLING SEA SURFACE TEMPERATURE

After Emery, Tracey, and Ladd, 1954

Reef data from L. Joubin with additions by J. W. Wells. Base map and seasonal shifts of isotherms from data furnished by Hydrographic Office.

1950

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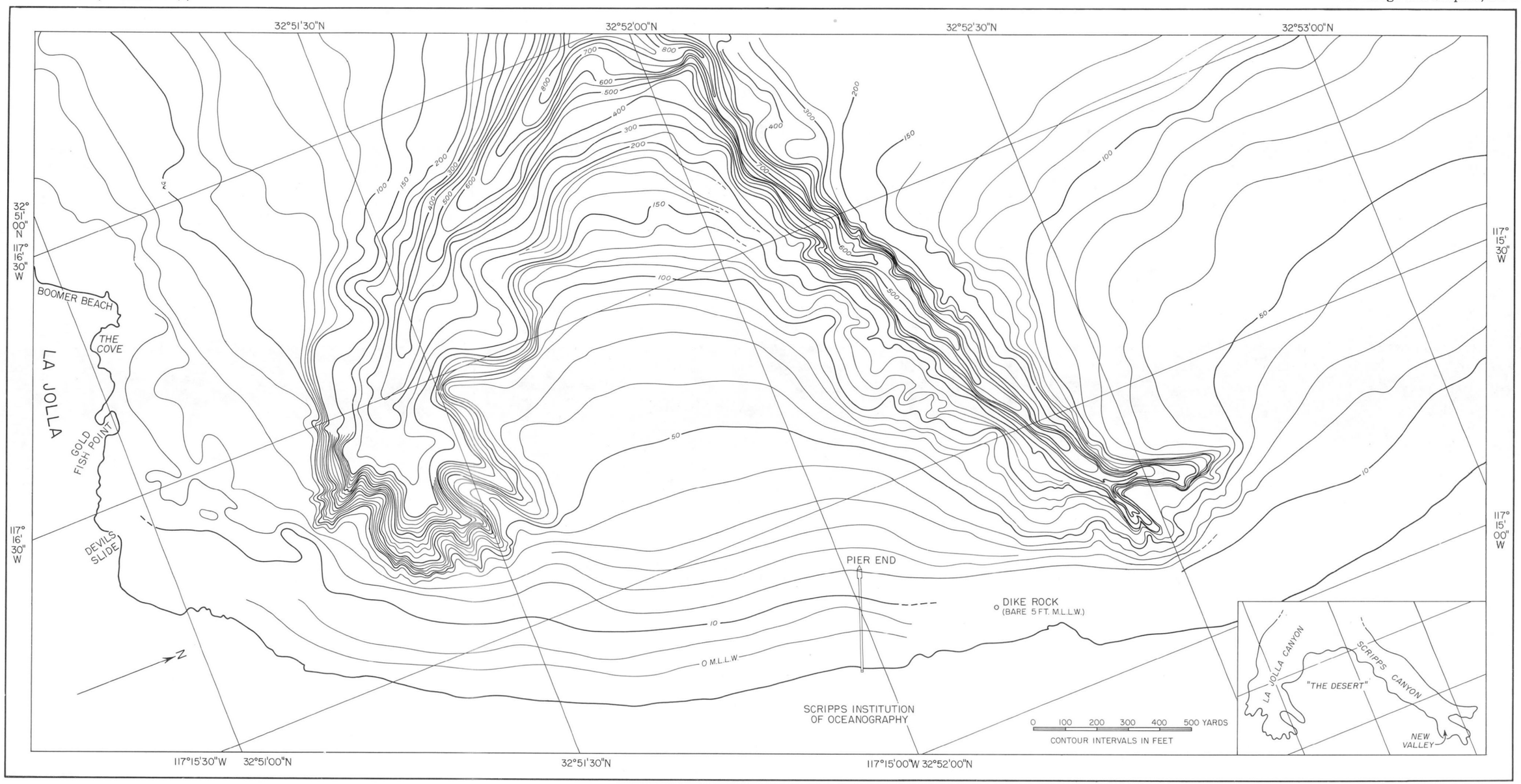

CONTOUR MAP OF SCRIPPS AND LA JOLLA CANYONS

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Chapter 21

Submarine Canyons*

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INTRODUCTION

Canyons of the sea floor have constituted for many years one of the most puzzling features on the face of the earth. Many of these valleys have been cut back into the continental shelf and extend virtually to the coast. Where best known they have the characteristics of river-cut canyons such as are found in mountain ranges or on the escarpments at the margins of plateaus. Thus most of them have rocky walls and are narrow and roughly V-shaped; their floors slope outward almost continuously toward the ocean basin, and they have many tributaries entering from the sides in the common stream pattern. Despite these stream-valley characteristics, geologists do not agree as to whether they were cut by streams or whether they are the product of present-day processes acting on the sea floor. The cause of these canyons will not be considered here, although references at the end of the chapter include some of the more recent articles and books on the subject. (*See* Ericson *et al.*, 1951; Kuenen, 1950; 1952; Shepard, 1948; 1952; Woodford, 1951.)

DESCRIPTION OF LA JOLLA CANYON

Before discussing the type of life which has been found within the canyons and especially on their walls, some description is needed of the characteristics of some of the best-known canyons. Those at La Jolla, California, have been explored more than any others. Their general setting is indicated in Plate 1, which shows the head of La Jolla Canyon and Scripps Canyon, out to the point where they join at a depth of 900 feet and approximately a mile from shore. Both canyons extend almost to the coast—*i.e.*, about 700 feet from low-tide line. Of the two, Scripps is the more spectacular because of its vertical or in places overhanging rock walls which occur along most of its length. The sedimentary rocks (Pl. 2, fig. 1) of Eocene age are similar to the rocks in the cliffs north of Scripps Institution. Ledges project from these rocky cliffs and provide cover for fish and other organisms in the recesses and caves underneath. At the top of the cliffs broad terraces are covered partly with sand and partly by a mass of boulders. The interstices between the boulders also provide other places for additional cover of organisms. The floor of the canyon in this area varies from place to place, and at the same place from time to time, from sand to mud, to plant debris. In most photographs and according to most accounts of the aqualung swimmers who have seen this floor, a conspicuous feature is a mat of kelp and surf grass (*Phyllospadix torreyi*) which commonly occurs along the floor. The decaying marine vegetation in this mat that has been temporarily buried may account in part for the

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trains of bubbles that can be seen rising to the surface above portions of the canyon center. However, recent observations by aqualung swimmers showed bubbles rising from rock ledges as well as from the sediments. According to an analysis of one sample, the gas consisted of 74 per cent methane, 24 per cent CO_2, and minor constituents.

The floor depths of this canyon head have been surveyed repeatedly, and a large variation in depth has been discovered. This is particularly well established in the inner sandy valley heads which lie shoreward of the vertically walled portion of Scripps Canyon. These valley heads fill rapidly with sand and detritus introduced largely by the longshore currents. However, the sediment does not stay permanently, and submarine landslides occur at intervals of about a year in one of the valley heads where frequent observations are made; the landslides cause deepenings which commonly amount to as much as 10 feet and in a few cases to 20 feet or more. After a slide the canyon refills rapidly, so that the exposure of the floor to the low level resulting from the slides is of rather short duration.

The heads of La Jolla Canyon (Pl. 2, fig. 2) have very little outcropping rock but are cut in most places in slightly consolidated alluvium. This alluvium consists locally of cobble beds and elsewhere of sand and muddy sediments intermixed. The walls of alluvium are commonly vertical, although for the most part this canyon head is less precipitous than is that of Scripps Canyon. Farther out in La Jolla Canyon rocky walls have been discovered, although most of the rock is soft shale which does not produce the cliffs which characterize the harder sandy rocks of Scripps Canyon. Where the alluvial walls have been subjected to landslides, talus slopes are found locally at the base.

CANYONS IN OTHER AREAS

The canyons described in the La Jolla area differ considerably from those in some other areas, notably in the very deep canyons which have been traced down the continental slope to the deep ocean floor. As far as is known, however, they are representative of the submarine canyons which extend in to shallow depths and close to the coast in many other localities. These canyons are common along the coasts of the Mediterranean, particularly along the Maritime Alps of southern France. They have been explored by aqualung swimmers from the University of Paris, and features have been described which are similar to those of the La Jolla, California, area (Bourcart, 1950). Along the eastern side of the Atlantic Ocean a number of canyons extend in to the shallow zone, notably at the mouth of the Congo, north of Cape Verde, at the fishing town of Nazarre, Portugal, and one at Cape Breton along the southwest coast of France.

The shallow-headed canyons are common in Asia. A considerable number of canyons hug the coast around the Philippine Islands of Luzon, along the east side of Formosa, in the vicinity of Tokyo Bay and in Tayama Bay on opposite sides of Honshu Island, and along the coast of Korea. In the Indian Ocean the canyons are found around the island of Ceylon and along a portion of the east coast of Africa near the Zanzibar River.

Along the west coast of North America and South America the canyons are best

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known off California and are especially abundant in southern California. The group heading in Monterey and Carnel bays are of enormous proportions and extend to within a stone's throw of the shore, as do several others farther south. A group of canyons close to shore is found around the southern tip of Lower California, and several are indicated along the west coast of South America, although very few soundings have been made in this area.

It can thus be seen that these shallow-headed canyons are not unusual and therefore must constitute important ecological environments. The significance is particularly great, since the topography of the canyons is in such great contrast to that of the surrounding continental shelves and slopes.

BIOTA OF THE LA JOLLA CANYONS

Aqualung divers have made observations to depths of about 50 meters, a few as deep as 75 meters, and one to almost 100 meters. These observations have been supplemented by dredgings and by photographs taken by a camera mounted on a tripod, with a mechanism which releases flash bulb and shutter as the tripod is swung at the end of a cable against the vertical canyon wall.

SCRIPPS CANYON

The flora at the head of this canyon is sparse, apparently because there are no horizontal surfaces or broad outcrops in depths of less than 40 feet. Plants have been observed in only two areas, the rim of North Branch and the head of New Valley.[1] Four species are common and conspicuous in this area—two red algae, *Rhodymenia pacifica* and *Gigartina* sp., and two browns, *Eisenia arborea* and *Macrocystis pyrifera*. *Eisenia* has a bushy growth on a stout basal stipe, resembling superficially the low-growing shrubs of a terrestrial environment. *Macrocystis* is a large kelp (up to 50 meters long), forming beds in 6- to 30-meter depths, which suggest groves when viewed below the surface. These grovelike stands provide a refuge for fishes. The tube-nosed fish, *Aulorhynchus flavidus*, spawns on this kelp in the vicinity of the canyons.

The attached or sessile fauna of the rocks is diverse and in some places forms a mat of living material and encrusted skeletal structures more than 6 inches thick, especially along the rims of the canyons and on the terraces below the rims. This growth thins out on the walls near the floor of the canyon. A similar thinning out of epibioses near the bases of subtidal rocks, resulting in a denuded zone ranging from a few centimeters to a meter in width, has been observed by Drach (1951) in various parts of the world. He attributes this to scour or erosion, and its width depends on the type of sediment and degree of turbulence in the region. Such a narrow zone in a submarine "gully" near Plymouth is attributed "presumably to abrasive action" by Forster (1954). It is possible that in a few localities the constant release of gas with a significant amount of CO_2 may influence the width of this denuded zone in the canyons.

The great concentration of attached animals near the rims of the canyons indicates that supplies of plankton and detritus upon which the organisms depend are probably most abundant in these regions. Drach (1951) considers that the principal factors

[1] So named because this feature is the result of a submarine landslide in 1950.

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influencing the development of such epibioses are light (especially important in governing the distribution of plants) and turbulence, which will of course affect the food supply as well as the amount of abrasive suspended matter in the water.

Among the more abundant animals are several anemones. Of these *Corynactis californica* is the most abundant and conspicuous, although the individuals are somewhat less than an inch in diameter. This species is gregarious, forming colonies of bright pink, white, or brownish polyps. Another abundant species is the common intertidal form, *Anthopleura xanthogrammica*. A few large solitary anemones occur: the brilliant red *Tealia lofotensis* and the white or pale-salmon *Metridium senile*. Small corals, common but inconspicuous, include solitary polyps of *Paracyathus*, *Caryophyllia*, or *Astrangia*, and small growths of the branches *Desmophyllum cristagalli*. There are several gorgonians, of which the most common is a low-branched form with white polyps and coral corallum (*Lophogorgia chilensis*). This is especially common on the rims and ledges, growing like sparse, scattered shrubs. Another common species in the reddish-purple *Eugorgia rubens*. Three species of sponges are common: the leaflike, orange *Hemectyon hyle*, the grayish *Geodia mesotriaena*, and *Tethya aurantia*, which forms low yellowish lumps. There are many polychaete worms, especially the large sabellids which occupy parchmentlike tubes in old burrows and in cracks. One of the conspicuous features of photographs taken at depths of about 300 feet is the large number of tube worms on the rock walls. One of the most abundant, but at the same time most inconspicuous, sessile organisms on the vertical and overhanging walls of the canyon is a large leathery tunicate (probably *Pyura haustor*). These tunicates are inconspicuous because they are irregular in size and covered with other organisms.

Other organisms attached to the rocks include a small brachiopod, *Terebratalia transversa*, and the clams, *Chama pellucida*, *Pseudochama exogyra*, and *Hinnites multirugosus* Barnacles are not commonly attached to the canyon walls, but small acorn barnacles are commonly attached to other organisms. Boring into the soft sandstone rocks are a large pholad and a small date mussel. These seem to be rare at the lower levels. The undermining activities of such crustaceans as the spiny lobster *Panulirus interruptus* and various crabs which dig under ledges and the holes excavated by these boring mollusks may cause the breaking off of portions of the sandstone ledges and accelerate erosion of the canyon walls. The heavy growth of organisms near the canyon rim and on ledges may to some degree retard the erosive action of the borers and diggers.

In the sandy areas immediately around the edges of the canyon many organisms more characteristic of the level bottoms are concentrated, possibly because feeding conditions are better. Most abundant of these are the sand dollars, *Dendraster excentricus*, which may be as dense as several thousand per square yard. Commonly they are arranged, standing on edge, in well-marked bands or rows, or they may occur as piles, lying flat, about 4 inches deep. At greater depths, colonies of sea pens, *Stylatula elongata*, are found in concentrations of up to a dozen per square yard. Numerous clams burrow into the sand.

Among the benthic, motile organisms are many worms and nudibranchs. Various shelled gastropods, including *Kelletia* and *Calliostoma*, and such echinoderms as

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Linckia, *Pisaster giganteus*, and *Stichopus* frequent the canyon walls. On the bottom and irregular surfaces there are a number of crustaceans, including *Panulirus interruptus*, *Loxorhynchus grandis*, *Cancer* spp., and smaller crabs. Many small fishes frequent these regions; some occupy rather limited territories.

The canyon heads provide nesting or spawning sites for many species. These include the cabezon, *Scorpaenichthys marmoratus*, the tube-nosed fish, and especially the squid, *Loligo opalescens*. Cabezon spawn each winter in the upper portions of the rock-walled canyons where they establish territories which they defend. The tube-nosed fish spawns in the *Macrocystis* at the head of New Valley. Canyon heads are the only places where squid have actually been observed to spawn in this immediate area, although they are known to spawn in other locations as well (McGowan, 1954).

Fish are abundant in the canyon, and the vicinity of the canyon is the best locality for angling as well as for spear-fishing with the use of the aqualung. At least 40 species of fish are commonly known to frequent the canyon. There are many rock-dwelling forms along the ledges and in the crevices as well as on the ridges between canyon heads. Sand-dwelling species occur near the rims, and at least 2 species more commonly associated with the *Macrocystis* beds, *Paralabrax clathratus* (kelp bass) and *Sebastodes atrovirens* (kelp rock fish), occur in great abundance in the canyon. Tagging experiments indicate that the kelp bass frequenting the canyons are a separate population from those of the near-by kelp beds.

Many squids live in the canyon heads and are found in the stomachs of fish. A few are observed by the divers, but more commonly only the ink clouds or spots are seen. At times hundreds of such black spots are seen, indicating that the squid have moved away from the approaching diver.

Plankton tows suggest that at some times there may be greater concentrations of plankton around the canyon heads than in near-by areas. Schools of anchovy and sardines, possibly feeding upon such concentrations, are frequently seen, or their presence is indicated by fathograms near the break in slope at the canyon or revealed by flocks of birds and herds of sea lions.

LA JOLLA CANYON

Because the substrate is poorly consolidated, the biota of La Jolla Canyon is markedly different from that of Scripps Canyon. Most of the sessile organisms characteristic of the harder surfaces are missing. Three species of plants are common at the canyon head. The most abundant is the eelgrass, *Zostera marina*, which occurs above the rim of the canyon on the south side. Isolated plants of Elkhorn kelp (*Pelagophycus porra*) and *Macrocystis* are attached to large cobbles. The most conspicuous organisms in this sandy region are large burrowing clams, *Schizothaerus nuttalli*, and a cerianthid (or possibly several species). The sand dollars and sea pens observed around the rim of Scripps Canyon are less abundant here. On a few rock outcrops there are numerous purple gorgonians and the worm snail (*Aletes*), as well as starfish, cucumbers, spindle snails (*Kelletia*), and a few urchins (*Strongylocentrotus franciscanus*).

In general, the motile benthic fauna is much sparser than that of Scripps Canyon, possibly because the attached biota upon which it may feed is sparser. Fish, however,

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seem to be as abundant on the south wall as in the other branch. On two occasions squid eggs were so abundant on the canyon rim that they looked like snowdrifts. Dead squid were found in the canyon below; apparently they were washed down into the canyon after spawning. In the winter of 1946–1947 a large herd of sea lions was observed near the head of one of the branches of La Jolla Canyon by Frank Haymaker. Apparently they maintained their position at the head of the canyon by swimming up the canyon and surfacing near the head.

GENERAL CONSIDERATIONS

These preliminary investigations of the environment and biota of submarine canyons suggest conditions not greatly different in most respects from those observed by Gislén (1930) and Drach (1951) on rocky surfaces in comparatively shallow depths of the subtidal zone. (Gislén used conventional diving gear; Drach used the "*scaphandre autonome*" developed by Cousteau-Gagnan.) Arrangement of communities in well-defined bands or zones associated with tidal levels, characteristic of the rocky intertidal region (*see* Chapter 18), is conspicuously absent. Instead, there is a dense growth of living material in favorable locations occurring in such a variety of associations that it is difficult to classify them. Gislén recognized over 40 "associations" in the Gullmar fjord; Drach developed a scheme of ordinal categories: the primary epibioses are those attached directly to the inorganic substrate, the secondary epibioses are those attached to the organisms of the primary epibioses, and so on. Since many epizoics appear to have rather narrow preferences (*see* Chapter 15A), it remains to be seen how useful such a subdivision will be in practice. The characteristic aspect of associations in this region is their high specific diversity. This adds greatly to the problem of studying these regions, as demonstrated by the bewildering variety of Gislén's epibioses.

Just as crevices and sheltered situations in the intertidal zone enable animals characteristic of lower levels to live well above their usual level (*cf.* Glynne-Williams and Hobart, 1952), so submarine canyons and narrow fjords provide sites for animals from deeper water in shallow depths. Gislén (1930, p. 108–111) describes the "ascent of animal communities towards shallower waters in the interior of the fjord". This may be explained in part by the reduction of algal growth, partly by hydrographical conditions. In the La Jolla canyons the most conspicuous vertical displacement is that of the gorgonians and certain fishes that reach their shallowest situations on the rim of the canyon. In fjords with sills, cold temperatures may be maintained beneath a discontinuity layer, as Gislén found, but a submarine canyon, opening into comparatively great depths at its lower end, provides a channel for the ascent of cold water, especially in a region like southern California where upwelling is a characteristic phenomenon of the hydrographic regime. A situation more suggestive of vertical displacement as a result of the absence of plants is encountered in grottoes, although the primary factor in such situations is reduced illumination (Pérès and Picard, 1949).

In the comparatively soft, relatively unconsolidated sediments of some submarine canyon heads, the activities of boring and digging animals, as mentioned above, may be an influential factor in the attrition of canyon walls, by weakening parts of the rim

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FIGURE 1. View or rock wall of Scripps Canyon.

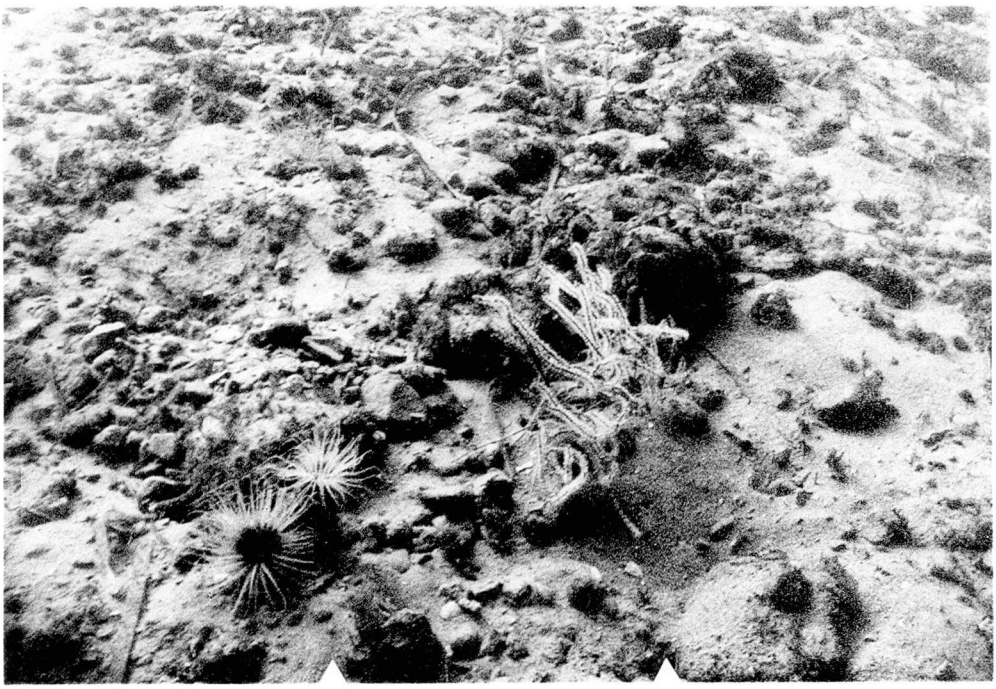

FIGURE 2. Alluvium near head of La Jolla Canyon, showing cerianthids and gorgonians.

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and by causing sand slides. The talus slopes from such action and the by-products of decomposing organic matter accumulated on the canyon floor probably prevent the development of epibioses on the walls near the bottom of the canyon in regions where deep waves may not set up scouring currents. Such action might produce an assemblage consisting of a mixture of fossils of different ages between otherwise continuous beds of the fossils of the earlier period; these assemblages, rich in sponge and alcyonarian spicules and similar evidences of an abundant epibiotic growth of an age subsequent to that of the neighboring rocks would suggest the head of a submarine canyon.

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Chapter 22

Deep Sea and Abyssal Depths

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ECOLOGICAL ZONATION OF THE DEEP SEA

As an introduction to the description of the life in the deeps and abyssal depths of the sea it may be useful to consider the main features of ecological zonation of the oceanic depths. This is especially true because the organisms of even the deepest trenches are dependent on the biological conditions of the overlying water masses, to the very surface of the ocean. As a generalized example we may consider a tropical or subtropical area (Fig. 1).

At the surface, light is the dominant factor in the epipelagic zone. The essential ecological feature of the photic zone is that the animals live in the same environment with the primary food source, the phytoplankton, whereas in the lower layers there is no primary production by plants. Although the endemic species of the epipelagic zone either do not migrate or perform only limited vertical migrations, there are many animals which invade the epipelagic zone from deeper layers during the night or pass their early developmental stages in the photic zone. In either case, the abundance of food is the primary factor.

The epipelagic zone is a very thin layer. In eastern parts of the oceans, with upwelling and high productivity, it may be less than 100 meters thick, and in clear subtropical areas it may be 200 meters thick.

The uppermost aphotic zone is the mesopelagic, inhabited by dark-loving (scotophilic) animals. Whereas temperature is an important factor governing the horizontal distribution of the animals of the epipelagic zone, in the lower zones of the sea temperature is more important in influencing the vertical distribution of animals. Some mesopelagic animals which are very rarely or never caught near the surface are probably limited by the higher temperatures of the upper layers. Downward, however, the limit set by temperature is much more pronounced. The division of the hydrosphere into a warm troposphere and a cold stratosphere, or the *Warmwassersphäre* and *Kaltwassersphäre* in the terms of Wüst (1950), is the most pronounced physical division in the oceanic water masses. In the following the terms thermosphere and psychrosphere are used for these divisions to stress this salient ecological factor.

There is a fairly pronounced discontinuity layer between these regions in most tropical and subtropical areas. The most useful ecological boundary is that marked by the 10° C. isotherm, since it is also the surface isotherm at the limits of the polar regions. The limit of the psychrosphere may be at about 100 meters in the eastern parts of the oceans where there is upwelling, whereas in western regions it may be as deep as 700 meters.

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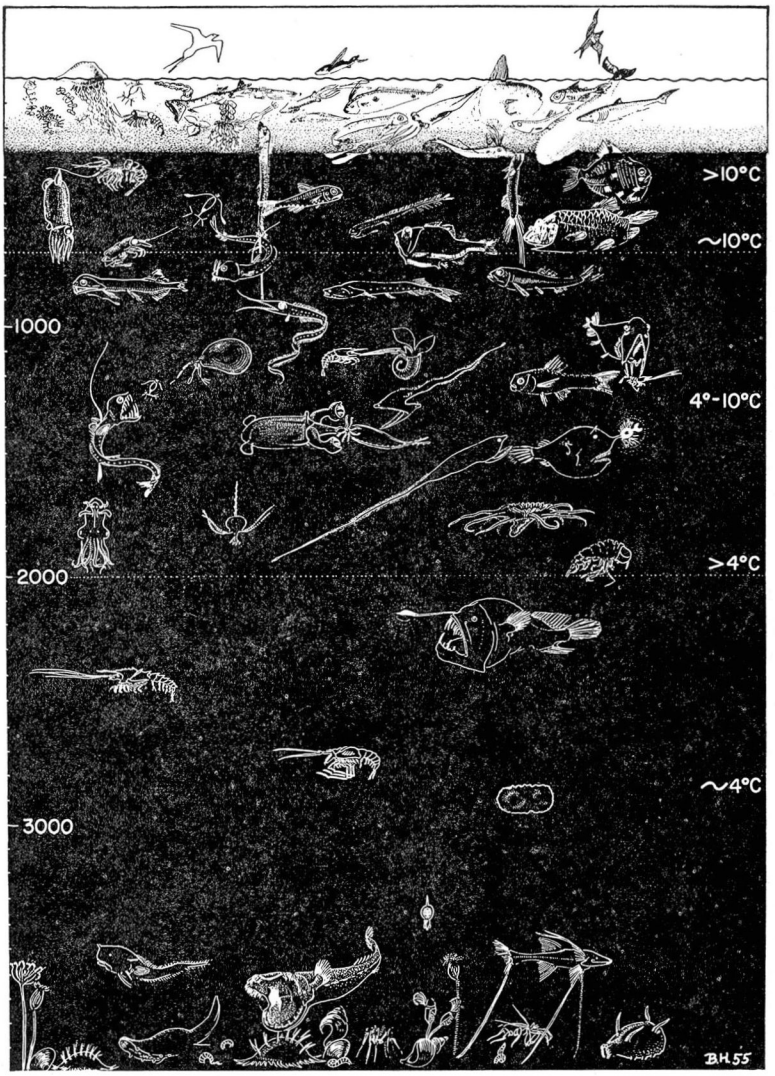

FIGURE. 1.—*Schematic representation of the ecological zonation of the deep sea in the tropical and subtropical regions*

From above: the thermosphere, temperatures > 10°C.; the epipelagic zone, downward as far as the sunlight penetrates during the day; this is the photosynthetic zone with the primary food, the phytoplankton. A zone of dim light leads down into the always dark mesolepagic zone, from which many species rise toward higher levels during the night. For food the mesopelagic animals, as those of deeper zones, depend on the food from the epipelagic zone. Downward the discontinuity layer separating the thermosphere from the psychrosphere leads into the bathypelagic zone at temperatures below about 10° C., where food gradually becomes scarcer; food becomes increasingly scarcer in the abyssopelagic zone from temperatures about 4° C. and lower. Close to the bottom an accumulation of organic debris from above starts a secondary production by heterotrophic organisms, serving as the first link of a new chain in the benthic abyssal zone.

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Among the typical animals of the mesopelagic zone, just above the psychrosphere, are such well-known fishes as *Idiacanthus*, *Chauliodus*, *Stomias*, and the lantern fishes (Myctophidae). In this zone there are a great many species in all animal groups with well-developed eyes and a great variety of luminous organs. Many of the animals are black or red. Most of these animals are currently referred to as bathypelagic, or upper bathypelagic. Many of these mesopelagic animals invade the epipelagic zone at night, and some of them, such as the fishes mentioned above, pass their larval stages there.

In the psychrosphere, which may be 100 to 700 meters beneath the surface depending on oceanic conditions, number of species and populations decrease greatly. This is the true bathypelagic zone, which has not been separated clearly from the mesopelagic zone, or has at best been called the lower bathypelagic zone.

Typical animals of this zone are *Pelagothuria*, *Bathothauma*, *Gnathophausia ingens*, *Eucopia grimaldi*, *Peraclis bispinosa*, *Limacina helicoides*, *Eupharynx*, *Saccopharynx*, *Cyema*, *Serrivomer sector*, *Malacosteus niger*, and most of the deep-sea anglers (Ceratioidea). The deep-sea radiolarians, such as *Tuscaretta*, may also be mentioned. Although the life histories of these bathypelagic animals are very poorly known, it is known that many of them rise to the upper layers to breed and that such fishes as *Eupharynx*, *Saccopharynx*, *Cyema*, and the ceratioids all spend their larval life in the thermosphere.

The bathypelagic zone merges into the abyssopelagic zone; the boundary between them appears to be that of the 4° C. isotherm, which also marks the division between the bathyal and abyssal benthic faunas. In the Atlantic Ocean this temperature is not reached until about 2000 meters, whereas in the Indian and Pacific oceans it is as high as 1500 or even 1000 meters. Much of the discussion about the vertical range of the bathyal and abyssal zones is undoubtedly due to these differences in the position of the 4° C. isotherm in the various regions.

The drop in the number of species and the quantity of animals is even more pronounced between the bathypelagic and the abyssopelagic zones. This may partly reflect lack of knowledge, but all the evidence confirms the impression of a poorly inhabited zone. As examples of abyssopelagic species, related to bathypelagic groups, we may mention the radiolarian *Protocystis*, the crustaceans *Eucopia australis* and *Gnathophausia gigas*, and such deep-sea anglers as *Melanocetus murrayi* and *Borophryne apogon* (Pl. 1, fig. 2).

Closer to the bottom are a number of species that depend on the concentration of food from the bottom, but the distinction between pelagic and benthic species in these depths is difficult in many cases and depends on how far from the bottom a species must live in order to be considered pelagic. Here, as in shallow regions of the sea, the intermediate mode of life, as exemplified by many shrimps and prawns, must be common. Species which have been caught abyssopelagically and are closely related to benthic groups are rare. The holothurian *Galatheathuria* and the fish *Macrouroides* are examples.

The lower limit of the abyssopelagic zone is unknown, but it may reasonably be expected to coincide with that of the abyssal zone, at about 6000 meters, which means a vertical range of 4000 meters for this region of the sea.

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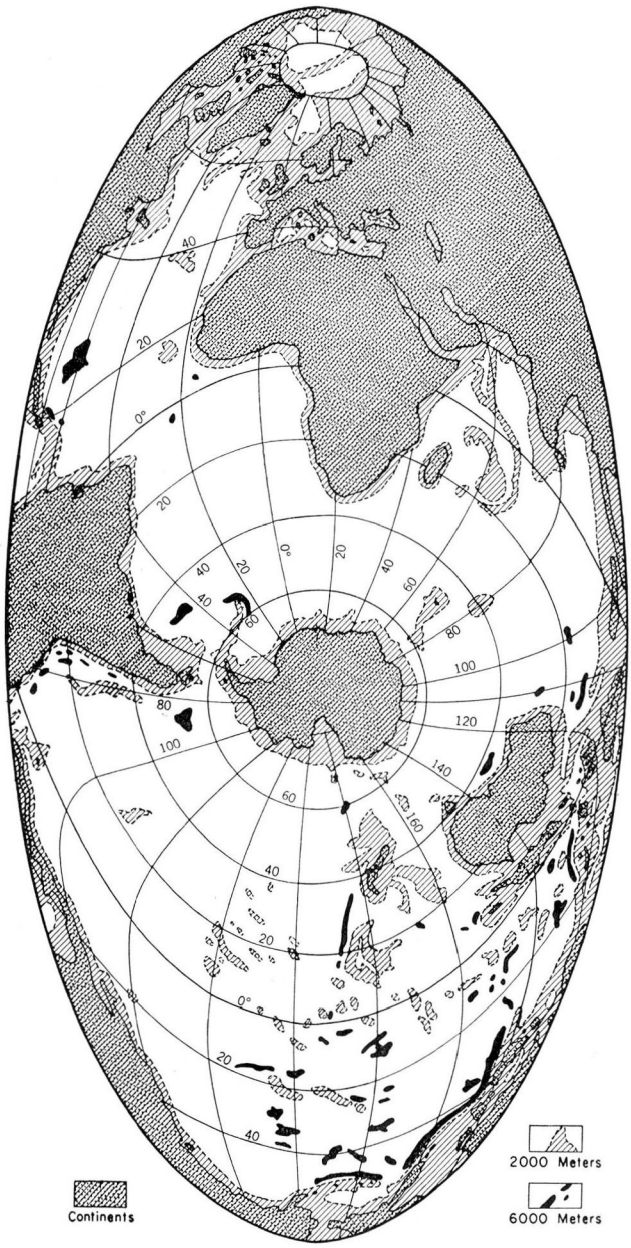

FIGURE 2.—*Map of the world ocean (Hammer-Aitoff projection) showing 2000-meter contour and depths greater than 6000 meters*

Note the essential continuity of the bathypelagic regions. Base from Spilhaus (1942)

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As yet nothing is known about pelagic animals from depths greater than 6000 meters—*i.e.*, from the trenches. If a hadopelagic fauna occurs, it is probably poor, as most of its species would be derived from a correspondingly meager hadal benthos.

The terms hadal and hadopelagic have been suggested to apply to the zones from 6000 meters to the greatest known depth (10,863 meters). The word is derived from hades, the Greek mythological underworld, to correspond with the terms bathyal and abyssal. It thus equals the *super-ozeanische Tiefen* of Zenkevich (1954).

CHARACTERISTICS OF THE ENVIRONMENT

Before describing the animal life of the deepest parts of the ocean it is necessary to give some picture of the conditions for life. This should not be a repetition of knowledge of the physics, chemistry, and geology of the abyssal depths but rather an attempt to evaluate the importance of various factors. Such an attempt can only be conjectural in the absence of observations upon living animals, and the current publication of the results of recent deep-sea expeditions will modify some of the viewpoints presented here.

AREA

The total area of the oceans and adjacent seas is 361 million sq. km. If the upper limit of the abyssal depths is set at 2000 meters, the area of the abyss would be about 84 per cent of this total area (Fig. 2). Even excluding the depths between 2000 and 3000 meters as some sort of transition zone between bathyal and real abyssal depths would subtract only 6.8 per cent; excluding the depths beyond 6000 meters would remove 1.2 per cent. Thus the area between 2000 and 6000 meters covers 76 per cent of all the area of the oceans, or 273 million sq. km. The total land area is slightly more than half of this, or 149 million sq. km. The total area of the globe is $510 \times 10^6 km^2$, so that more than half the globe is occupied by the abyss.

BOTTOM SEDIMENTS

By far the greater part of the abyssal region is covered with a soft bottom, fine ooze or clay. For all practical purposes it can be considered covered by the pelagic sediments (Kuenen, 1950). The calcareous oozes occupy 128 million sq. km, the siliceous oozes 38 million sq. km, and the abyssal clay 102 million km (red clay is better called abyssal clay, because most of it is not red, but brownish).

Plate 3 shows that the oozes, especially *Globigerina* ooze, dominate in depths less than 4000 meters, whereas the abyssal clay is found only in depths exceeding 4000 meters.

It may be expected that the composition of the substratum will influence the animal life, but at present it is not possible to delineate the special communities confined, *e.g.*, to *Globigerina* ooze or abyssal clay. Other factors are probably sufficient to account for the rough picture of distribution of the animals, so far as known at present.

LIGHT

Sunlight disappears high above the abyssal zone, so no photosynthesis is possible. Bioluminescence can hardly be of much importance; the magnificent display of luminous organisms that occurs in the surface layers is probably rare in the deep. Some animals, like *Umbellula*, produce light, but the general rule that true abyssal animals have reduced eyes or are blind must mean that any form of light is sparse and of little ecological importance.

PRESSURE

The hydrostatic pressure, the weight of the overlying water, is a simple function of depth. For purposes here it is sufficient to reckon 1 atm. as equal to 10 meters of water. There is, therefore, the wide range of 200–600 atm. in the abyssal zone, increasing toward 1100 in the hadal zone. Direct

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observations on the effect of these high pressures on the deep-sea animals are practically lacking. That the animals are dead when they come up in the dredges or trawls is primarily caused by the change of temperature, especially within the region of the thermosphere. But even in or close to the polar regions the variations of temperature and salinity may overshadow the effect of the decreased pressure.

There is no evidence that the general shape of animals is changed when the pressure is decreased, and there is nothing like the "explosive effect" commonly supposed.

The effect of pressure on the abyssal animals must, however, be of great physiological importance, as judged from observations on shallow-water animals. The classical experiments were carried out by Regnard (1891), when he showed that the fermentation of sugar by yeast was almost normal at 400 atm. but was stopped at 600 atm., and that eggs of trout hatched normally after having been under a pressure of 300 atm. for 6 hours, whereas 400–650 atm. had a lethal effect.

In 1930 Fontaine asked why there is a special deep-sea fauna. As a physiologist, he considered the three dominating peculiarities of life in the deep sea to be: (1) absence of sunlight; (2) low temperature, close to 0° C.; (3) high pressure. The two first are not peculiar to the abyssal fauna, since light disappears at 400 meters at the most, and the low temperatures are normal for the polar regions. The unique dominating factor is pressure.

Among Fontaine's experiments may be mentioned the parallel he draws between the effects of tetanization and pressure on muscles of the frog and his discovery of an increased metabolism in *Pleuronectes platessa*, *Gobius minutus*, and *Palaemon serratus* under pressure.

Of equal interest is the varying resistance in different animal groups. In Fontaine's experiments some actinians which survived after 1 hour under 500 atm. died after 4 hours under the same pressure; *Phascolosoma* could survive 500 atm. for several hours, whereas fishes like *Pleuronectes*, *Gobius*, and *Ammodytes* died at pressures below 200 atm., depending on the duration of the experiments, but survived at 100 atm. for 20 minutes or even for somewhat longer periods.

Fontaine also finds that the larvae of a frog are more resistant than an adult frog, and a newt (*Triton*) more resistant than a frog.

Ebbecke (1935) followed with similar experiments, and he gives a list of animals, arranged according to increasing sensibility toward pressure: actinians, asteroids, echinoids, Medusae, ctenophores, Amphioxus, prosobranchs, polychaetes, shrimps, and fishes. He adds that paralysis occurs in the most sensitive (shrimps and fishes) at 200 atm. and at 500–600 atm. in the most resistant organisms tested.

Based on experiments on isolated organs of the frog Ebbecke (1936) gives the following:

Compressed organ	*Paralytic pressure, atm.*
Central nerve system	250–300
Myoneural-connection	200–400
Peripheral nerve system	about 500
Heart	800
Isolated nerves	1000
Ciliated cells, leucocytes	1500

Many interesting details on viscosity and solubility may be found in Bridgman's comprehensive study (1949). Ebbecke and Haubrich (1936) conclude that from a physiological point of view the increase of viscosity by increased pressure does not influence the proteins or protoplasm but affects the fats and lipoids of the cell. Ebbecke (1944) gave a comprehensive review of his own studies and of the literature on the effect of high pressure. Since then Kitching (1954) has studied this effect on a suctorian protozoan. From his own experiments and from those of others quoted by him, he concludes that the proteins are also affected by pressure, and that several reactions or processes, differentially affected, have a common basis in the folding of protein molecules.

Thus, pressure has an important physiological effect. Fontaine's conclusion that life (living organisms as known at the time of his experiments in 1930) might have a lower limit at about 7000 meters (except for microbes) was possible. Now that life has been found at 10,000 meters, it must be concluded, until experiments demonstrate otherwise, that organisms from the greatest depths have some physiological adaptations which determine an upper limit of occurrence. Fontaine's and Ebbecke's experiments show a varying tolerance in different animal groups in good agreement with the empiri-

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cal finding of eurybathic and stenobathic animals. ZoBell's unique cultures of barophilic bacteria (ZoBell, 1952; 1954; Oppenheimer and ZoBell, 1952) lead to the supposition that more highly organized animals are still more sensitive toward pressure, in much the same general systematic order as found by Ebbecke (1935).

SALINITY

The variation of the salinity in the abyss is, from an ecological point of view, extremely small. An average figure may be set at 34.8‰, and the variation is only about 0.2‰. This applies in time to a single place, as in the Bay of Biscay (Kiilerich, 1953), where at 4500 meters in 1922, 1930, and 1950 the salinity was 34.89‰, 34.92‰, and 34.90‰. It also applies when passing from one ocean to another, if special cases like the Mediterranean are excluded.

It does not seem that the very slight variations in the salinity close to the bottom (Koczy, 1950; 1952) can be of biological importance.

TEMPERATURE

The abyssal zone was delimited toward the bathyal zone by the temperature of about 4° C.; in general it is therefore a typical cold-water zone, which has its corresponding counterpart in shallow water only in the polar regions. The variation must be called small from a biological point of view; this is particularly true if a limited area is considered from repeated observations. The Bay of Biscay (Kiilerich, 1953) from the years 1922, 1930, and 1950 may again serve as an example. Temperatures at 4500 meters were 2.56°, 2.53°, and 2.53° C. The very slight increase of temperature in the water layers very close to the deep-sea bottom, as observed in several cases (Koczy, 1953), is also without any biological importance.

OXYGEN

Generally the bottom water contains sufficient oxygen to support at least some animal life, as indicated by the fact that azoic areas are unknown in the abyssal and hadal depths. A correlation between the varying concentration and the distribution of the species may be expected, but at present it is not possible to demonstrate this, and it may be upset by the ability of many organisms to live anaerobically for short periods or to contract an "oxygen debt" when invading an oxygen-poor region. Koczy (1950; 1952; 1953) has shown sudden decrease of oxygen in the water layers from about 20 to 50 meters above the bottom down to the layers 1 meter above the bottom. This decrease may amount to values around 4.0 ml/l down to around 3.6 ml/l in the Indian Ocean (Fig. 3). Such a decrease is of great importance in areas where the oxygen content in the water some distance from the bottom is close to the limit of tolerance of the animals. At present, however, the only observations available are from the Swedish Deep-Sea Expedition, quoted above, and they should be regarded in the light of the investigations of Brouardel and Fage (1953; 1954) who examined the oxygen content in the meter of water immediately above the bottom and found that at a depth of 460 meters there was a decrease of 0.15 ml/l from 70 cm above the bottom down to the bottom; these measurements were carried out at five consecutive levels at the same time and showed the greatest decrease in the 14 cm of water directly in contact with the sediments. Similar measurements from still greater depths would be very interesting.

ALKALINITY, pH, CARBON DIOXIDE, PHOSPHATE, AND SILICATE

There is no indication so far that the slight variation of these factors is of any importance to the distribution of animals. As in the case of oxygen, however, they show a definite gradient close to the bottom. Again reference is made to the results of the Swedish Deep-Sea Expedition, as published by Koczy (1950; 1952; 1953) and Bruneau, Jerlov, and Koczy (1953).

Generally, the phosphate, silicate, and carbon-dioxide concentrations decreased downward from the layers about 20 meters above the bottom, and the alkalinity increased. An example of this is given in Figure 4 from 4522 meters in the Atlantic Ocean, but the same phenomenon was also observed in the Indian Ocean. Koczy (1953, p. 98–102) discussed two hypotheses: one suggests that elemental concentrations in the ocean change with regard to time; the other, assuming a constant content of the elements, leads to an estimation of eddy diffusivity and vertical transport. Koczy

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shows that in Recent time the main factor for carbonate dissolution at the sediment surface is the oxidation of organic matter, probably by bacteria.

In any case the decrease of P, Si, and O_2 points toward a binding of these elements at the bottom. Koczy mentions the possible role of siliceous sponges and other benthic animals and states that the phosphates may be assimilated by bacteria or partly adsorbed by particles of the sediments. Many

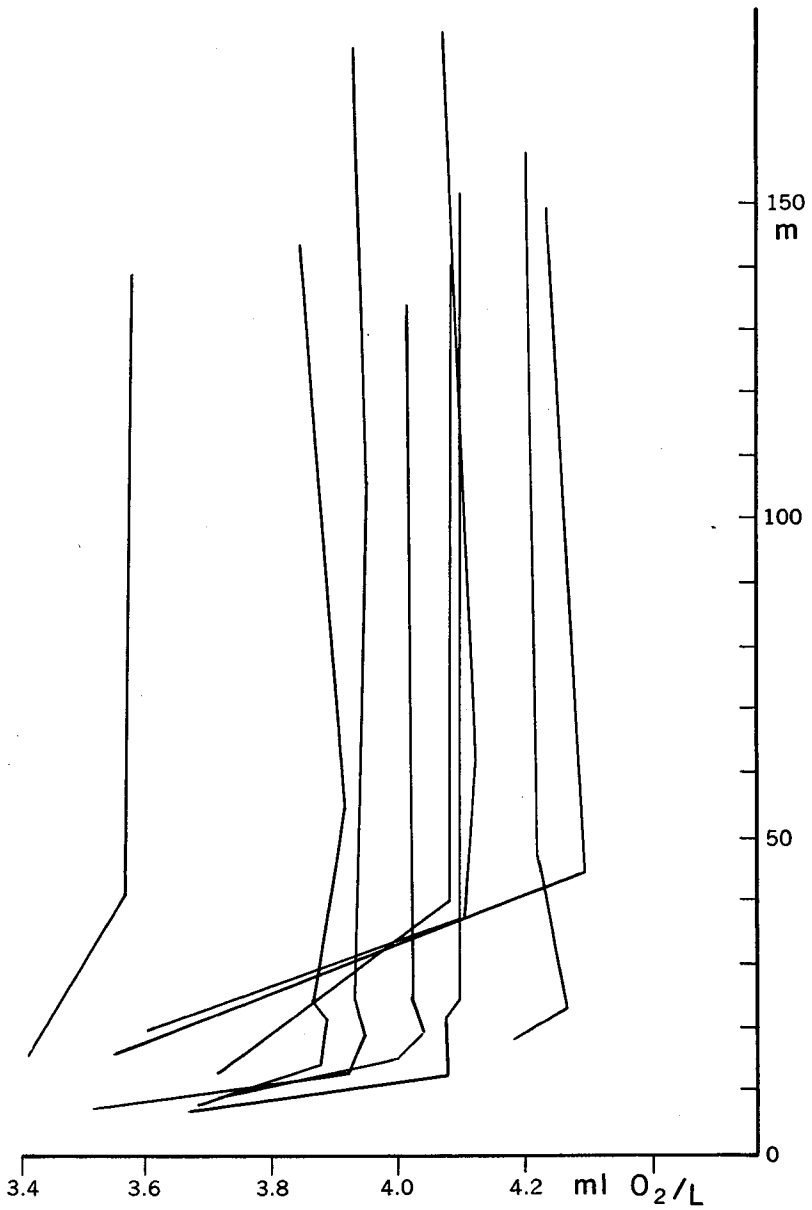

FIGURE 3.—*Oxygen content of the water from about 150 meters above the bottom to 1 meter above the bottom*
All deep stations in the Indian Ocean from the Swedish Deep-Sea Expedition. From Koczy (1953)

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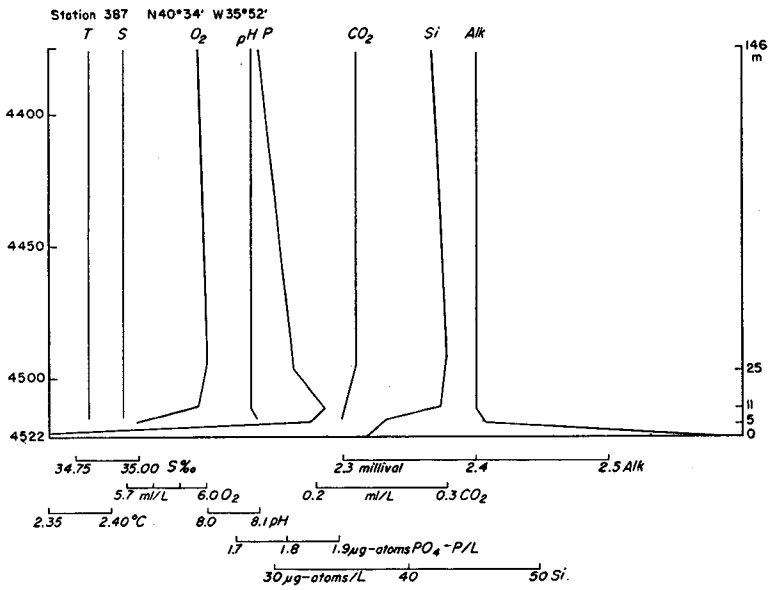

FIGURE 4.—*Various characteristics of the water as observed by the Swedish Deep-Sea Expedition at the indicated station in the Atlantic*

The constant values of temperature and salinity indicate that these factors are not influenced by the proximity to the bottom. From Koczy (1953)

more observations on the quantity of abyssal animals are necessary before their role in geochemical processes may be evaluated.

FOOD

All organisms living below the photosynthetic zone must depend upon the food that falls from this uppermost zone. The word food should in this connection be understood as energy stored in organic matter, because such energy can be utilized by heterotrophic bacteria when they assimilate plant and animal remains or dissolved organic matter. According to ZoBell (1954, p. 21), bacteria oxidize approximately 60–70 per cent of organic carbon to carbon dioxide, whereas the remaining 30–40 per cent of the organic carbon is converted into bacterial cell substance (particulate protoplasm), consisting primarily of proteins and lipids that may ultimately serve as an important source of food for deep-sea animals. Many marine animals, particularly protozoans, bottom grazers, filter feeders, and mud eaters, ingest and digest bacteria. Certain animals can survive and thrive on an exclusive diet of bacteria. This general view of ZoBell's is strongly supported by Fage (1955), who considers the bacteria to be a most important source of food for the deep-sea animals. Ekman (1955, p. 6) is of the opinion that bacteria probably play an important role but adds that for the mud eaters, like certain echinoderms, food incorporated in the sediments ("*die im Sediment eingeschlossene Nahrung*") is available, and such particles may also be eaten by certain polychaetes and crustaceans. Finally, he maintains that siliceous sponges, octocorallians, and crinoids live on the sinking dead bodies of plankton organisms.

These views illustrate the current opinions which have replaced the formerly prevalent idea of a rain of dead plankton bodies falling to the deep-sea bottom from the surface.

Before studying the various sources of organic matter at the bottom in the abyssal and hadal zones, the influence of depth should be considered. It is commonly asserted that a greater depth means a lesser supply of organic matter from the surface. This would be true if there were more links in the food chain at 6000 than at 2000 meters, for example. But it is probably not true, because the

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zones below the bathypelagic layers are so poorly populated that there may not be even a single full link in the chain. Even bacterial decomposition is probably much inhibited, because of the increasing pressure, while the particles are sinking toward the bottom. A bacterial flora derived from the species flourishing at the given pressure can develop only when the particles have come to rest at the bottom. Therefore, the amount of food available is largely independent of the depth, below the bathypelagic zone. Organic matter reaching the bottom is closely correlated with the primary production at the surface and the secondary source of dead organic debris carried by the currents from the coastal areas, especially from the mouths of the rivers. This is the case whether the organic matter reaching the bottom is directly available for the benthic animals or has to be assimilated by bacteria first.

Directly available sources.—Some abyssal animals live close to the surface in their larval stages. Typical of those are the various benthic deep-sea eels, all of which pass an epipelagic *Leptocephalus* stage in tropical or subtropical regions, as has been studied in the case of *Synaphobranchus* (Bruun, 1937). In this genus the *Leptocephalus* may grow to a length of 7 cm before the larva suddenly metamorphoses and starts the benthic life; of the unknown, but large, number of small eels that descend, only a fraction return to the surface as mature eels to spawn and continue the species; the rest must serve as food for bottom predators (Pl. 2, fig. 2).

A rain of dead bodies has often been mentioned in the literature, but no observation seems to support this idea. It seems more likely that any weak animal falls prey to predators in the upper layers. The only exceptions imaginable would be bodies too large to be swallowed, such as those of big fishes or big sharks, whose teeth indicate the last remnants of such bodies; this could well be in part an explanation of the spotty distribution of bottom animals. A dead whale of 50 tons must attract scavengers for a long time and thus form a local focus of abundant food for predators; all their excrements would undergo bacterial assimilation and enter new food chains.

Indirectly available sources.—Several sources of this kind can be mentioned, but it is difficult to estimate their relative importance. The content of dissolved or colloidal organic matter, which may be about 0.5 mg per liter, is probably most important (ZoBell, 1954, p. 21–22), especially because it seems to be rather uniformly distributed. The particulate organic matter may be of any size, from huge water-soaked logs carried to the sea by the rivers, down to suspended particles. This source varies greatly from one region to another.

An example of particles of animal origin that could not be digested by animals is much of the excrements of the animals living between the surface and the bottom; in this case there must be a kind of rain coming down, for instance in the offshore waters of Peru. The same phenomenon must be displayed by the enormous amounts of chitin, produced especially by crustaceans. It is doubtful that any animals can assimilate chitin without the aid of micro-organisms (ZoBell, 1946, p. 143–144). Most of the tunicin of the test of the tunicates must also be left to bacterial activity, because no animal seems to produce a tunicinase. Recent observations have proved this; Edgerton (1955, p. 534) reports that he passed an area thick with moulted shrimp shells in the bathyscaphe (See Houot and Willm, 1954; 1955). The "Marine Snow" mentioned by Inoue, Sasaki, and Oaki (1953, p. 60) may be of a similar origin.

Remnants of land plants, such as branches, leaves, or fruits, or marine algae from the coastal belt, have been seen in many hauls from deep water (Agassiz, 1888, p. 291); Mortensen 1938, p. 225). They were also observed from several places during the GALATHEA Expedition, even at the bottom of the Philippine Trench. Mortensen thought that these sunken remains of land plants served as food for such deep-sea echinoids as *Hydrosoma luculentum*, because their intestines were filled with bits of

PLATE 1.—ABYSSOPELAGIC FORMS

FIGURE 1.—*Vampyroteuthis infernalis*

FIL: filament; FLO: fin light organ; E: lid of the light organ, which may be drawn forward to occlude the organ; FP: posterior fin rudiment; FU: funnel opening; MA: mantle aperture; OP: olfactory papilla. From Pickford, DANA Report (1949).

FIGURE 2.—*Borophryne apogon*

A dwarfed parasitic male, without light organ, attached to the much larger female (Poul H. Winther del.)

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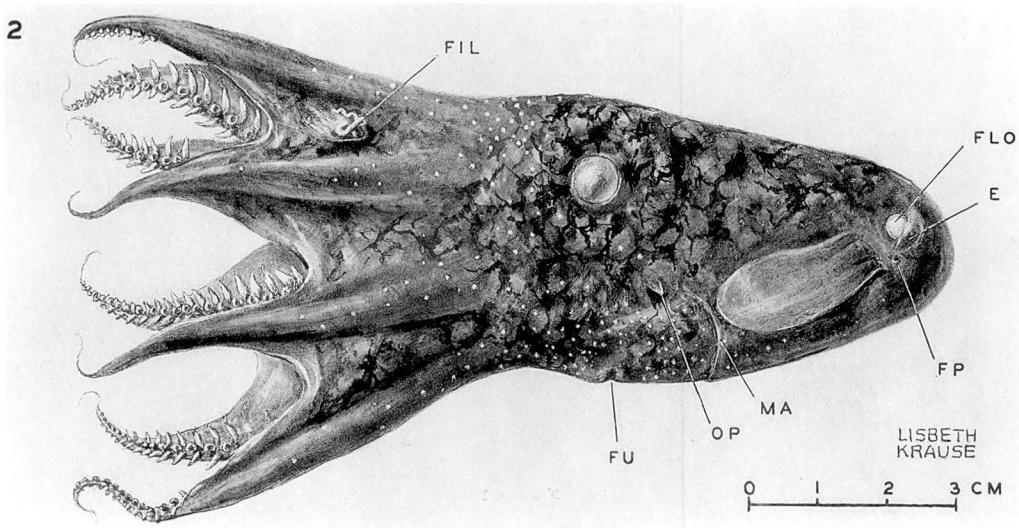

FIGURE 1

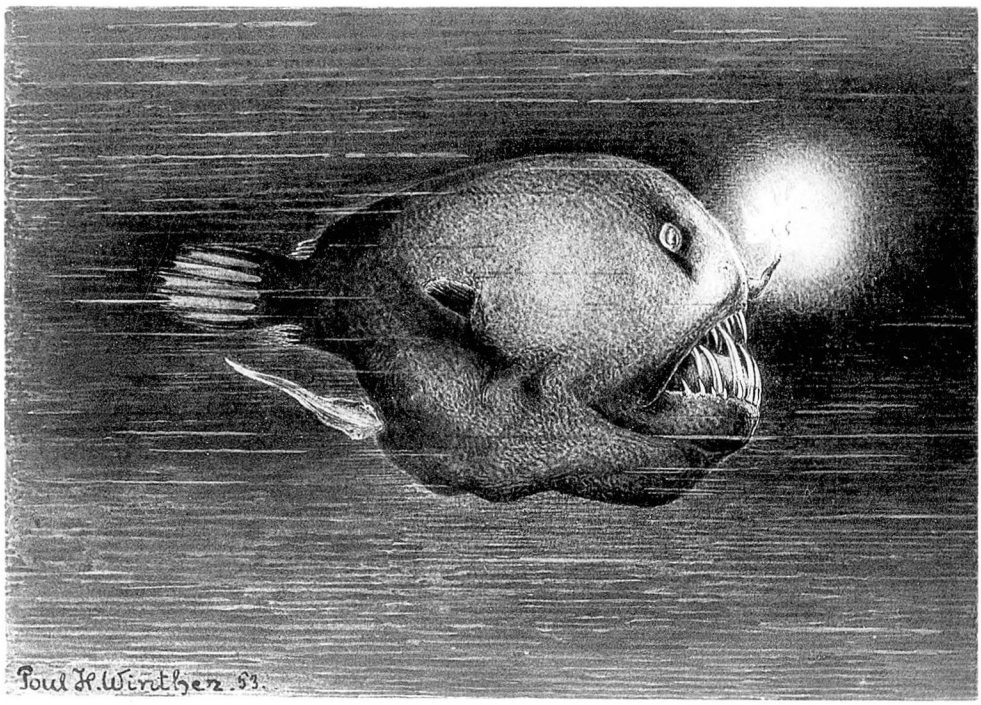

FIGURE 2

ABYSSOPELAGIC FORMS

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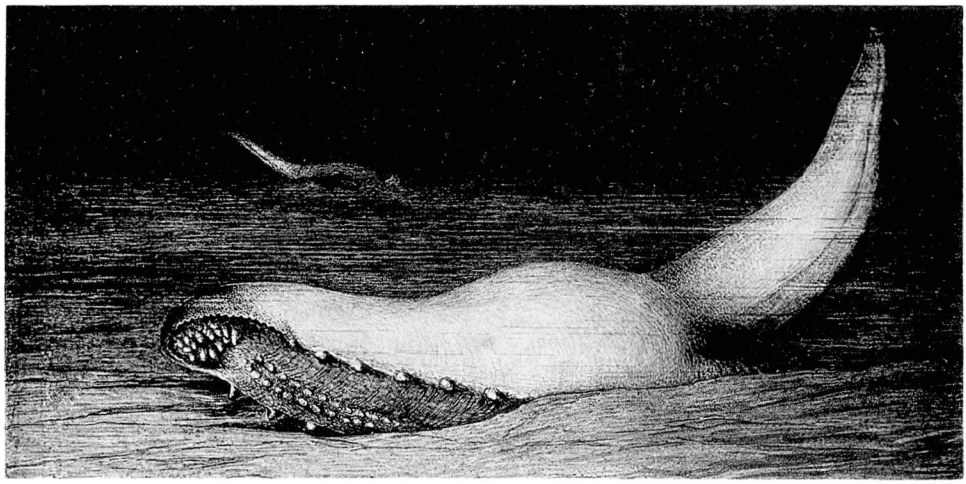

FIGURE 1

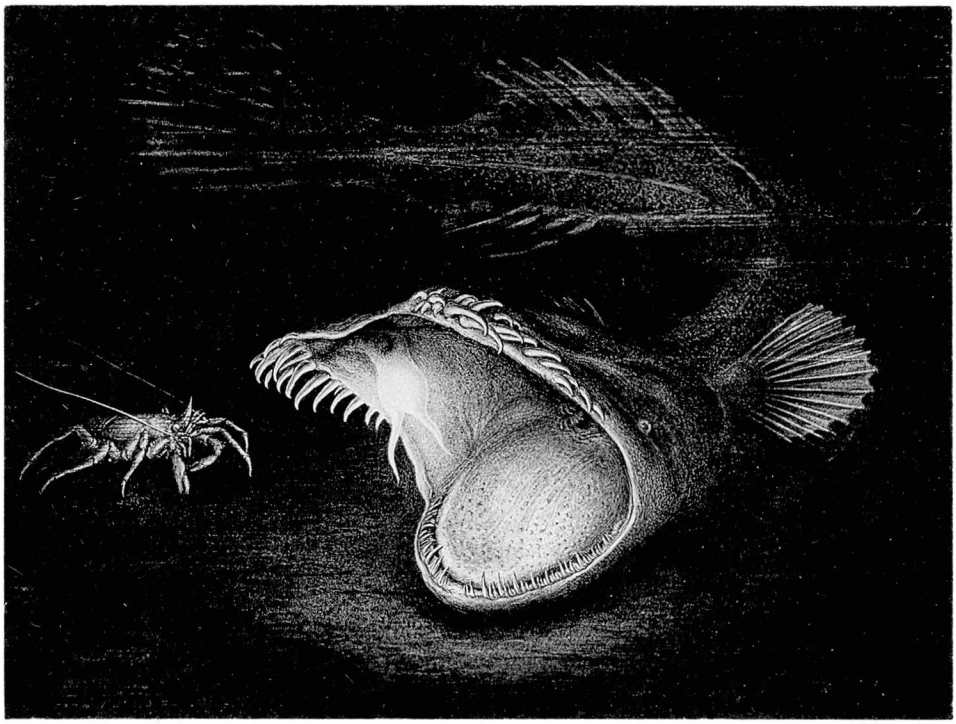

FIGURE 2

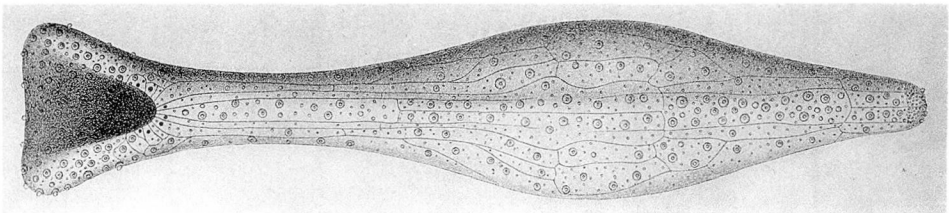

FIGURE 3

ABYSSAL FORMS

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plants. It is possible that the soft parts of the plants serve as food directly, but it seems more likely that animals would digest the bacterial and protozoan organisms living on the plants. Most of the cellulose, at least, would have to be assimilated by bacteria; as in the case of the carcass of a big animal, a sunken tree trunk would form a focus of abundant life for a long time. Mortensen mentioned a great variety of animals found with the plant remains, and on the GALATHEA Expedition it was found that a haul rich in plant debris was also rich in animals.

On the whole the food supply in the abyssal and hadal zones is not plentiful; it may even be called precarious (Fage, 1955, p. 14), but it is no more scarce than in any other region of the ocean below the layers that are in fairly close contact with the photosynthetic zone. The actual depth is of minor importance in comparison with the nearness of land and the productivity at the surface; the amount of dissolved organic matter represents a fairly uniform supply, so that no abyssal desert, without animal life, is found because of lack of food, where other life conditions are fulfilled.

ANIMAL COMMUNITIES

A description of the abyssal and hadal communities in any detail approaching what has been done in the case of the shelf fauna (Chapter 17) is not possible at the present stage of knowledge. A very general picture must suffice, because of lack of observations, especially concerning the quantitative distribution in relation to the ecological factors.

The description of the deep-sea fauna given by Ekman (1935; 1953) and Marshall (1954) may be consulted for a more detailed picture, but both authors do not always distinguish clearly between what is here called the abyssal and hadal animals and those living in the bathyal zone (archibenthal of Ekman).

Le Danois (1948) gave a detailed analysis of the ecological zonation of the fauna off the coasts of France, including the deepest parts of the Bay of Biscay, down to more than 5000 meters. As this area of the abyssal region is perhaps the one that has been studied more than any other, the lists of Le Danois enumerating all the species recorded in relation to depth are of particular interest.

All three authors give a complete list of the pertinent literature. (*See* also the semipopular account by Günther and Deckert, 1950; 1956.)

Before describing the abyssal and hadal faunas it should be stated that Le Danois (1948, p. 226) concludes that, even in the fairly restricted area of the Bay of Biscay, the costal, shelf, and slope zones, and even his semiabyssal zone, can be split into ecological units, but it is impossible to make any clear faunistic distinction below 2500 meters; the horizontal distribution of the abyssal organisms is considerable, and most of the species are found all over the North Atlantic, and several in other oceans (Pl. 2, fig. 3).

PLATE 2.—ABYSSAL FORMS

FIGURE 1.—*Psychropotes, a holothurian*

Long caudal appendage probably used in respiration (Poul H. Winther del.)

FIGURE 2.—*Galatheathauma*, an angler

From tropical West America, depth 3590 meters. Note light organ well inside the mouth fringed with depressible teeth. Natural size 47 cm, only specimen known (Poul H. Winther del.)

FIGURE 3.—*Echinosigra paradoxa*, a spatangoid sea urchin

The test has been cleaned of the almost hairy spines to show this most irregular shape. This abyssal species, formerly known only from 1515 meters in the North Atlantic, was found by the GALATHEA Expedition at 3300 meters in the Central Indian Ocean. From Mortensen (1907)

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ABYSSAL COMMUNITY

Most descriptions of the abyssal fauna have been of a faunistic character, but it may be useful here to consider first the contents in a single haul with a 96-foot trawl. The locality chosen is a GALATHEA station between Madagascar and Mombasa, where a very even abyssal plain covers a huge area at depths around 5000 meters. This particular haul was made at 4820 meters on a light-colored Foraminifera ooze.

The dominant group of animals was the echinoderms, consisting principally of 30 specimens of bulky holothurians. They represented at least 7 species, of which 8 specimens belonged to *Psychropotes* and 8 to *Deima*. Both genera belong to the order of Elasipoda, which is typical of the abyssal fauna, since no less than 88 species, or about two-thirds of the species described, have been found in depths exceeding 3000 meters (Madsen, 1953, p. 166). The *Psychropotes* showed a delicate reddish-violet color, except for a single specimen with a lemon-yellow dorsal side. The semicylindrical body (Pl. 2, fig. 1) has a peculiar caudal appendage, supposed by some to be used for swimming, but more likely serving a respiratory function as the animal ploughs its way more or less imbedded in the ooze. The length of these animals is about 20–30 cms, whereas the whitish *Deima* are about 10–15 cms long. *Deima* carries rows of prolongations on the dorsal side which may also serve in respiration.

The Elasipoda were also represented by one *Benthodytes* and one *Euphronides*. The rest of the holothurians were 5 Molpadiidae and 4 Synallactidae, all typical abyssal species, and 3 indeterminable specimens.

The other group of echinoderms which dominated the catch was the ophiuroids, of which 58 specimens were caught; this was a rather small number, as many other hauls yielded several hundreds. In any case many of these brittle organisms must have been lost because of the rough treatment during towing and hauling the trawl. Again the greater number, 54 specimens, belonged to a typical abyssal family, the Ophiolepididae; this family is represented by 49 species in depths exceeding 3000 meters or as many as the remaining 5 families recorded in these depths (Madsen, 1951, p. 110). Most of these ophiuroids were pale, even white.

The catch contained 12 specimens of asteroids representing 3 species. Six belonged to the genus *Styracaster*, 5 to *Goniaster*, and 1 was a species of brisingid. Furthermore, there was 1 spatangid sea urchin and 1 crinoid.

The mud- or filter-feeding holothurians, echinoids, and crinoids were thus outnumbered by the predatory ophiuroids and asteroids.

Various sedentary stalked animals were found, such as an *Umbellula*, still able to emit a faint bluish light when they came up. Other coelenterates were some colonies of hydroids and a fragment of an isisidid octocoral; 14 white Actinaria were found on the stems of siliceous *Hyalonema*-type sponges.

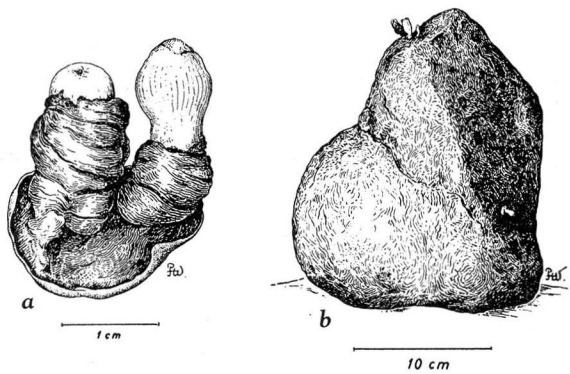

FIGURE 5.—*Hadal sea anemone Galatheanthemum representing a separate family of Actinaria*

(a) Two specimens with a common base. (b) Four specimens sitting on a stone. Philippine Trench, 10,190 meters. From Carlgren (1956)

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Some of the animals mentioned represented some sort of epifauna, as was the case with the cirripede *Scalpellum*, found on the *Hyalonema* stems.

More than 60 specimens of the ascidian *Culeolus*, with long thin stalks, were also typical abyssal types. The polychaetes were numerous, especially those of the family Oweniidae; Opheliidae, Maldanidae, Glyceridae, and Capitellidae were also represented.

Mollusca were represented by several specimens, including 9 Scaphopoda, 14 Pelecypoda, 4 Prosobranchiata, and 4 Tectibranchiata; one of the bivalves was of the peculiar predatory or scavenging genus *Cuspidaria*.

Among the crustaceans there were 13 hermit crabs, *Parapagurus*; of these 12 were overgrown with a reddish-violet actinian and 1 with zoantharia.

One crab, an *Ethusa*, was a female carrying orange-yellow eggs.

Some of the shrimps or prawns in the trawl were definitely pelagic types, but some of them, as well as certain amphipods, did belong to types which were seen only in trawls towed on the bottom.

The same applies to the fishes; species of myctophids, *Sternoptyx*, *Argyropelecus*, *Gigantura*, *Stylephorus*, and cetomimids could at once be discarded as coming from the pelagic zones, and the remaining 8 specimens were real benthic species. One was a semitransparent fish, 8 cm long, of the rarely caught brotulid genus *Aphyonus*, with the eyes reduced to barely visible minute black spots under the skin; another specimen was also a brotulid related to the genus *Microlene*, another typical abyssal type.

Still more interesting were the remaining 6 specimens, belonging to the iniomid genus *Ipnops*, known since the days of the CHALLENGER expedition, but also very rarely caught. Pictures of this species have been reproduced very often, probably because of the pair of big yellow plates covering the flattened head; the fish itself is blind, but the peculiar honey comblike structure of the plates is commonly supposed to represent luminous organs which are perhaps attractive to small animals with a feeble light perception.

This short description of an abyssal haul should give the impression of a fairly varied fauna, not rich in comparison with those of the shelf and the slope, but still far from being a poor fauna. This special haul was not a particularly rich one. A haul with the same gear at 4820 meters the following day gave 20 specimens (8 species) of benthic fishes, 83 pagurids, and about 300 ophiuroids; another haul 2 days later at 3970 meters gave 9 benthic fishes (4 species), 27 pagurids, about 500 ophiuroids, and many more invertebrates as well.

For comparison a haul of the Swedish Deep-Sea Expedition Station 329 in the Atlantic may also be considered. The locality was 9°38′ N. Lat., 26°20′ W. Long., the depth 5600 meters. A 30-foot trawl was used so that even though Nybelin (1951, p. 14–15) describes the haul as the richest of the expedition it is still more impressive when the size of the GALATHEA trawls (96 feet) is kept in mind. The bottom is described as calcarous red clay. Of the 22 benthic fishes, 11 were *Bathypterois*, 7 were small macrourids, and 4 were brotulids (1 large brotulid (?), 1 *Grimaldichthys*, 1 *Bassozetus*, 1 *Leucochlamys*); all these are preliminary identifications by Nybelin. Except for fragments of siliceous sponges, the following invertebrates have been studied by specialists (the year the species were established has been added to show how many of the species became known in the very early days of real deep-sea research): 1 actinarian, *Paredwardsia abyssorum* (Carlgren 1951); empty tubes of chaetopterids (Eliason 1951); 1 *Bathycrinus aldrichianus* Wyville Thomson 1877 (Gislén 1951); 13 holothurians plus fragments, namely 5 *Peniagone lugubris* Théel 1882, 7 *Scotoanassa translucida* Hérouard 1899, and 1 *Euphronides kerhevei* (Hérouard 1902), (Madsen 1953); 11 asteroids, namely 5 *Porcellanaster coeruleus* Wyville Thomsen 1877, 2 *Eremicaster pacificus* (Ludwig 1905), 3 *Styracaster horridus* Sladen 1883, and 1 *Freyella tuberculata* Sladen 1889 (Madsen 1951); 63 ophiuroids, all *Amphiophiura bullata* (Wyville Thomson 1873; Madsen 1951).

The high proportion of predators like the fishes, asteroids, and ophiuroids should indicate that other gear used in the same locality would bring up many more specimens and species of mud- or filter feeders, on which these predators thrive.

Le Danois (1948, p. 196–203) gives a list of the species caught from 3000 meters and downward in the Bay of Biscay; it comprises 3 Spongiaria, 3 Coelenterata, 7 Polychaeta, 2 Echiuroidea, 13 Holothuria, 3 Ophiuroidea, 8 Asteroidea, 3 Prosobranchia, 4 Scaphopoda, 8 Pelecypoda, 1 Cephalopoda, 16 Crustacea (including 4 *Scalpellum*), and 6 neopterygian fishes. Four species of fishes and 1

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cephalopod from Le Danois' lists have been excluded, because the writer considers them to be at most abysso-pelagic (Pl. 1). Le Danois attempts to split up the abyssal zone according to depth: (A) between 2000 and 3000 meters; (B) between 3000 and 5000 meters; and (C) from 5000 meters downward. Some zonation is indicated by a number of species disappearing toward the depths and other species replacing them to some extent and making the decrease in total number of species toward the depths a little less marked. However, generalizing about the whole abyssal region of all oceans from this single area is not justified. But for comparison with the examples given from the Indian and Mid-Atlantic oceans it is very interesting to notice the abundant species as given by Le Danois from 3000 meters and downward.

Again the holothurians are the most common animals: species of *Oneirophanta*, *Psychropotes*, *Benthodytes*, *Scotoanassa*, *Trochostoma*, and *Protankyra* are the most important; next in importance are such asteroids as *Dytaster spinosus*, *Crenaster spinolosus*, *C. semispinosus*, *Styracaster horridus*, and *Freyella sexradiata*, and then the ophiuroids, *Amphiophiura bullata*, *A. convexa*, and *Ophiomusium planum*. Representatives of other phyla include: coelenterates, *Kophobolemnon macrospinosum*, *Bathytrochus hexagonus*, and *Chitonanthus abyssorum*; sponges, *Abestopluma pennatula*, *Hyalonema lusitanicum*, and *Chondrocladia guiteli*; the bivalve *Syndesmya profundorum* and the cephalopod *Cirroteuthis umbellata*; the echiuroid *Phascolosoma flagriferum* and the polychaete *Laetmonice filicornis*; among crustaceans, the crab *Geryon tridens*, the anomuran *Opophorchynchus parfaiti*, the peneid prawn *Benthesicymus longipes*, and some cumaceans and *Lepas*; the fishes *Bassogigas* (*Bythites*) *crassus*, *Alexeterion parfaiti*, and *Leucochlamys cryptophthalmus*.

Zenkevich (1954) and Zenkevich, Birshtein, and Belyaev (1954; 1955) have summarized recent Russian investigations in the Kurile-Kamchatka region, revealing the same general picture of the fauna of the abyssal zone as the examples given above.

HADAL COMMUNITY

Knowledge of the hadal fauna dates back only to 1948, when the Swedish Deep-Sea Expedition made a haul from the eastern slope of the Puerto Rico Deep in depths between 7625 and 7900 meters (Nybelin, 1951, p. 19–20). This was nearly 2000 meters deeper than the haul at 6035 meters made by Prince Albert of Monaco at the beginning of this century. Agassiz (1902, p. 60, 77) recorded a haul from 7631 meters containing siliceous sponges, but in view of recent knowledge of the topography of trenches and the special difficulty they present for trawling it seems unlikely that the sponges really came from the depth supposed. Continuous recording of depths with an echo sounder is indispensable for determining the depth of an abyssal haul in most places, without exception in the trenches.

The hadal fauna has been studied in only seven of the trenches of the world, and much of the material has been studied only in a preliminary manner. The investigations of this fauna, as represented by the GALATHEA collections and including the Swedish and Russian results, are summarized in Table 1. Whereas the hauls between 2500 and 4500 meters contained about 50–60 species, the number of species fell sharply with increasing depth, and only about 20 species were taken from 8210–8300 meters. Some of these, however, occur in surprising abundance: 3000 specimens of a holothurian, *Elpidia glacialis sundaensis*, were taken in one haul from the Sunda Trench. Such hauls, however, are the result of several hours trawling, and the actual populations per unit area may not be excessively high (Fig. 8). The qualitative composition of the trenches is even more interesting. Sponges are nearby absent, and ophiurans, which are so abundant at lesser depths, are known from only a single station; the most abundant and characteristic animals are holothurians, certain polychaetes, and anemones. Asteroids and crustaceans, principally isopods and amphipods, are not rare, and there are also a few bivalves (Figs. 5–8). Gastropods are at present known only from the Kurile-Kamchatka trench. There are a few ascidians, hydroids, echiuroids and fish.

Kurilo-Kamchatka Trench. The following account of the fauna of this trench is based on Zenkevich (1954) and Zenkevich *et al.* (1954). It is what has been called the ultra-abyssal fauna and the fauna of the *Tiefseerinnezone* or *superozeanische Tiefen*. These authors expect to find final proof for the existence of such a special fauna when a full systematic treatment of the material is available and when it is shown that the trenches contain species which do not occur in other parts of the oceans, not even in other trenches (Zenkevich *et al.*, 1954, p. 72).

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The investigations were carried out with a 2.5-meter Sigsbee trawl and a special dredge. Between 1000 meters and close to 10,000 meters, 14 trawlings were carried out, 6 of which were in depths exceeding 6000 meters.

Of the coelenterates 2 species of Actiniaria were found down to 9050 meters, and 1 octocorallian at 8660 meters. Some nemerteans were taken down to 7200 meters, and from the same depth 3 specimens of *Priapulus* were taken; *Thalassema* (an echiuroid) was found down to 9950 meters. The polychaetes were quite numerous, errant as well as tubicolous species. Of special interest from 6860 meters to 9950 meters was a very large errant species, as yet unidentified, of typical deep-sea appearance, whitish and with very long and fragile dorsal cirri of the parapodia, which carry setae 15 mm. long. Another genus, *Travisia*, was found down to 8400 meters.

Several bivalves were living at 7000–8000 meters, in appearance resembling such genera as *Portlandia*, *Nucula*, and *Axinus*; colorless *Propeamussium* with paper-thin shells were also found. From 6860 meters some prosobranchs of the Buccinidae were extracted from deep holes in lumps of clay.

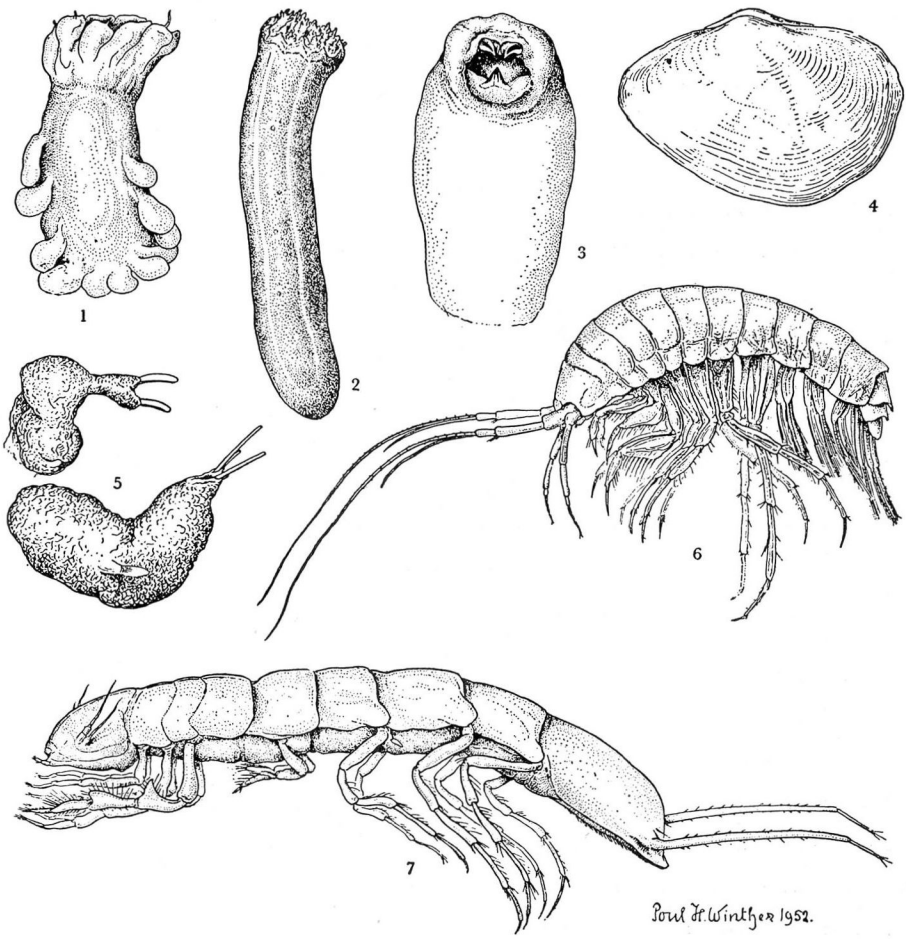

FIGURE 6.—*Hadal community of the Philippine Trench at 10,000 meters*

(1) holothurian (*Scotoplanes*), 17 mm. (2) holothurian (*Myriotrochus*), 7 mm. (3) pharynx of a polychaete (Macellicephala), 7 mm. (4) bivalve (*Glomus*), 7 mm. (5) fragments of an echiuroid worm, about 5 mm. (6) amphipod crustacean, 3 mm. (7) isopod (*Macrostylis*), 6 mm. The eighth species, an actinarian sea-anemone, is seen in Figure 5.

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TABLE 1.—*Hadal Fauna (a preliminary catalogue)*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
	7625–7900 m	6740–7160 m	6490–6650 m	7250–7290 m	6140–7000 m	8210–8300 m	8810–8940 m	9790–10210 m	6860–7230 m	8330–9050 m	9700–9950 m
PORIFERA					+				+	+	
COELENTERATA											
Hydroidea											
Aglaophenia (?) *galatheae* Kramp 1956		+									
Halisiphonia galatheae Kramp 1956						+					
Anthozoa											
Bathydactylus kroghi Carlgren 1956						+					
Daontesia mielchei Carlgren 1956				+							
Galatheanthemum profundale Carlgren 1956					+	+					
Galatheanthemum hadale Carlgren 1956								+			
Hadalanthus knudseni Carlgren 1956					+						
Paredwardsia lemchei Carlgren 1956		+									
Actiniaria										+	
Antipatharia		+									
Octocorallia									+		
Umbellula					+						
Scyphozoa					+				+		
Stephanoscyphus sp.					+						
NEMERTEA									+		
POLYCHAETA											+
Macellicephala abyssicola Fauvel 1913		+		+	+						
Macellicephala hadalis Kirkegaard 1956				+	+	+		+			
Macellicephala mirabilis McIntosh 1885									+		
Macellicephala zenkevitchi Ushakov 1955										+	
Macellicephaloides grandicirra Ushakov 1955										+	+
Macellicephaloides verrucosa Ushakov 1955									+		

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TABLE 1.—*Continued*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
	7625–7900 m	6740–7160 m	6490–6650 m	7250–7290 m	6140–7000 m	8210–8300 m	8810–8940 m	9790–10210 m	6860–7230 m	8330–9050 m	9700–9950 m
Macellicephaloides vitiazi Ushakov 1955									+	+	
Macellicephala sp.	+										
Ancistrosyllis constricta Southern 1921			+								
Nereis profundi Kirkegaard 1956				+							
Nephthys elamellata Eliason 1951					+						
Ninoë fusca Moore 1911					+						
Tharyx multifilis Moore 1909			+								
Ilyophagus bythincola Chamberlin 1919		+									
Travisia profundi Chamberlin 1919			+	+							
Travisia sp.										+	
Kesun abyssorum Monro 1930		+			+	+					
Ammotrypane galatheae Kirkegaard 1956				+							
Notomastus sp.						+					
Maldanella harai (Izuka) 1902					+						
Petaloproctus cirratus (?) Monro 1937				+							
Myriochele sp.					+	+					
Owenia lobopygidiidiata (?) Ushakov 1956				+							
Ampharetidae gen. 1					+						
Ampharetidae gen. 2		+									
Terebellidae	+										
Terebellides eurystethus Chamberlin 1919					+						
Jasmineira sp.				+		+					
Serpulidae					+						
ECHIURIDA								+			
Thalassema sp.											+
SIPUNCULIDA									+		

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TABLE 1.—*Continued*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
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PRIAPULIDA											
Priapulus sp.									+		
BRYOZOA											
Bugula sp.						+					
ECHINODERMA											
Crinoidea											
Bathycrinus australis (A. H. Clark 1907)						+					
Bathycrinus sp.									+	+	+
Echinoidea											
Pourtalesia (?) *aurorae* Koehler 1926				+							
Asteroidea											
Eremicaster pacificus (Ludwig 1905)		+			+						
Eremicaster sp.									+		
Styracaster sp.									+		
Thoracaster sp.									+		
Brisingidae									+		
Freyella mortenseni Madsen 1956					+						
Hymenaster blegvadi Madsen 1956					+						
Ophiuroidea									+		
Ophiura loveni (Lyman 1878)					+						
Holothurioidea											
Hadalothuria wolffi Hansen 1956							+				
Benthodytes sanguinolenta Théel 1882			+	+							
Ceraplectana trachyderma H. L. Clark 1908			+								
Elpidia glacialis sundensis Hansen 1956		+									
solomonensis Hansen 1956							+				

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TABLE 1.—*Continued*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
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kermadecensis Hansen 1956					+	+					
Elpidia sp.										+	+
Euphronides verrucosa Ludwig 1894				+							
Mesothuria murrayi (Théel, 1886)			+								
Myriotrochus bruuni Hansen 1956								+			
Myriotrochus sp.											+
Paroriza grevei Hansen 1956			+	+							
Peniagone vedeli Hansen 1956					+	+					
Peniagone sp.	+										
Periamma naresi (Théel 1882)		+									
Pseudostichopus villosus Théel 1886					+	+					
Scotoplanes galatheae Hansen 1956								+			
Scotoplanes globosa Théel 1879					+						
Scotoplanes sp.									+		
MOLLUSCA											
Gastropoda-Prosobranchia										+	
Buccinidae									+		
Odostomia						+					
Pelecypoda		+								+	
Glomus								+			
Nucula									+		
Portlandia									+		
Pectinidae					+						
Propeamusium									+		
Axinus									+		
Kelliella					+	+					

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TABLE 1.—*Continued*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
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Teredinidae			+	+							
Cuspidaria			+	+							
Scaphopoda		+									
ARTHROPODA											
Crustacea											
Ostracoda									+		
Cirripedia									+		
Scalpellum					+				+		
Isopoda										+	
Eurycope nodifrons Hansen 1916					+						
Eurycope madseni Wolff 1956					+						
Eurycope galatheae Wolff 1956					+						
Macrostylis galatheae Wolff 1956								+			
Macrostylis hadalis Wolff 1956				+							
Bathyopsurus nybelini Nordenstam 1955	+										
Ischnomesus bruuni Wolff 1956					+						
Ischnomesus spärcki Wolff 1956					+						
Ilyarachna antarctica Vanhöffen 1914					+						
Storthyngura benti Wolff 1956					+						
Storthyngura pulchra Hansen 1897					+						
Storthyngura furcata Wolff 1956					+						
Leptanthura hendili Wolff 1956			+								
Tanaidacea					+	+					
Apseudes galatheae Wolff 1956					+						
Neotanais serratispinosus hadalis Wolff 1956					+	+					
Herpotanais kirkegaardi Wolff 1956					+						
Amphipoda	+	+	+	+	+	+		+		+	
Cumacea		+									
Mysidacea									+		
Pycnogonida									+		

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TABLE 1.—*Continued*

	Puerto Rico Trench	Sunda Trench	Banda Trench		Kermadec Trench		New Britain Trench	Philippine Trench	Kurile Trench		
	7625–7900 m	6740–7160 m	6490–6650 m	7250–7290 m	6140–7000 m	8210–8300 m	8810–8940 m	9790–10210 m	6860–7230 m	8330–9050 m	9700–9950 m
Nymphon galathea Fage 1956			+								
POGONOPHORA										+	+
TUNICATA											
Ascidia					+		+		+		
PISCES											
Bassogigas sp.		+									
Pseudoliparis amblystomopsis Andriashev 1955									+		
Liparidae					+						

Cirripedians were represented by *Scalpellum* down to 6860 meters. Between 7800 and 8400 meters a very large white asellote isopod, and large white Amphipoda and Mysidacea, were found. Of the Echinodermata a species of *Bathycrinus* was found between 5070 and 9050 meters. In a single haul from 9050 there were 150 specimens. Two species of ophiuroids descend to 7230 meters, at which depth 1 species of an asteroid is also found; at 6860 meters there are still 4 species represented. But the holothurians were the most varied and numerous. Deepest down, between 8600 and 9950 meters, *Elpidia* superseded all other species by weight and number: 2 hours' trawling at 9000 meters yielding 2850 specimens. Also at 9950 meters was a small holothurian, probably related to *Myriotrochus*, and *Scotoplanes* was found down to 6860 meters. The very peculiar Pogonophora, presumed to be Hemichordata, were very numerous; a single haul from 9000 meters contained almost 2000 specimens of 2 new species. Some ascidians were caught at 7200 meters, and at the same depth a rather large fish, a pinkish liparid species with small eyes, was caught; this is the deepest record of any fish.

The number of species of the six hauls were as follows: (A) 6860 meters, 43 species; (B) 7210–7230 meters, 40 species; (C) 8330–8430 meters, 20 species; (D) 8610–8660 meters, 8 species; (E) 9000–9050 meters, 17 species; (F) 9700–9950 meters, 6 species; these extreme depths were inhabited only by polychaetes, echiuroids, and holothurians.

Very remarkable is the haul from 9000 meters containing the following number of animals: 2850 Elpidia, nearly 2000 Pogonophora, 84 echiuroids, 150 crinoids, 160 polychaetes; the 5700 specimens represented 17–18 species.

ECOLOGICAL GROUPS

The abyssal and probably the hadal animals can be divided into two ecological groups. The first group is the true abyssal species, those which live in the abyssal zone for their entire life from egg to death; all such species are sessile or have very limited mobility, such as the free-living species of echinoderms, mollusks, polychaetes, and many others (Fig. 7). The second group consists of the probably relatively few species which spawn close to the surface, even epipelagically; such species must be

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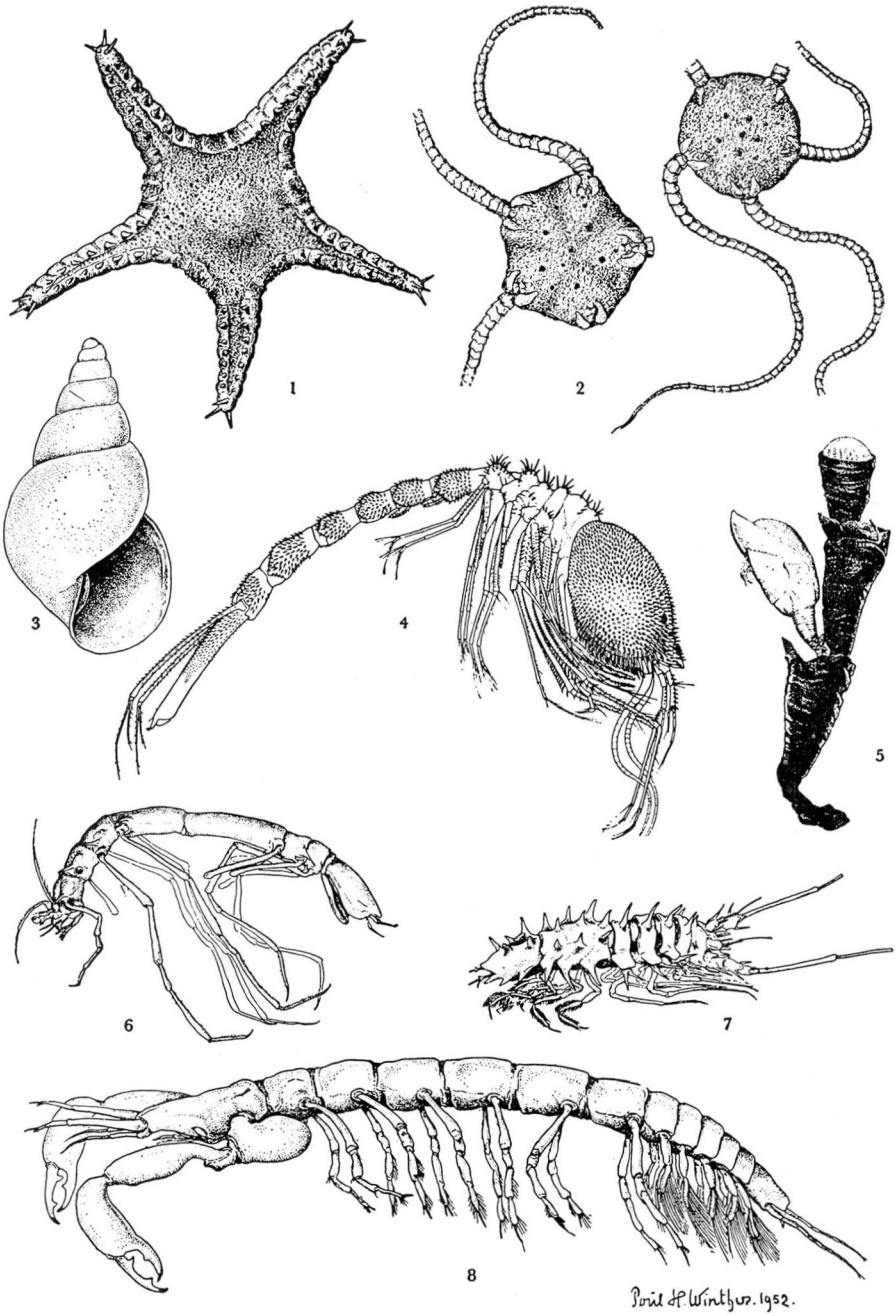

FIGURE 7.—*Various abyssal and hadal animals from their deepest known occurrence*

(1) sea star (*Eremicaster pacificus*), 56 mm, 7630 meters. (2) brittle star (*Ophiura loveni*), disc 13 mm, 6660 meters. (3) prosobranch (*Odostomia*), 4 mm, 8210 meters. (4) cumacean (*Diastylis*), 30 mm, 7130 meters. (5) cirriped (*Scalpellum*), 30 mm, attached to the cuticle of an actinarian sea anemone (*Galatheanthemum*), 6660 meters. (6) isopod (*Ischnomesus*), 13 mm, 6960 meters. (7) isopod (*Storthyngura*), 5 mm, 6960 meters. (8) tanaid (Neotanais), 15 mm, 8210 meters. (1–3, 6–8 Poul H. Winther del., 4–5 P. Larsson del.).

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fairly good swimmers, and again the abyssal species of the apodal fish family Synaphobranchidae may be mentioned (Bruun, 1937). These deep-sea eels live their early life pelagically in the thermosphere, and the breeding places seem to be rather restricted, *e.g.*, in the North Atlantic to the Sargasso Sea; but their leptocephali live somewhat deeper than by far the greater number of other species of leptocephali. The synaphobranchid leptocephali have peculiar cylindrical-telescopic eyes, another feature rare among the leptocephali.

A similar case may be found in another fish family, the Macrouridae, but here too little is known about the life history of the single species found in the abyssal zone. Most of the macrourids live in the bathyal zone; even for them almost nothing is known of the larval development and where it takes place.

Most of the eryonid crustaceans are also bathyal, but some have been found in the abyssal zone down to more than 3000 meters. In this case also too little is known about the life history, except that a fair number of larvae have been described (Bernard, 1953) from pelagic, probably bathypelagic, or abyssopelagic, hauls.

Finally, some animals are caught in the abyssal zone which just manage to live, but can never reproduce, there. It must often happen that pelagic stages of bathyal animals are carried downward into the abyssal zone by turbidity currents; even bottom stages may be brought downward in this way, and, if they are not killed by the increased pressure or lower temperature, they will form a foreign element in the abyssal zone, disturbing zoogeographical considerations as long as they cannot be separated from the true abyssal species. Ekman (1953, p. 276) gives many examples of extreme eurybathy. A close study of the sexual development of all the species which have such a very wide vertical range is necessary; specimens from the lowermost limit may never mature.

It has often been pointed out that a shortened larval life or viviparity is typical of Artic or Antarctic species. Very little is known about this in abyssal animals, except that as far as known the same ways of reproduction seem to be common, which is not surprising, since the environment is similar. Some abyssal animals must have a free-swimming larval stage, as for example the parasitic Rhizocephala, which were found by the GALATHEA Expedition to infest abyssal crabs. A pelagic life of some duration would seem necessary for the parasite to spread to other crabs.

The geographical distribution of the abyssal fauna has been treated at length by Ekman (1953) and by Ekman and several other authors. (For the reference, *see* Ekman, 1954.) Ekman divides the abyssal fauna into Atlantic, Indo-Pan-Pacific, Antarctic, and Arctic regions. On the basis of the echinoderms Madsen (1954) suggests two main regions, the Pacific and the combined Atlantic and Indian, from which may be separated an Antarctic region with some features of its own.

It is not possible to reconcile such different opinions at a time when much new evidence is being accumulated, but some considerations indicate that the true abyssal species are cosmopolitan, which is a return to the view held in the early days of deep-sea research.

Scanty collections and a hopeless taxonomic situation in very many cases explain much of the conflict. Again the problem of a clear definition of the term abyssal species turns up, because the distribution of those species which breed outside the

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abyssal zone depends on the requirements for the breeding places. Thus the various species of the deep-sea apode, *Synaphobranchus*, have a distribution corresponding to their pelagic breeding places in the thermosphere, in the same way that the distribution of the fresh-water eels (*Anguilla*) is governed by the breeding places and not by the conditions in fresh water where they grow up.

It is easy to give examples of the scantiness of the collection of abyssal animals:

In 1875 the CHALLENGER Expedition caught a new pycnogonid, *Nymphon procerum*, west of South America (33°31′S., 74°43′W.), at 3948 meters. The second specimen was not recorded until 1948, when it was caught by the Swedish Deep-Sea Expedition in the North Atlantic (40°33′N., 35°24′W.) at 4540 meters. These two specimens, taxonomically very critically treated by Fage (1951), are sufficient to characterize the species as a cosmopolitan; moreover, they show an example of a widely distributed species with nonpelagic development, in conflict with the view of Ekman (1954, p. 10) that benthal abyssal animals with a planktonic juvenile stage should have a wider distribution than those without such a stage.

Even if an animal is known from several specimens and localities caution is required. Ekman (1953, p. 298) mentions some holothurians characteristic of the Arctic Sea and adds: "But even more characteristic for the Arctic deep-sea fauna is *Elpidia glacialis* (about 20 localities), although it occasionally ascends in high-Arctic regions to the lower shelf; most finds, however, come from abyssal depth down to 2800 m."

This statement could be made only by disregarding Perrier's (1902) and Heding's (1940) records from off the Moroccan coasts (2210–2480 meters) and Théel's (1882) record from south of Australia (4750 meters). Now, with Hansen's (1956) abundant material from the Indian and Pacific oceans at hand, *Elpidia glacialis* should be called a cosmopolitan eurybathic abyssal species with a certain tendency toward subspecific segregation, especially under hadal conditions.

It therefore seems likely that the future will show that in general the true abyssal species are cosmopolitan in accordance with the fact that the abyssal zone of the oceans forms an ecological unit with no barriers, except for isolated areas like the Sulu Sea.

This does not necessarily mean that any abyssal species is equally distributed all over the abyssal area; an ecological factor such as competition under the conditions of the varying supply of food from one area to another is probably very important, and the varying tolerance toward pressure must also be considered. Some species are found over a very large range of depth: *Elpidia glacialis*, as already mentioned, is a typical eurybathic species and may be expected everywhere within the abyssal depth range and even outside. In contrast, the sensitivity of more highly organized animals, which was indicated by laboratory experiments, might show a zonation of the abyssal zone. This seems to be the case with the fishes: the group barely enters the hadal zone; only stray specimens have been caught down to 7200 meters. Within the abyssal zone there seems to be a change toward other species around 4000 meters, so that there is an upper and a lower abyssal fish fauna. This distinction has been summarized by Nybelin (1955) and may be illustrated by examples compiled from literature and the GALATHEA collection.

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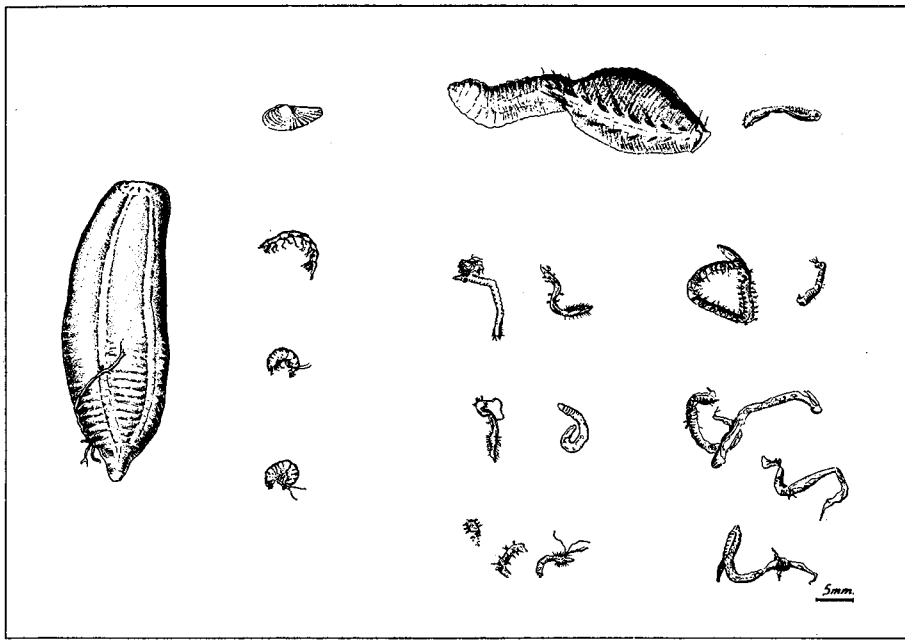

FIGURE 8.—*All the animals from 0.2 square meter at 6580 meters in the Banda Trench*

One holothurian (*Ceraplectana*), one bivalve (*Cuspidaria*), one isopod (*Leptanthura*), two amphipods, six polychaetes + fragments (*Travisia, Tharyx, Ancistrosyllis,* Oweniidae sp.). Altogether eight species, 11 + individuals, 2.1 g. (Bent Hanskov del.)

In Figure 9 the distribution of two different species is shown. The material is small, but the abyssal depths have been very little explored, especially those depths exceeding 4000 meters. Therefore, it is still more striking to note that the relatively well-fished North Atlantic yielded 8 specimens of *Bathymicrops regius* and that the sporadic fishing of the Galathea in the Indian and Pacific gave 3 specimens, thus making the species cosmopolitan, but only between 4000 and 6000 meters. In contrast, the GALATHEA found two specimens of *Acanthonus*, one in the Gulf of Guinea and one in the Gulf of Panama; both specimens were found at depths from about 2000 to 4000 meters, as were the specimens found earlier. Thus, these two species may be termed stenobathic cosmopolitans of the abyssal zone: *Bathymicrops* represents a lower, and *Acanthonus* an upper subzone. In the case of *Acanthonus* one is also led toward the conclusion that this species may require a fair supply of food, because it has been found only in regions where food is relatively abundant; in the East Atlantic and East Pacific below very productive surface layers, and in the Indonesian area with plenty of terrestrial debris.

The very peculiar Pogonophora, which Ivanov (1955b) proposed as a new phylum, the Brachiata of the Deuterostomia, may be especially restricted in their distribution because of food requirements. They have been found in great numbers in the North Polar, the Bering, and the Okhotsk seas and even in the abyssal and hadal zones of the Kurile region. Furthermore, they have been recorded from the abyssal

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zone in Indonesia as reviewed by Zenkevich (1955, p. 80). The GALATHEA Expedition found a new genus in the Celebes Sea at 5000 meters (Kirkegaard, 1956b), and, more remarkable, two species in the central American Pacific. One of these two species, *Lamellisabella zachsi*, was formerly known from the Bering and Okhotsk seas (Kirkegaard, 1956b). Inasmuch as this group was first recognized as most extraordinary in 1937, much more will have to be found out about the distribution of its 16 species so far described. The unique mode of extraoral feeding described by Ivanov (1955a) may require a fairly high concentration of food, which is a feature common to the northwest Pacific, Indonesian region, and central American Pacific occurrences.

The means of distribution of the abyssal fauna may not be as varied or efficient as those of the animals living close to the surface with strong currents. However, abyssal rises are found swept clean of sediments by currents which would also carry any small pelagic stage of a benthic animal far and wide. Turbidity currents, starting perhaps as slides on the slopes, may also carry small animals in suspension for long distances.

Finally, the time factor working with the constant huge bottom currents, forming a continuous pattern in the world-wide abyssal zone below 2000 meters (Fig. 2), must lead toward a continuous mixing of the abyssal populations and must prevent the isolation necessary for large-scale formation of species endemic to a single ocean.

The hadal fauna may eventually show the contrast. If an abyssal species becomes physiologically adapted to the hadal pressures in the same way as the bacteria and thus becomes to a certain degree stenobathic it also becomes isolated, and the possibility of the formation of species endemic to a single trench arises. The account of the hadal community as given for the few trenches explored shows examples of such endemism. Perhaps the most striking is that of the new family of actinarians, the Galatheanthemidae, represented by one species in the Philippine Trench and another in the Kermadec Trench. In any case, the trenches are isolated (Fig. 2), and it is therefore not surprising that their faunas show examples of endemism parallel to those of the mountain regions on land.

ADAPTATIONS OF DEEP-SEA ANIMALS

Morphologically the abyssal and hadal animals are in many ways characteristic at first glance: the lack of bright colors characteristic of shallow-water animals, the reduction of the eyes, often total blindness, and several other characters are conspicuous; closer inspection reveals that probably each single character or complex of characters is also found in some related animal from the bathyal zone or even coastal regions or fresh water, especially caves.

The abyssal species of the apode fish *Synaphobranchus* look in all respects much like any other muraenoid fish; they even have well-developed eyes and a darkish-brown color. They perform an ontogenetic migration, spawning near the surface, and have an epipelagic larval stage. *Synaphobranchus* therefore is simply an eel fish, which, without obvious change of morphology, has overcome the physiological stress of descending to the abyss, much as the species of fresh-water eels (*Anguilla*), leading the same epipelagic larval life, have entered fresh water and are the only repre-

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sentatives of the large order of Apodes to overcome this physiological stress. In contrast, another apodal fish, *Heterenchelys microphthalmus* Regan, lives burrowing in the mud along the coast of tropical West Africa; it is fairly small, about 30–40 cm long, with eyes reduced to barely visible black spots, with transparent unpigmented skin, to which the blood gives a pinkish tinge. If it came up from abyssal depth this fish, rather than the *Synaphobranchus*, would be called a typically deep-sea species. It could also be called a typical cave fish. The fish family Brotulidae is represented by several abyssal species, blind or with reduced eyes (*Acanthonus*, *Typhlonus*), and by others (*Stygicola*, *Lucifuga*) which have entered the caves of Cuba.

Thus, it appears impossible to point out any single character of morphological adaptation, which could definitely be referred to the abyssal or hadal life condition.

As for the physiological adaptation reference has already been made to present scanty knowledge of the special life condition of the deepest zones, the pressure.

ORIGIN OF THE DEEP-SEA FAUNA

In comparison with the bathyal fauna the abyssal and hadal fauna is poor in number of species. Many species and also some higher taxonomic categories are endemic to the abyssal zone, but there is no question that the abyss has been populated from the bathyal zone.

In the early days of deep-sea exploration the great expectation was to find living fossils in the deep. The finding of stalked crinoids in the West Indies, the *Encrinus* brought up by fishermen on hooks from deep water and later, in 1835, the remarkable *Holopus rangii*, especially inspired such expectations. The discovery of *Rhizocrinus lofotensis* from the Norwegian coast in 1864 undoubtedly inspired some of the intensive work in the following years.

The stalked crinoids, formerly known only as fossils from past geological periods, were followed by quite a number of parallel cases. There were the hexactinellid sponges and the crustacean family Eryonidae; these, and several more examples (recently the coelacanth fish *Latimeria*), are all of the highest zoological interest,

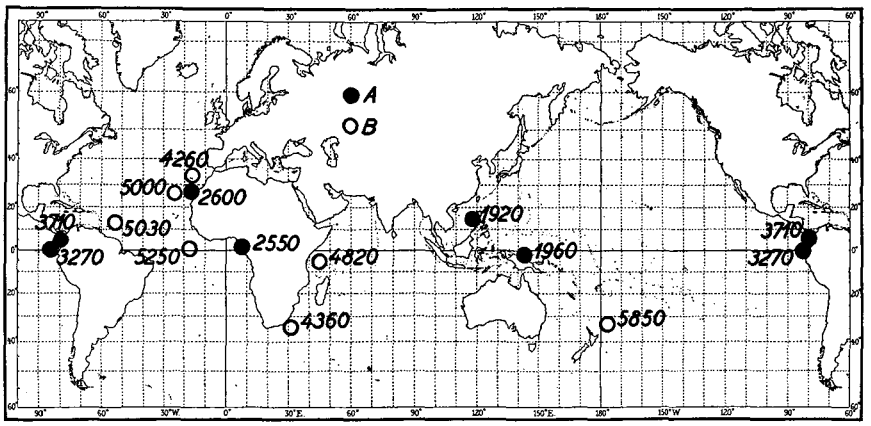

FIGURE 9.—*Distribution of two cosmopolitan abyssal fishes which have different depth ranges* (A) *Acanthonus*; (B) *Bathymicrops*. Depths indicated in meters.

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but they all come from the lower shelf or the bathyal zone. Perrier (1899, p. 340), in his attempt to divide the marine fauna into zones, inappropriately suggested the name paleozoic zone for the depths around 400 to 2000 meters because of the many similarities of its fauna with that of the secondary [Mesozoic] period.

In the abyssal zone such relics are only a few species, derived from the bathyal groups, which have become adapted to live under abyssal conditions. The same is true for the hadal faunas: they must have been derived from the general abyssal fauna, for they have features in common; at the same time a certain amount of endemism has already developed. Most species of the abyssal and hadal faunas are probably of fairly recent geological age.

Before the glacial age, when there were no constant polar icecaps, the temperatures in the abyssal and hadal depths must have been considerably higher, perhaps between 4° and 10° C., as in the present bathyal zone.

Emiliani and Edwards (1953, p. 888) examined the oxygen isotopes of benthic Foraminifera of probable Oligocene age from a core from the Eastern Central Pacific at 4725 meters depth. The concentrations of O^{18} indicate the following temperatures:

Depth below top of core (cm)	*Temperature C.°*
2–10	10.3 ± 0.5
282–290	11.5 ± 0.5
339–346	9.4 ± 0.5

The temperature at the same depth in this region at present is about 1.3° C. In preglacial times, the thermosphere must also have been much greater, horizontally as well as vertically. If a certain number of animals had developed into a barophilic (or stenobathic) fauna of the present abyssal and hadal zones, the relatively sudden appearance of the glacial age and its cooling of oceanic deep water to temperatures below 4° C. must have been catastrophic for the fauna. Only the relatively eurythermic or eurybathic species could survive—the first group on the spot under less competition from the second group, which was pushed upward into the bathyal zone.

The present composition of the hadal fauna may indicate the types of animals which survived; if higher taxa than subspecies will stand up as exclusively hadal in occurrence, they are probably relics of a preglacial abyssal or hadal fauna. In addition to these old components, the abyssal fauna may have had a new invasion, which started simultaneously with the first glacial cooling and must still be in process. This would consist of species becoming adapted to the abyssal and hadal life conditions, especially the low temperature and the pressure. The interglacial periods must have caused fluctuations of the bottom temperatures but probably of a much smaller range than that between preglacial and glacial periods.

The species which possess a certain degree of eurybathy must be considered as preadapted for an abyssal life under the cold conditions. Among such species, which also possess a certain degree of eurythermy, are those which could move downward from any part of the bathyal zone. Examples of this type are the Hexactinellida, the stalked crinoids or the Eryonidae, and, in short, all the groups which have the majority of their species in the bathyal zone.

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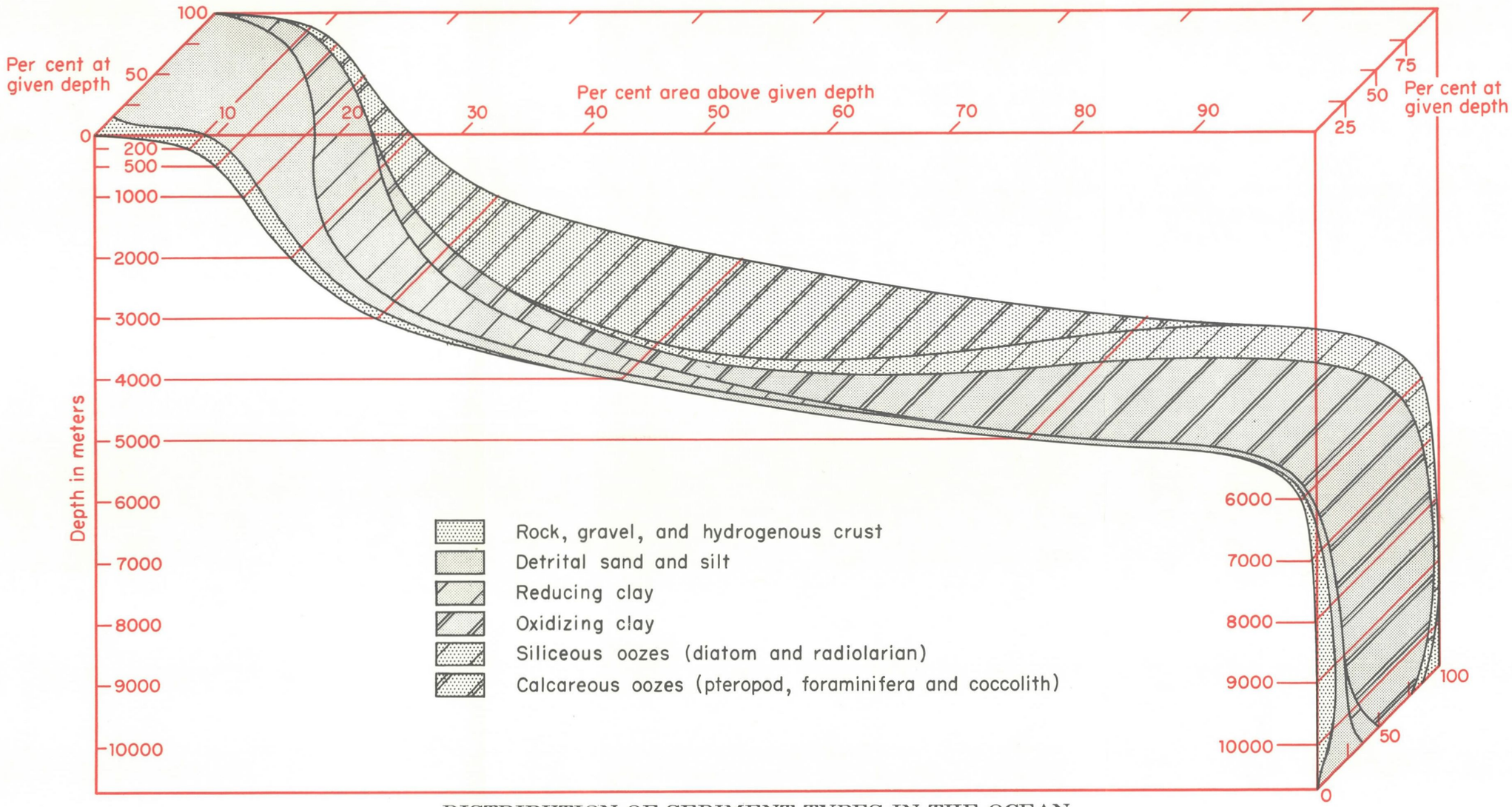

DISTRIBUTION OF SEDIMENT TYPES IN THE OCEAN

Distribution plotted on hypsographic curve to indicate approximate percentage at a given depth and approximate area occupied by various indicated types. (Compiled with the assistance of G. O. Arrhenius).

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In the Arctic and Antarctic seas are also stenothermic species, adapted to temperatures below 4° C. In ages past they must have spread poleward from lower latitudes, possibly even in preglacial time, because the polar areas must always have been fairly cool; these species could thus descend into the abyss as soon as the temperature became suitable.

The extremely cold water, below 0° C., of the Arctic and Antarctic seas, is not thought of in this connection, because it must have spread to its recent extent during the glaciation; it remains to be seen if the endemic species of its abyssal zone are stenobathic or simply represent a relatively late invasion of eurybathic species from the corresponding slopes and shelves. It does not seem reasonable to expect that species which have first become specialized to live at temperatures below 0° C. should afterward easily give up this adaptation.

Therefore the conclusion is that the glacial and postglacial invasion of the abyssal zone consists of eurybathic species of the continental slopes, and even the shelves, where the temperature tends to be around 4° C.

These considerations on the origin of the abyssal and hadal faunas are intentionally kept in very general terms. This must remain the situation until the present initial stage of the study of bathyal and deeper zones is passed. The pressing need of a thorough study of the taxonomic composition of the deep-sea faunas in the oceans in general must not be overshadowed by the badly needed study of the physiology and other aspects of deep-sea animals; such studies can add to understanding of the ecology of the animals only when the species are well defined and their full life history, as well as their distribution, is well known.

The abyssal depths of the oceans represent a very monotonous environment, yet the relatively small adjacent seas like the Mediterranean, the Sulu Sea, and the Arctic and Antarctic seas constitute large-scale ecological experiments by Nature, which will still reveal many facts of the utmost importance to understanding the household of the open oceans.

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Note: The most interesting discovery made by the GALATHEA Expedition did not come to light until the specimens had been critically examined. This is the living monoplacophoran mollusk *Neopilina*, representing a class thought to be extinct since Devonian time. It was taken from 3590 meters in the Acapulco Trench off Central America. For details see the entry under Lemche, 1957, in the annotated bibliography of Mollusks in this volume.

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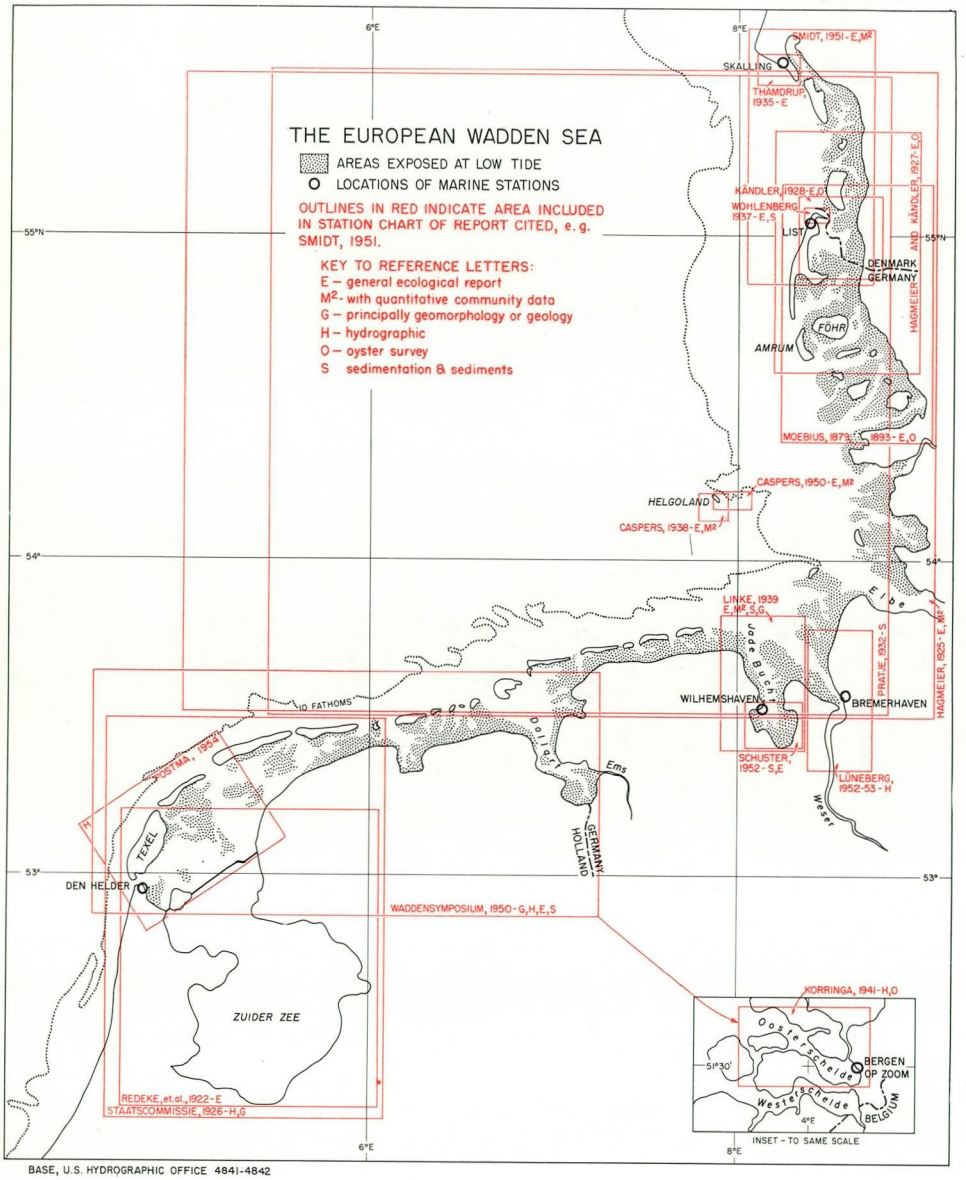

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LOCATION MAP OF THE EUROPEAN WADDENS

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Memoir 67, Vol. 1, 1957
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Chapter 23

Estuaries and Lagoons

I. Physical and Chemical Characteristics*

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An estuary is the wide mouth of a river or arm of the sea where the tide meets the river currents, or flows and ebbs (L. *aestuarium*, fr. *aestuo* to boil or foam, *aestus*, heat, tide). Or, "an estuary may be defined as a body of water in which the river water mixes with and measurably dilutes sea water." (Ketchum, 1951b). A lagoon is defined as a shallow lake or sheet of water connected with the sea or a river (L. *lacuna*, fr. *lacus*, a lake). These dictionary definitions are not mutually exclusive, since a lagoon connected with the sea may also be affected by the tide. Some ecologists prefer to describe the environment in terms of the salinity (as saline, brackish, or fresh), but saline water is not restricted to marginal marine areas, and such a description of the environment does not consider the most characteristic aspect of the estuarine environment—that it is a region of steep and variable gradients in environmental conditions (Fig. 1).

Physiographically, estuaries are bodies of water bordered by and partly cut off from the ocean by land masses that were originally shaped by nonmarine agencies. They are usually perpendicular to the coast line, and most of them occupy the drowned mouths of stream valleys and are, therefore, usually considered as evidence of submergence.

Lagoons are bodies of water separated in most cases from the ocean by offshore bars or islands of marine origin and are usually parallel to the coast line. They have usually been considered a result of emergence, but they can also form as a result of submergence of a flat coastal plain. Both estuaries and lagoons are reached by the tide, yet both have areas of quiet water that favor deposition of stream-contributed sediment. These sediments form deltaic deposits that may eventually fill the estuary or lagoon. After the deposits have built up to an intertidal position, where they tend to be stable for a long time, their top surface is called a tidal flat. If the tidal flat is covered by emergent brackish or salt-water vegetation, it is termed a salt marsh (Anglo-Saxon *mersc*, a marsh or bog; allied to Latin *mare*, sea), and, if barren, it is a mud flat or a sand flat. In the tropics, the same zone is usually a mangrove swamp.

PHYSIOGRAPHY

ESTUARIES: When first formed, estuaries and lagoons approach their ideal triangular and elongate shapes to a degree that depends on the irregularity of the original topography. Sedimentation and marine erosion soon change this early shape.

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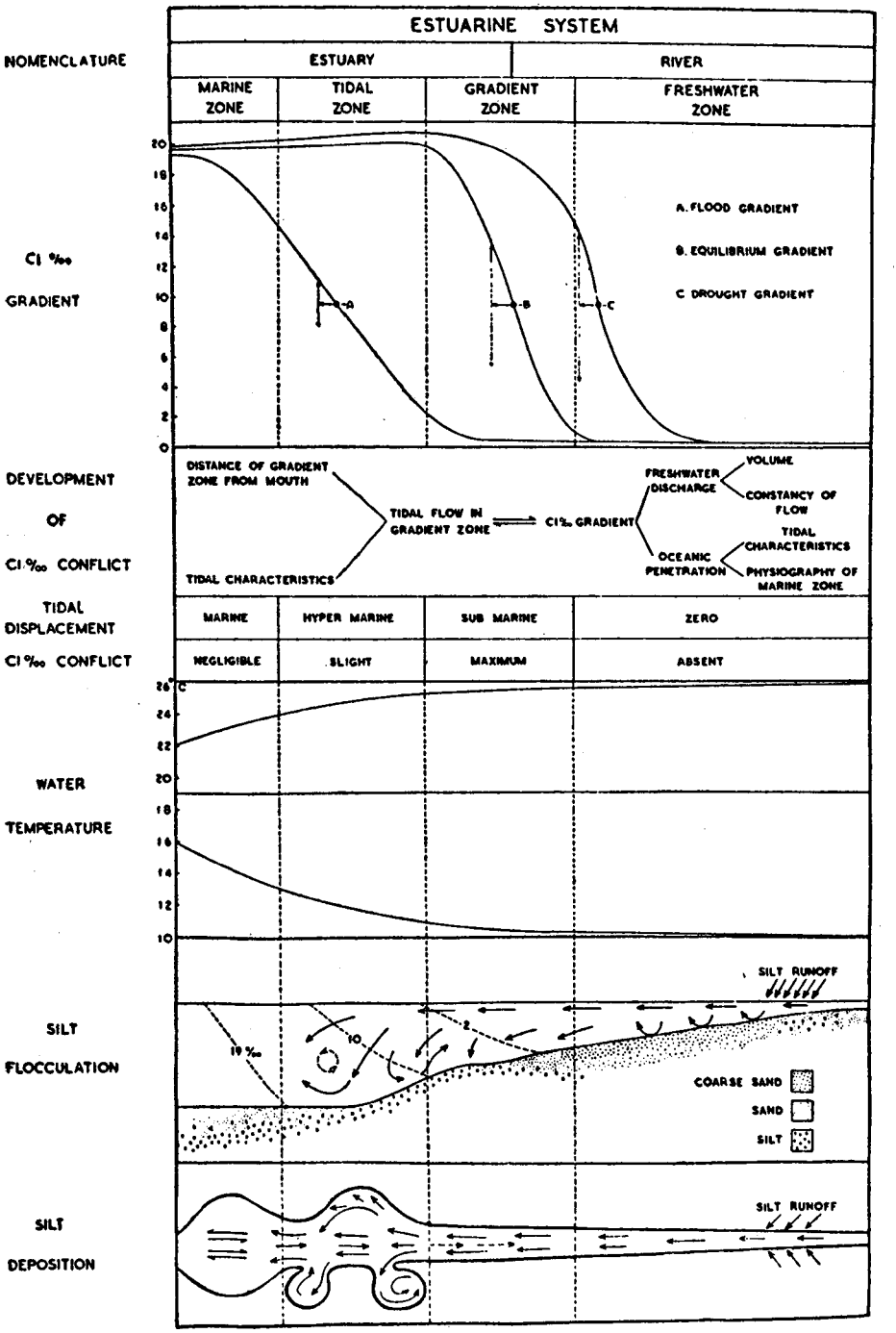

FIGURE 1.—*Diagram showing some of the zonal features of a composite Australian estuarine system*
From Rochford (1951)

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Erosion of the headlands at either side furnishes sediment for beaches and for baymouth bars that help to provide a quiet environment for the deposition of finer sediments in the estuary. As most estuaries occupy drowned river mouths, the shortened river immediately begins to build a delta at the head of the estuary near the new river mouth. The top surface of this delta is a tidal flat. Somewhat similar tidal flats form along the sides of the estuary from sediments contributed by small tributary streams, by cliff erosion, and by the main river from which they may be carried during floods in a layer of fresh water overriding the sea water. Some of these marginal deposits become reworked by waves into sand beaches and spits. In small estuaries the main source of waves is the open sea, so most of the spits can be expected to curve up-estuary. The bulk of the sediments is deposited on the deep floor of an estuary. The ratio of the volumes of subaerial and subaqueous sediments depends on the original depth and the stability of the estuary during its period of filling.

With passage of time the delta shortens the estuary by deposition at the head, while wave erosion of the cliffed headlands and of baymouth bars shortens it at the mouth. The relative size of the estuary when it becomes filled by sediments must be a function of the relative rates of deposition and erosion. Such factors as time of submergence, past rate of stream erosion (which controlled the original size of the estuary now being filled), and present rate of stream erosion above the estuary (which controls the present volume of deposition) are among the more important factors in determining the rate and degree of filling. After marsh or deltaic deposits have prograded some distance into an estuary, a new stage commences, that of accumulation of alluvial-fan or river flood-plain deposits. In Table 1 is the sequence of physiographic stages in an estuary as related to shoreline processes outlined by Johnson (1919). The degree to which this sequence is followed depends on the homogeneity of the headlands; marine erosion of nonhomogeneous rocks can produce a more irregular shore line (Shepard, 1937).

LAGOONS: Most lagoons are elongate parallel to shore and lie athwart the mouths of one or more streams. The quiet water behind the offshore bar, or barrier island, is an ideal site for small deltas built of stream-contributed sediment. After the deltas have prograded completely across the lagoon, continued growth is mainly along the long axis of the lagoon. Some lagoons may be filled largely from the seaward side by sand washed through the tidal inlet and forming tidal deltas (Lucke, 1934) or by sand washed over the offshore bar by storm waves and forming washover fans (Price, 1947). On both the landward and the bar sides of the lagoons, marginal tidal flats are built largely by entrapment of fine sediment by plant growth. Thus, in a general way, the lagoonal depositional area is similar to that of the estuarine area.

Lagoons are commonly shallower than estuaries, and the lagoon floor is usually subject to reworking by waves, whereas in larger estuaries, at least, the bottom is not much affected by waves. Studies by Price (1947) suggest that the depths of lagoons are controlled by the opposing forces of deposition of stream-derived sediment and removal of sediment by wave and current action. Recent work by F. P. Shepard (1953) indicates that deposition is the greater force, at least in bays along the Texas coast. Johnson's concept of the physiographic sequence in lagoons (Table

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TABLE 1.—*Sequence of estuaries and lagoons as shown by development of shore lines of submergence and emergence*
According to Johnson (1919)

Estuary	Lagoon
Initial stage: deeply embayed	Initial stage: straight shore line; no lagoon
Early youth: cliffed headlands	Early youth: offshore bars separating shallow lagoons from open ocean
Later youth: formation of beaches and spits, baymouth bars, beginning of marsh	Later youth: lagoon largely filled by marsh
Submaturity: straight coast with bars extending across estuary mouths, estuary largely or entirely filled by sediments	Submaturity: lagoon almost filled by marsh, erosion of bar on seaward side and deposition of sand on landward side, resulting in landward migration of bar over the marsh
Maturity: straight cliffed coast, cliff recession resulting in removal of the estuary	Maturity: continued landward migration of bar so that marsh is eroded away and shore is straight and cliffed

1) has been modified by recent work, particularly in regard to movement of the offshore bar or barrier island.

Many environments are more complicated than those outlined above, because there are relatively few "pure" estuaries and "pure" lagoons. Instead, many are compound and consist of estuaries adjoining lagoons. Such complex environments may be the result of submergence, followed by emergence, or of construction of a barrier island by longshore currents. Examples of such combinations are to be found in many of the extensive systems of the Atlantic and Gulf coasts and on a smaller scale on the Pacific coast of North America and Central America.

ENTRANCES: The entrance to an estuary or lagoon is restricted where it consists of a tidal inlet through a bar, or, in the case of some estuaries, of a narrow strait between headlands. Tidal inlets through bars and barrier islands are generally formed by storm waves, kept open by tidal currents, and moved or closed by longshore currents. Storm waves cut notches across the bars or islands, commonly at gaps between dunes, and distribute the sand as washover fans within the lagoons (Price, 1947). The Beach Erosion Board, in studies of the North Carolina coast (1935; 1948), has found numerous examples of new and usually temporary tidal inlets formed by high waves and by water flowing over barrier islands or bars during storms. Nichols and Marston (1939) have described the cutting of inlets by the 1938 New England hurricane and their subsequent natural filling. In addition, inlets are formed during the rainy season through bars built across the mouths of some estuaries in regions of pronounced seasonal drought.

A large part of the volume of water in the prism between low and high tide has to pass in and then out through the mouth of an estuary or lagoon in only a few hours. In order to accommodate this discharge, at least where there is a large fresh-water runoff, a narrow entrance is deep, usually the deepest part of the estuary. Where the entrance is entirely through sediment, the depth is in equilibrium with the tidal volume, so that only slight erosion or deposition occurs. During the filling of an estuary or lagoon by sediment over a long period of time, however, the entrance

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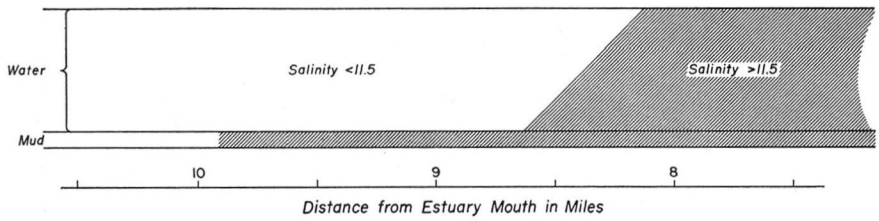

FIGURE 2.—*Diagram illustrating the distribution of salinity at low water in the water and muddy foreshore of an estuary*
After Alexander, Southgate, Bassindale 1935

gradually shallows because the amount of tidal water that must pass through the entrance is diminished, although it usually remains the deepest part of the estuary. Where the entrance is through rock, equilibrium with tidal volume has not usually been reached, the cross-sectional area is relatively small, and the tidal currents have high velocities, sometimes exceeding 5 knots. With such velocities the current is capable of considerable erosion, and the entrance slowly deepens.

Longshore currents that carry sediment along the offshore bars or islands deposit some of it in or at one side of an inlet. Where the longshore current is more active than tidal currents the inlets are filled, and a "tidal delta" is built up inside the inlet, but, where it is weaker, the inlets remain open but usually migrate along the bar.

SUBSTRATE: Since estuaries and lagoons are usually regions of low topographic gradient and active sedimentation, most of the bottom materials are unconsolidated muds and sands in various combinations. Mud is usually characteristic of the upper reaches and regions of reduced current action, whereas sand is found near the mouth and in the channels. A feature of many estuaries is the development of extensive tidal flats; in estuaries free from industrial pollution these flats are inhabited by extensive communities of burrowing and tube-building organisms, feeding on suspended matter, detritus, and, in some cases, the organic materials in the mud itself. Rocky surfaces may be rare in an estuary and when present on the bottom may be covered with fine silt if not buried in sediment, inhibiting the settlement of organisms depending on rocks. The distribution of soft-bottom species will, as in the sea, be associated with the respective bottom types.

One of the most ecologically significant properties of the muddy bottom of estuaries is its tendency to retain the water of higher salinity as the tide recedes (Fig. 2). As a result of this, organisms living within the substrate or burrowing into it are able to penetrate a greater distance up an estuary than those which are subject to the salinity conditions of the overlying water (Fig. 3).

TIDAL FLATS: The tidal flats which line and finally fill the estuaries and lagoons consist mostly of mud. Their surfaces are intertidal and thus periodically exposed to air and then covered by water. A large proportion of the prism of water that covers the flats at high tide travels via large tidal channels. Minor channels adjoining them act both as tributaries and distributaries. Although the large channels are fairly straight, the minor ones meander even more than old-age streams, and,

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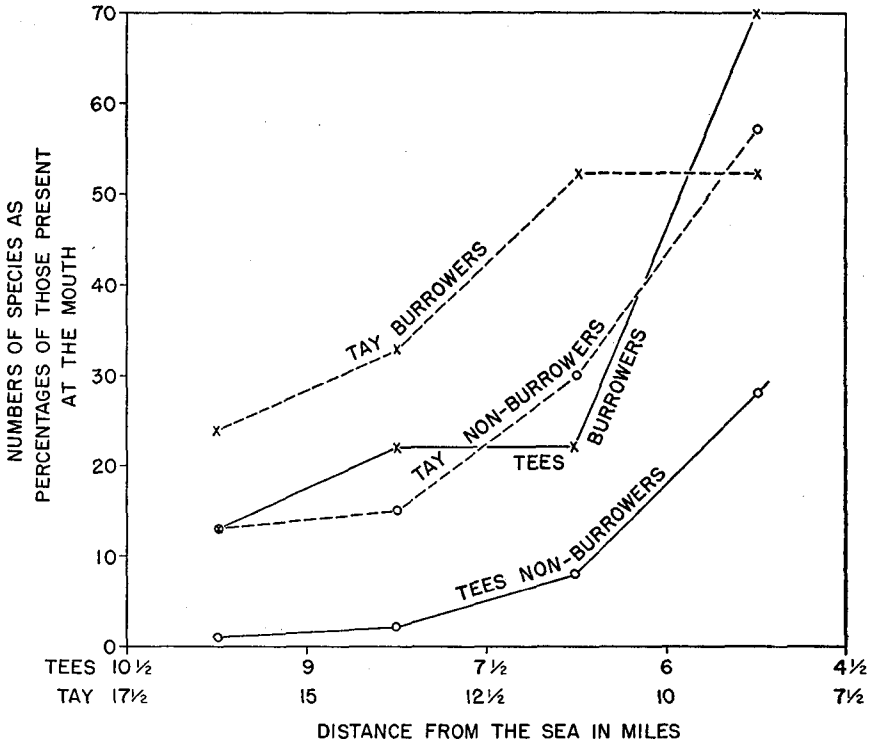

FIGURE 3.—*Penetration of burrowing and nonburrowing animals in the estuaries of the Tees and Tay* After Alexander, Southgate, Bassindale (1935)

because they are wide compared to their length, they taper much more than do streams. Their meanders appear to follow characteristic patterns. Near the mouth of large channels, where a great volume of water passes with a relatively high velocity inward at flood and outward at ebb tide, they are commonly cuspate in shape, with the outside of the bends broadly concave and the inside pointed. Farther into the flat, where less water passes, their pattern changes into a more sinuous one with nearly equal radii of curvature of both sides. Some marshes that have abundant vegetation are characterized by channels that wind around among roughly circular patches of vegetation. As shown by Lüders (1934), Van Veen (1950), and Van Straaten (1949; 1950b), the winding channels (*Priele*) migrate considerably over a period of several years. Their patterns can often be detected from aerial observation of completely filled former marshes. Along the Atlantic coast the marks of older channels bordering narrower present-day ones appear to indicate relatively recent minor uplift of the land in much the same manner as stream terraces would. Linke (1939) found that sediment texture and other factors caused considerable variation in cross-sectional shape of the *Priele*, and he developed a classification on that basis.

Along the sides of the larger channels natural levees are commonly present; locally they rise to a height of a foot or more. Where the channel meanders strongly,

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its natural levee may nearly completely enclose an area of marsh which then supports a small pond in its center.

ENVIRONMENTAL FACTORS

TIDE: The tide is the most important ecological factor in an estuary, since it is the agent which effects the exchange of water, and its vertical range determines the extent of tidal flats which may be exposed and submerged with each tidal cycle. The action of the tides against the volume of river water discharged into an estuary results in a complex system whose properties vary according to the structure of the estuary as well as the magnitude of the river flow and range of tide.

In most estuaries except those in regions where stream discharge is light and evaporation is high, there is a net discharge of water from the estuary equal to the amount of river discharge. Because of tidal action, however, the exchange of water in large estuaries is not completed in a single tidal cycle, and it may require several days or tidal cycles for a given particle of river water to reach the sea.

A typical exchange pattern is that illustrated in Figure 4, where there is a net upstream movement of salt water in the lower water layers and a net downstream movement of fresh water at the surface. Under such conditions the upstream movement of larvae, and plankton, as particles in the system is possible in the lower water layers of an estuary, although large numbers will inevitably be lost downstream (Pritchard, 1953). That is, even though larvae may be distributed throughout the water column of a turbulent estuary, they will tend to be more concentrated, on the average, at some particular depth determined by factors which tend to act in opposition to the dispersing effect of the turbulence. Thus larvae so concentrated will spend a statistically greater proportion of the time in the lower levels, which have a mean flow up the estuary, than in the upper layers. Such a causal explanation of upstream dispersal satisfies the observed conditions more adequately than Carriker's (1951) explanation that oyster larvae tend to drop near the bottom on the ebb and rise during the flood, thus "migrating" upstream. Somewhat similar studies by Yasuda (1952) suggest that the greater frequency of mollusk larvae found during the flood at a given observation station may actually be the net accumulation during the tidal cycle carried by the flood, although Yasuda concluded that the larvae moved upward on the incoming tide, coincident with a diurnal vertical migration. Although such migration patterns are not necessary to account for the upstream migration of larvae (and possibly small adult organisms), Rogers (1940) suggested that negatively phototropic larvae, which are usually more abundant in the water during the spring and summer, would migrate upstream as a result of the longer time spent in the lower levels of the estuary because of the greater duration of daylight during that time of the year.

It is possible to recognize two types of estuaries on the basis of tidal and salinity characteristics: (1) a "normal" or "positive" type, in which salinities are reduced

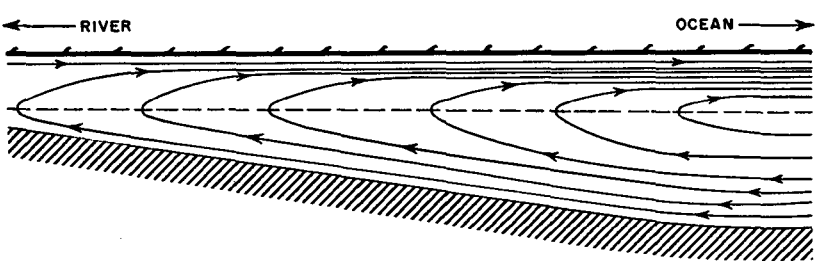

FIGURE 4.—*Schematic presentation of streamlines in a longitudinal section down the central axis of an estuary*
After Pritchard (1952)

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upstream as a result of adequate river discharge mixing; and (2) a "hypersaline" or "negative" estuary, occurring in arid regions of poor runoff, where exchange is poor and salinities are higher than in the ocean (Fig. 5). There are many varieties of the "normal" estuary; Stommel and Farmer (1952) recognize at least four, which they refer to simply as Type I, Type II, etc., on the basis of salinity structure (Fig. 6). Guryanova *et al.* (1926) recognized three types of estuaries in the Russian Arctic, based on salinity and biological characteristics. Only two of these, however, are characterized: Type I, in which the salinity is strongly variable and in which such organisms as *Mya arenaria, Cardium edule, Microspio theeli,* and *Eteone arctica* are abundant; and Type II, with less variable salinity during the tidal cycle and characterized by such organisms as *Gammarus duebeni* and *Fucus* spp. Their Type III is exemplified by the estuary of the Ob, a large boreal-arctic fjord.

The classification suggested by Stommel and Farmer is designed to indicate the hydrodynamic characteristics of the various types which may be analyzed by different equations, as illustrated by the exchange-ratio method of Ketchum (1950; 1951b), the analysis of Alberni Inlet by Tully (1949), and of Chesapeake Bay by Pritchard (1952). Still other schemes of classification have been proposed. Rochford (1951b) has divided Australian estuaries into three primary groups on the basis of river-discharge characteristics: (1) dominated by summer flood and winter drought discharges; (2) dominated by winter flood and summer drought discharges; and (3) a mixture of (1) and (2), showing no regular annual flood cycle. While of limited hydrographic use, this classification is of some ecological value. Day (1951) recognizes three types of estuaries in South Africa: a type with a vertical salinity gradient, a reversed gradient type, and the blind estuary.

The less extreme conditions of salinity, temperature, pH, etc. are generally found near the tidal entrance to an estuary, where there may be an almost continuous resupply of sea water, and the extreme conditions generally occur near the head of the estuary where the supply of sea water is discontinuous. The geographical position of the transition point between saline and fresh-water conditions depends on the balance between tidal range and runoff; that is, the transition is near the entrance of an estuary having a small tidal range and large runoff, and near the head of one having a large tidal range and small runoff. The effect of tidal action under conditions of similar runoff is shown by the studies of Habe (1949), who found that bays on the Pacific Ocean side of Japan, where the tidal range is greater, have a more oceanic fauna than those of the Japan Sea side, although the runoff is about the same in both areas.

In a large estuary whose opening to the sea is not at the end but near the middle, the environment is complex and not easily classified. This is especially true of San Francisco Bay, where the major influx of fresh water is at the north end while evaporation is greater than the inflow at the south end of the bay. Salinities and temperatures are higher on the average in the southern end of the bay, but salinities do not attain values much above 28 ‰ because the southward-flowing currents past the Golden Gate at slack tide carry some of the less saline water from the northern part of the bay to the south. Without such currents, hypersaline conditions might be established at the lower end of the bay, where evaporation is sufficient to enable the solar extraction of salt in evaporating ponds, and salinities taken at the time of ebb are slightly higher than those at flood tide (Miller *et al.*, 1928). The complexities of tidal exchange in San Francisco Bay were brought out in the study of mining debris by Gilbert (1917).

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In some of the larger estuaries the periodic flooding action of the tide is supplemented by seiches, or long stationary waves. The simplest of these is one whose node is at the opening to the sea and whose antinode, or point of maximum vertical movement, is near the landward end of the body of water (Sverdrup *et al.*, 1942, p. 538–542; Neumann, 1950). The period of the seiche is controlled by the length and depth of the body of water, and where this natural period nearly coincides with that of the tide, as at the Bay of Fundy, a very great fluctuation of sea level occurs (Marmer, 1926, p. 217–226). In the Bay of Fundy the seiche has an amplitude of about 50 feet, but in most lagoons and estuaries it is only a few inches high and is obscured by the much greater tidal amplitude.

The periodic changes in sea level produced by the tides and seiches subdivide the estuaries and lagoons into ecological zones having nearly horizontal boundaries. The height of these zones varies with the distance from the tidal inlet. In most small estuaries and lagoons the tidal range decreases away from the entrance, but in those having dimensions favorable for large seiches, such as the Bay of Fundy and San Francisco Bay, there may be a greater range of sea level at a distance from the entrance. The action of the tide is observable a great distance upstream, far beyond the upper limit of salt water, where the gradient is low. The greatest reported distance is 600 miles up the Amazon (Andree, 1920, p. 116), and in other large rivers such as the Yangtze, Mississippi, Euphrates, and Nile there are tidal effects at least 100 miles upstream. In such situations the succeeding tide arrives before its predecessor has ebbed, so there may be several discrete tidal waves along the estuary of a large river.

WAVES: Ordinary wind waves in estuaries and lagoons are small because of the short fetch and relatively shallow bottom. Because they are rarely higher than 1–2 feet, most of them erode only a minor amount. In the shallow coastal lagoons of eastern Australia, usually parallel with wind direction, waves 8 feet high are common. Locally, they stir up the muddy sediment at the edge of a tidal flat so that the finer constituents may be carried away, leaving the coarser ones behind as a small sand bar or sandy beach (Johnson, 1919, p. 325–327). Similar beaches and bars are formed at the margin of deltas (Russell and Russell, 1939). The waves also transport some of the sand in a down-wave direction and, because the largest waves come chiefly from the widest part of a lagoon or estuary, they form spits pointing upstream in tidal channels.

A second kind of wave, effective chiefly on the upper reaches of a tidal flat, is the tidal bore—a wave of translation. Bores are common in tidal channels with narrow or shallow entrances; as a result of this shape and of bottom friction the flooding tide is held back for a time until the water finally rushes forward into the head of the channel as a steep wall of water from a few inches to many feet in height. A height of 10 feet was reported at the mouth of the Tsientang River in China by Marmer (1926, p. 84–85), although Andree (1920, p. 117) wrote that it sometimes reaches a height of 25 feet and moves at 12–13 knots. The character of a tidal bore is determined in part by the river discharge, which must be sufficient to hold back the tide for a period. If the river flow is reduced by natural or artificial causes, the tidal bore may be reduced or obliterated. According to Sykes (1937, p. 30, 39) a

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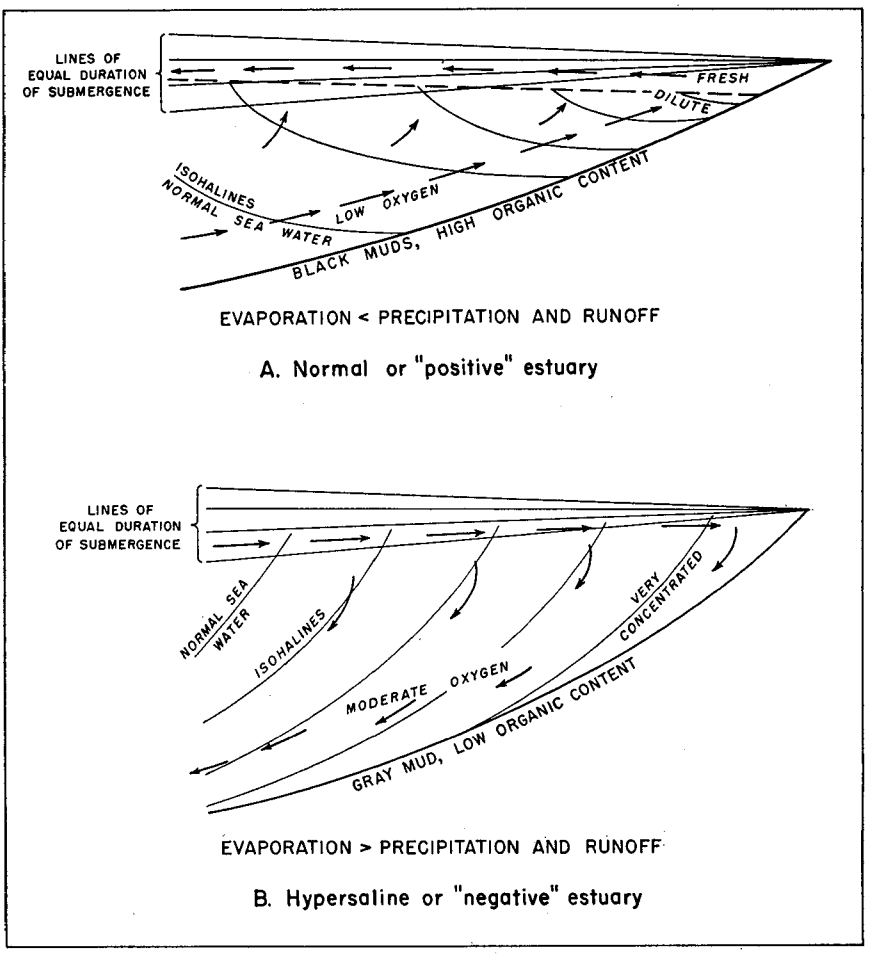

FIGURE 5.—*Schematic sections of the two basic types of estuaries*

bore nearly 10 feet high occurred at the mouth of the Colorado River; at the present time, since the construction of large dams on the river, only a rather rapid tidal rise, about 50 cm in 1½ hours, is to be observed.

CURRENTS: The chief cause of currents in estuaries and lagoons is the tide. In the open sea the tidal-current velocity reaches its maximum in the direction of progress of the tide wave at high tide and its maximum in the opposite direction at low tide (Sverdrup *et al.*, 1942, p. 565). At the entrance of a bay or river having no constriction the same phase relation between current and tide may exist, as shown by Marmer (1926) for the Hudson River entrance. In the narrow entrance of a large bay the friction may be so great that the water is largely held back until a hydraulic head develops, so that the maximum current comes near mid-tide, or near the time when the tide is changing fastest. Examples of this relationship are presented at Loch Scotnish (Nutman, 1950) and probably at San Francisco Bay

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(Sumner *et al.*, 1914). There are probably varying phase relationships of tidal height and current velocity, depending on degrees of closure of the bays. Of course, at the head of a bay the flooding and ebbing currents also are zero at high tide and low tide; otherwise the tide would continue to rise or fall. A similar frictional retardation exists on the shallow mud flats off the Netherlands (Postma and Verwey, 1950) and elsewhere. On tidal flats these currents are largely confined to the deeper tidal channels, where velocities of 2–3 knots are not uncommon. Much higher velocities, even of more than 5 knots (Marmer, 1926), exist at the entrances of some estuaries and lagoons. The greater strength of tidal currents near the entrance in lower depths of an estuary may inhibit the development of animal populations as compared with areas farther inland (Spooner and Moore, 1940).

Some slow currents are produced by excessive evaporation within the shallow waters of estuaries or lagoons. The loss is replaced by water from the open sea. A well-known example of such condition is the Gulf of Kara Bugaz, into which water flows continuously from the Caspian Sea, contributing most of its load of salts to the floor of the gulf (Twenhofel, 1932, p. 499). In contrast, an estuary or lagoon that receives more water from runoff by streams and direct precipitation than is lost by evaporation has an excess of water that may leave in the form of a continuous outward current. More commonly, this excess merely modifies the tidal current, decreasing the rate and duration of flood current, and increasing the rate and duration of ebb. Where much fresh water is supplied to a relatively deep estuary, such as Chesapeake Bay, there is a general outward movement of fresh water at the surface and an inward movement of sea water at the bottom (Fig. 4). As shown by Pritchard (1950), Nelson (1947), and Cowles (1930), both the outward-flowing fresh water and the inward-flowing sea water are deflected to their right in the northern hemisphere because of earth rotation (Fig. 7). This should result in stronger flood

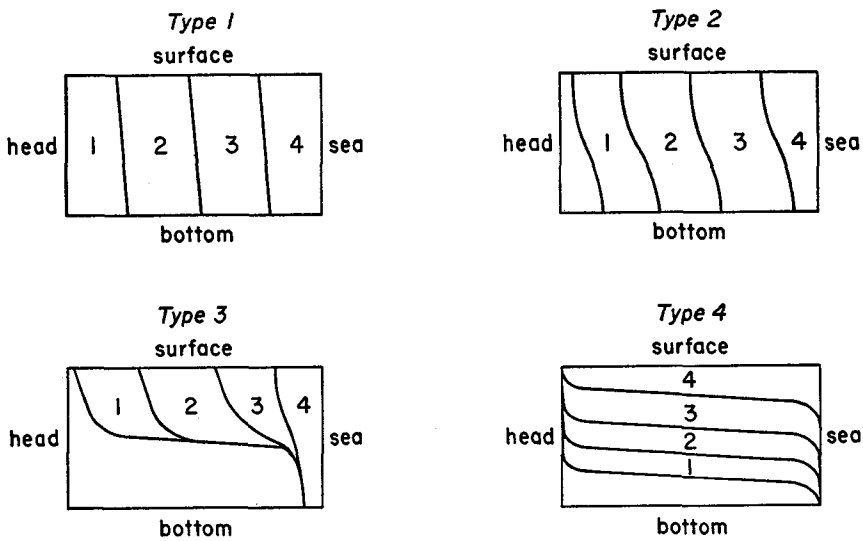

FIGURE 6.—*Classification of estuaries, according to Stommel and Farmer (1952)*

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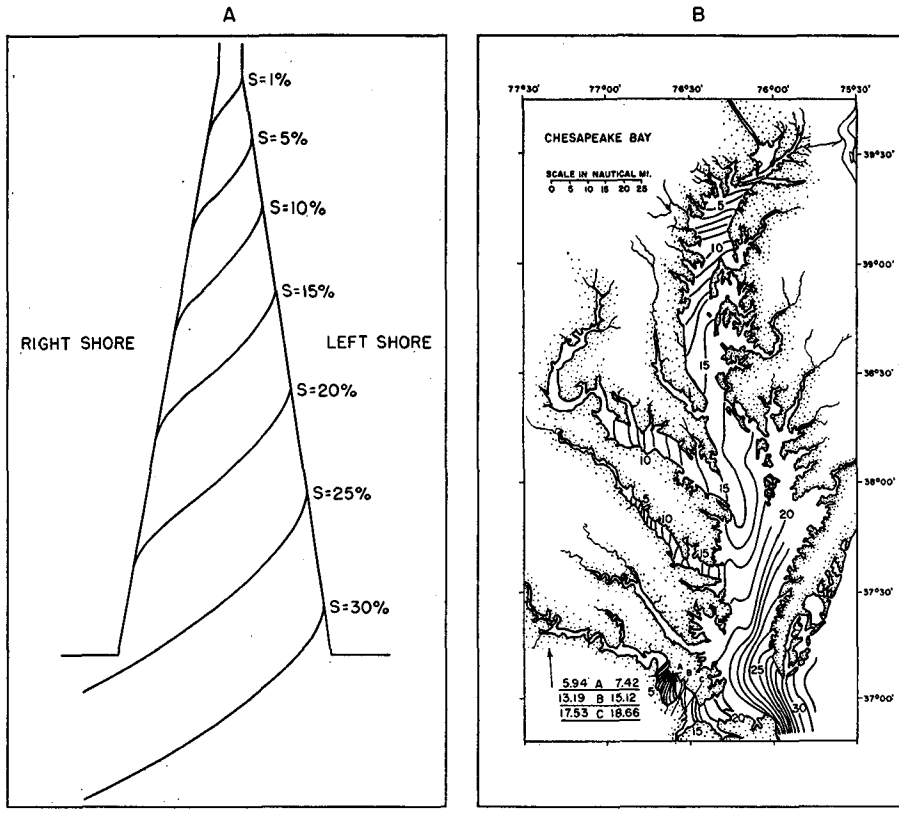

FIGURE 7.—*Idealized and actual isohalines in an estuary in the northern hemisphere*
After Pritchard (1951; 1952)

currents on the left-hand side of an estuary (looking down estuary) and stronger ebb currents on the right-hand side. In the southern hemisphere the currents should be of opposite signs.

Still other currents are produced by wind, particularly during the piling up of water on one side of a lagoon or estuary during storms (Haurwitz, 1951).

TEMPERATURE: The layer of water overlying estuaries and lagoons, and especially their tidal flats, is relatively thin, so it follows variations in the temperature of the atmosphere more closely than does the water of the open sea. Shallow waters are therefore much colder in winter and much warmer in summer than is the open sea. The diurnal variation is also greater, especially where the water has flowed over previously exposed mud flats. Because of interchange at the entrance of an estuary or lagoon, the water there is nearly the same temperature as the open sea, while greater departures are exhibited at progressively greater distances from the entrance. This is well exemplified in a study of San Francisco Bay by Sumner *et al.* (1914, p. 28–56). The wide range in temperature, especially in back-bay areas, eliminates

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stenothermic organisms and is probably also the chief cause of the large seasonal difference in flora and fauna of these areas.

In addition to horizontal temperature variations, there is a pronounced vertical variation. During the winter, the water is generally cold and nearly isothermal at all depths, although during short periods of cold weather the surface water may become a degree or so colder than the deeper water. During the summer, solar heating and low-velocity winds produce a high temperature at the surface with less change at depth. The difference between surface and bottom temperature may also be augmented by warm or cold river water flowing out over the denser sea water. Some estuaries and lagoons undergo so much evaporation during the summer that the surface water, though warm, is salty enough to sink to the floor and flow out the entrance beneath incoming new sea water, and the temperature of the deeper water may then be greater than that of the surface water. The greatest annual range of temperature occurs at the surface.

In northern fjord-type estuaries lacking complete exchange with the sea, the overlying layer of fresh or slightly saline water may act like the glass of a greenhouse, heating up the underlying water. This circumstance has been exploited in Norway, where oysters are cultured in small bays or "Pollen" (Gaarder and Spärck, 1932). The formation of ice at high latitudes in such regions as the Baltic and subarctic fjords is an important ecological factor, especially in the littoral zone, where it removes the organisms by mechanical action. The occurrence of winter ice does not, however, mean an impoverished shore; in such regions as the Kola Fjord the common littoral forms migrate to lower levels during the winter but flourish during the summer months at the edge of the sea (Guryanova *et al.*, 1929).

SALINITY: On the basis of salinity characteristics, estuaries and lagoons may be regarded as marine, brackish, or hypersaline, but often the designation must change according to the season. The various classifications proposed for brackish waters (Chapter 2) are of limited value in application to estuaries because the range of salinities at a given point may run through all the categories of such a scheme of classification. The ecologically significant aspect of salinity in an estuary is not the mean condition but its range on a daily and seasonal basis, and its rate of change through the tidal cycle. A daily, repeated change of salinity in an estuary may have a cumulative effect upon an organism, restricting it to higher salinities in nature than it may withstand under experimental conditions (Bassindale, 1943). This range of salinity may differ in various parts of an estuary. Milne (1938) observed that in the Tamar estuary the range, rate, and duration of change in salinity were greater in the deeper part of the estuary, and the fluctuation was less and was distributed over the higher part of the total salinity range in the intertidal part of the estuary. Under such circumstances it may be possible for marine intertidal organisms that can withstand exposure to air to penetrate an estuary somewhat farther than can organisms restricted to the bottom. In a stratified estuary, where the less saline water is more persistent in the upper layers of the estuary, such penetration along the intertidal margins is reduced (Fig. 8).

As a result of the tendency of the inward-flowing sea water and the outward-flowing fresh water to flow to their respective right sides, salinities are usually higher

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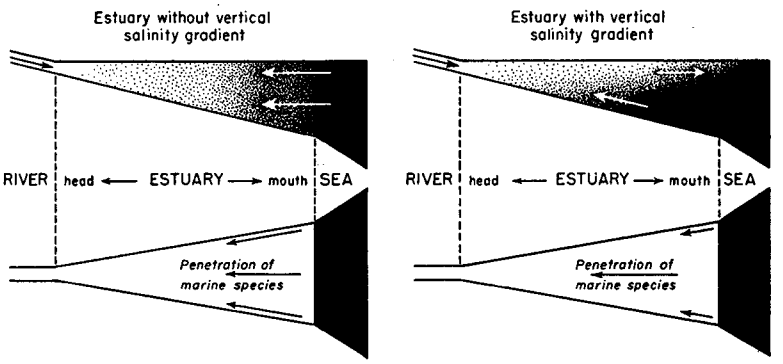

FIGURE 8.—*Diagrammatic sections showing penetration of sea water at high tide (above), and surface views (below)*

Showing penetration of marine species along shore and in midchannel in two types of estuaries. After Yonge (1949), with the permission of Collins, London

on the left side of an estuary in the northern hemisphere. (Also in the Baltic Sea, *see* Chapter 24). In smaller estuaries this difference may be obscured by local conditions, but Pritchard (1952) found that the salinity on the left side of the James River was on the average 1 ‰ higher than on the right (Fig. 7). The effects of these differences on the distribution and abundance of organisms has not been studied in detail, but the distribution of stomatopods in the Chesapeake Bay as given by Cowles (1930) suggests that they have penetrated the bay along the more saline side. According to Pritchard (1951) the most productive oyster bars in the James River occur on the northeast (left) side of the river.

In some smaller estuaries, such as the Tamar (Milne, 1938), the isohalines are convex with the direction of tidal flow, suggesting an effect of bottom friction in limiting water movement at the edges of the estuary. In deeper holes near the head of larger estuaries and in fjords with sills, sea water may remain for some time, perhaps years, and when conditions bring about overturn of this stagnant water there is a resultant mortality of organisms and a turnover of populations (Chapter 29).

Estuaries and lagoons in regions of high evaporation and low rainfall and runoff are subject to a different hydrographic regime. In such environments the high rate of evaporation increases the salinity of the water, and its resulting greater density carries it to the bottom where it may flow seaward if there is no sill at the mouth. To replace this loss, sea water flows in at the surface. This results in a salinity gradient, that increases with depth and with distance from the mouth with the isohaline surfaces sloping seaward (Fig. 7*b*). Salinities may exceed 100 ‰, or three times that of sea water. Around the margins of the lagoon the salinity may be even higher, and salt may be deposited on the shallow flats. Especially high concentrations occur in lagoons where the entrance is restricted by a bar or shallow sill, as in the Laguna Madre (Fig. 9), or the Gulf of Kara Bugaz, where salt is deposited on the bottom as well as along the shores (Twenhofel, 1932, p. 498–503; Clarke, 1924, p. 168, 169). Plankton and nekton may be carried into such an environment with the surface

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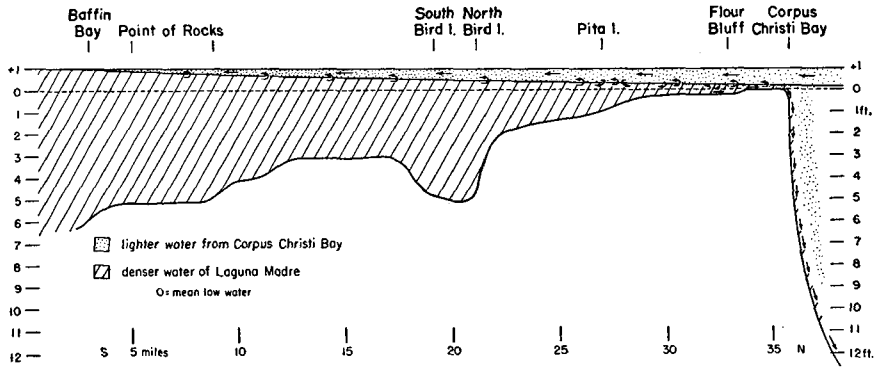

FIGURE 9.—*Schematic profile of salinity conditions in the Laguna Madre, Texas, at 1.0 tide* Before excavation of the Intracoastal Waterway. From Hedgpeth (1950)

current, although the organisms cannot survive in the regions of highest salinity into which they may be carried. Similarly, organisms may be brought in during seasonal or other periodic inflows of sea water and killed by the resulting increase of salinity in lagoons where hypersaline conditions are seasonal.

Some ecologists have considered that the waters of estuaries and lagoons have the same relative abundance of the various salts as sea water though with a greater or lesser total concentration (Howes, 1939). In most environments, however, the runoff usually has quite different salts from those of sea water, and in hypersaline environments the evaporation leads to differential deposition of salts. In general, in estuaries there is a higher ratio of carbonate and sulfate to chloride and of calcium to sodium than in normal sea water as a result of runoff, whereas evaporation causes these ratios to be lower than in normal sea water (Clarke, 1924, p. 63–121, 219–221; Schachter, 1950). In extreme examples, the composition of the water could be a significant ecological factor that would escape detection by the usual chloride titration or total salinity determination by hydrometer. Considerable dependence of land vegetation on the composition of ground water, and dependence of terrestrial mollusks on the composition of fresh water (Boycott, 1936), has been shown, and such may also be true of marine organisms (Nelson, 1947).

OXYGEN, CARBON DIOXIDE, AND PH: During the night, both plants and animals increase the carbon-dioxide content of the water by respiration, but during the daytime in a balanced system the plants convert this carbon dioxide back into oxygen (Sargent and Hindman, 1943). The oxygen content of water in estuaries and lagoons should, therefore, reach a minimum at night and a maximum during the day; measurements of carbon dioxide should be exactly opposite. In mangrove swamps and probably also in peat bogs this cycle may be partially masked by continuous loss of oxygen during decomposition of the rich deposit of organic matter (Orr and Moorehouse, 1933).

An example of the results of oxygen measurement in a large estuary is given by Newcombe *et al.* (1939) for an arm of Chesapeake Bay. They found a range for the surface waters from 85 per cent saturation before daylight to nearly 115 per cent in the late afternoon. Results obtained at San Francisco Bay show that this diurnal

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cycle can be masked by tidal changes (Miller *et al.*, 1928). In shallow water of the marshes, where the volume of organisms makes up a larger proportion of the volume of the water, the range is much greater. Nicol (1935), for example, found a variation in tide pools from about 40 per cent saturation at about sunrise to 200 per cent in the afternoon. In a Dutch *Zostera* bed Broekhuysen (1935) measured a range from zero oxygen (with hydrogen sulfide odor) at night to 260 per cent saturation of oxygen. Commonly, algae of the quiet shallow water are covered with numerous small bubbles of oxygen during the afternoon (Nelson, 1947).

The lower limit of dissolved oxygen adequate for normal respiration of many marine animals appears to be 1.0 or 2.0 ml per liter, although some forms are present even where the oxygen content is as low as 0.1 ml per liter. The latter animals either have a low oxygen requirement, such as *Arenicola*, a polychaete worm (Hecht, 1932), and some fish, such as sea bass (Baldwin, 1923), or they make only temporary stays in oxygen-deficient waters. Newcombe *et al.* (1939) have shown that the deeper waters of part of Chesapeake Bay usually contain near or below 2 ml per liter during the summer, when the salinity stratification of the water is so marked that it inhibits turbulent mixing of oxygen to depth. In industrial areas the situation is further aggravated by the dumping of chemically reduced wastes that take up oxygen from the bottom water during their oxidation (Olson *et al.*, 1941; Tully, 1949).

Norwegian fjords (Strøm, 1939) also have estuarine characteristics, though they are not true estuaries. The dilute surface waters contain oxygen and support commercial quantities of oysters grown on racks. The deeper waters contain no oxygen but instead have much hydrogen sulfide. When the surface water moves seaward owing to storm winds or to summer heating (Saelen, 1947), the deeper water rises, and the oysters are killed. Miyadi and Habe (1949) reported an interesting case of oxygen deficiency in Japan, where Yosanaikai Lagoon became practically isolated from the ocean by natural building of a sand bar. Inflowing streams diluted the surface water, and the sea water at the bottom could not be replaced because of the shallow barrier, so it became stagnant and devoid of oxygen. An abundant fish population was destroyed. Deepening the opening by dredging proved successful in restoring circulation and allowing repopulation by fish. A somewhat similar example in a Scottish loch was described by Raymont (1949).

Few measurements of total carbon dioxide are available because the analysis is rather time consuming, but Emery (1946), working with still shallower tide pools, found a range of carbon dioxide from 94 ml per liter before sunrise to 43 ml per liter in the late afternoon.

A close approach to the variation of carbon dioxide is that of the pH since, roughly speaking, the higher the content of carbon dioxide, the higher is the concentration of carbonic acid and the lower the pH. Thus, photosynthesis should tend to make the pH low at night and high during the day. As pH is an easy factor to measure, there are many such determinations in the literature, but most of the diurnal series are incomplete owing to a general reluctance to make observations throughout the night. Actually, some erroneous conclusions regarding pH tolerance have come from the use of only daytime observations. A variation of 0.2 pH unit from low at night to high at day was found by Moberg (1927) at the entrance to Mission Bay,

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California, in contrast to a variation of only about 0.05 pH unit for the open sea. In shallower water of Newport Bay the range was one unit (7.6 to 8.6), agreeing with the general results obtained by Powers (1920) in a small lagoon of Puget Sound. Nicol (1935), working on a British salt marsh, also found a range of about one pH unit. A diurnal range of 1.5 pH unit in tide pools only a few inches deep was noted by Emery (1946) in southern California and by Gail (1920) in Washington. Although these tide pools are in rock, their water is influenced by biochemical processes similar to those of marshes. The tide-pool values range from about 7.5 to 9.0, departing from the normal pH of sea water of 8.0 to 8.2. For a detailed discussion of CO_2, pH, etc., *see* Chapter 10.

In addition to the diurnal cycle of oxygen, carbon dioxide, and pH there is a seasonal cycle. During the summer, when the sunlight is most intense, there is more plant growth in lagoons and estuaries, producing a greater range of these values. Such has been found at Port Erin Bay, Isle of Man, by Bruce (1925), in a lagoon near Essex, England, by Howes (1939), and probably also at Chesapeake Bay by Newcombe *et al.* (1939). Nicol (1935) found an additional intermediate irregular variation that she related to hours of sunshine. Also, rain dilutes the water, reducing the alkalinity (approximately the carbon dioxide) as does runoff from a region of only slightly calcareous rocks, whereas runoff from a region of limestone increases the alkalinity relative to chlorinity (Lucas, 1929; Brust and Newcombe, 1940).

Perhaps the most significant aspect of the oxygen distribution is its decrease with depth. Near the bottom of the photosynthetic zone there is a depth at which oxygen production is exactly balanced by oxygen consumption in respiration of the plants (Ketchum, 1951a); *see also* Chapter 6). Below the photosynthetic zone plants are unable to manufacture any oxygen, but animals still use it in their respiration, liberating carbon dioxide. Similarly, aerobic bacteria oxidize hydrocarbons of the bottom, reducing the oxygen and pH and increasing the carbon-dioxide content of the deeper waters. In an estuary or lagoon where fresh water flows out above sea water, there is only very slow replacement of the bottom water and that by subsurface water from the open sea, itself sometimes relatively low in oxygen. Accordingly, the bottom water of this kind of estuary or lagoon may become quite stagnant and inhospitable to oxygen-consuming life (Strøm, 1939; Saelen, 1947; Nash, 1947; Miyadi *et al.*, 1950b). A less extreme oxygen decrease with depth occurs in Alberni Inlet, a small fjord of western Canada (Tully, 1949). Organic remains which fall to the bottom in such estuaries stand a good chance of being buried without undergoing much decomposition, giving rise to sediments of high organic content.

Many hypersaline lagoons should have water relatively high in oxygen because, as in the Mediterranean Sea, the bottom water has only recently sunk from the surface because of increased density through evaporation. If the salinity is not too great, bottom-living organisms such as scavengers and aerobic bacteria can exist, so the organic content of the bottom is not apt to be very great. Other lagoons and estuaries of this type have a sill depth that is too shallow to permit easy exit of the bottom water. If there are marked seasonal variations in the rate of evaporation, a density stratification should exist, and the bottom waters should become

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stagnant and devoid of oxygen. Unfortunately, oxygen data for hypersaline estuaries and lagoons are not available. In marginal cases, particularly where the water is shallow, one might expect that the normal increase of pH and oxygen content during the day, and the reverse at night, would mask any secular change, and such is indicated by a few measurements by ZoBell and Feltham (1942) on the marshes of Mission Bay, California.

Much remains to be learned of the biochemical changes in the water of estuaries and lagoons, and the effects of the changes on the organisms and bottom sediments. Only enough scattered information is now at hand to provide a sketchy picture of the environments.

TURBIDITY: The turbidity of the surface waters, particularly in normal estuaries and lagoons, varies widely throughout the year and reaches a maximum during floods of the rainy season. At all seasons there is a gradual decrease of turbidity (increase of transparency) with distance from the river mouth. In Chesapeake Bay, for example, Olson *et al.* (1941) found the same light intensity at 3 meters in the open bay as at 0.3 meter near the Patapsco River mouth. Similar qualitative relationships have been observed in the estuaries of San Diego Bay and San Pedro Bay in California, Jade Bay in Germany, and elsewhere. The effect of turbidity is, of course, to decrease the thickness of the photosynthetic zone, thereby decreasing the abundance of phytoplankton and attached algae. Settling of the turbid suspension also forms a thin layer of silt and clay on the bottom that may prevent the attachment of molluscan spat. A similar layer on algae tends to suffocate them (Dahl, 1948, p. 133).

An important source of sediment for making the water turbid, other than stream load, is the tidal channels; consequently, the water over a tidal flat is likely to be most turbid just before high tide, whereas that in the deep water of an estuary or lagoon is most turbid at or before low tide and least turbid at high tide (Francis-Boeuf, 1941).

Plankton organisms occasionally become so abundant that they color the water red, yellow, or green and considerably increase the turbidity, thus limiting their own abundance. In some estuaries and lagoons so much tannic and other organic acids may be produced from organic decomposition that they impart a brown or tea color to the water. This phenomenon occurs in temperate and polar as well as in tropical waters, and it also limits the depth of photosynthetic activity.

NUTRIENTS: In general, the nutrient cycles of estuaries are similar to those of shallow coastal waters (Chapter 11), but the influence of land drainage is more immediately apparent. In various studies of the phosphate content of Chesapeake Bay waters it was found that phosphorus was highest in the surface water at night when there is no photosynthetic activity and at times of turbid water when light penetration is low (Newcombe and Brust, 1940; Newcombe *et al.*, 1939; Nash, 1947). The phosphorus content increased with depth and became exceptionally high in the deeper water where there was insufficient light for plants and insufficient oxygen for most animals (Rochford, 1951a; 1951b). Much of this phosphate was released during the breakdown of organic materials in the sediments by anaerobic bacteria (Stephenson, 1951). However, phosphorus also increased toward the head of the

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estuary, showing that it was largely contributed by streams. This relationship is the same as that found by other workers off the Mississippi River (Riley, 1937), off the Fraser River (Lucas, 1929), and in Varna Bay on the Bulgarian coast (Caspers, 1951). As a result of contribution by the streams, the phosphorus at the head of the estuary and in the bottom waters ranges up to 2.0 milligram-atoms per cubic meter, in contrast to only about 0.1 for the surface of the open ocean. Even higher values have been found in estuarine channels (Howes, 1939). The characteristic estuarine phenomenon of concentration against the gradient may be in part responsible for the concentration of phosphorus, especially in estuaries where the contribution of land drainage is low, as in the Australian estuaries studied by Rochford. One would expect phosphorus to be as low or lower than that of the open sea in a hypersaline environment where the principal source of water is from the phosphorus-poor upper layer of the sea. While such appears to be the case in the Sivash (Zenkevich, 1947), the tendency of phytoplankton to take up excess phosphorus in the water may interfere with accurate determinations in such a circumscribed environment, where there is a large seasonal growth of phytoplankton.

The phosphate cycles in estuaries are complex and as yet incompletely understood but in general are adequately represented by Rochford's diagram (Fig. 10). The existence of an active release of phosphorus from the bottom at the mud-water interface has been utilized by Rochford (1951c) to increase oyster production in Australian estuaries by adding superphosphates to the bottom. According to Gneri and Angelescu (1951) bottom feeding or ilyophagous fish may be capable of extracting 1 gr of phosphorus from 100 gr of mud, thus returning it to the system

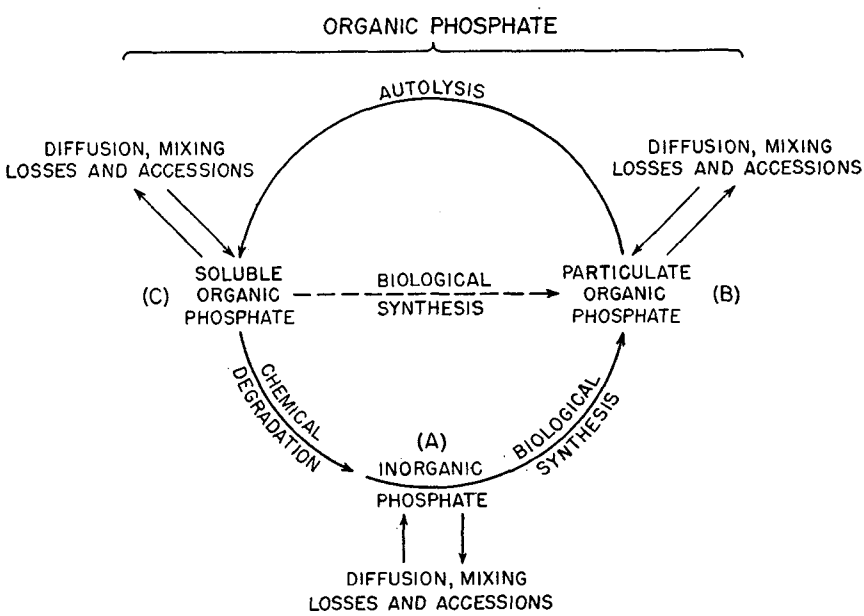

FIGURE 10.—*Simplified cycle of phosphorus transformation within a relatively isolated water mass*
After Rochford (1952)

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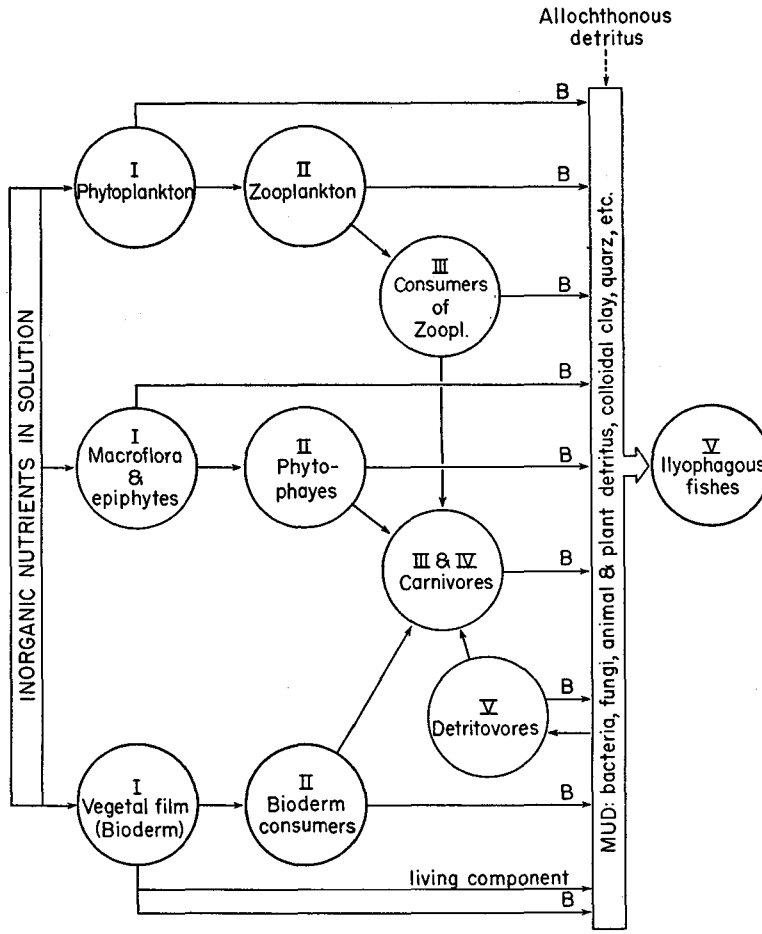

FIGURE 11.—*Diagrammatic representation of the food chain of ilyophagous fishes*
After Gneri and Angelescu (1951)

and playing a more active part than had been expected in the cycle of an estuary (Fig. 11).

Nitrogen in the sea is present (in order of decreasing abundance) as organic matter, nitrate, nitrite, and ammonia. Little information, however, is available regarding the abundance of these forms of nitrogen in estuaries and lagoons, except that they, like phosphate, appear to be more abundant than in the surface water of the open sea. These areas also show a greater annual variation of nitrogen than does the open sea (Phifer and Thompson, 1937). The resulting concentration of plankton in the near-shore brackish high-phosphate and nitrate waters off the Mississippi Delta is well shown by the greater abundance of chlorophyll there than farther offshore (Riley, 1937). Nitrogen is low in the Sivash (Zenkevich, 1947) and probably also in other hypersaline environments.

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Silica, as silicate, has been found off the Fraser River and in Chesapeake Bay in amounts many times greater than in the surface water of the ocean. There is also a well-defined increase toward the headwaters to values as great as 120 milligram-atoms per cubic meter, in contrast to less than 10 for the open sea. This is in general agreement with the well-known fact that rivers generally contain a much higher concentration of silica than does the ocean (Clarke, 1924, p. 138). Possibly some of the load of silica is deposited by rivers when they enter the estuaries and lagoons, giving rise to masses of gel on or in the bottom, such as those on the Mississippi River Delta that were briefly described by Russell (1936, p. 143), though much of the silica is rapidly utilized by diatoms.

The relatively high concentration of nutrients in estuaries and lagoons is evidently the result of nearness to the supply provided by the land runoff and the continuous replacement of nutrient-rich water to growing plants. The continuous supply of nutrients and the presence of shallow bottom in the photosynthetic zone lead to concentrated life off the rivers. This abundant life also contributes much organic matter to the bottom, giving rise to organic shales where accumulation takes place under anaerobic conditions.

The high organic content and numerous dead shells in brackish water off rivers have led to an erroneous belief that such areas are inhospitable to life. Yet, as Brockmann (1929; 1937) and others have recognized, it is the very fact that these areas are favorable to life that permits the high population required for rapid death and entombment of organisms.

II. Biological Aspects*

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1. THE COLONIZATION OF ESTUARIES

As regions of transition and sharp gradients, estuaries support a fauna recruited principally from the sea, but with a few components from fresh-water environments. The various attempts to classify the fauna (and flora) of estuaries have emphasized this composite origin (Table 2). Several writers (*see* Pearse, 1950) have commented upon the monotony of estuarine populations, and, while it is true that the number of species in estuaries, as compared with the sea, is greatly reduced, the number of individuals is often large. Consequently few students have been willing to agree with Annandale (1922) that estuaries are "the last refuge of spent races." Such a view ignores the importance of estuaries, especially to the economy of neritic subtropical regions, as nursery and feeding grounds.

To survive in an estuary an organism must adapt to a wider range of fluctuations in environmental factors than in the sea or fresh water. Optimum development or successful colonization in an estuary may well depend on the interaction of several

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TABLE 2.—*Classifications of the faunal components of estuaries*

Redeke (1922) (Holland)	Robson (1925) (Thames)
Oligohalinophil	1. Permanent indigenous element
Mesohalinophil	2. Seasonal migrants
Polyhalinophil	3. Stragglers

Spooner and Moore (1940) (Tamar)	Panikkar (1951) (S. India)
A. Essentially marine	1. True estuarine species
B. Estuarine, but occasionally marine	2. Marine, euryhaline species
C. Predominantly estuarine	3. Fresh-water, salt-tolerant species

Day (1951)
(S. Africa)

A. Fresh-water component
B. Stenohaline marine component
C. Euryhaline marine component
D. Estuarine component
E. Migratory component

factors, as Day (1951) contends: "The point to be emphasized . . . is that the distribution of animals in estuaries cannot be based on any single factor of the environment." A diagram of the selective action of factors in combination, especially as applied to marine organisms on a nontemporal basis, was devised by Day (Fig. 12). Nevertheless, the limits of distribution may be controlled by any one of several factors, and excess variations in salinity, temperature, or turbidity have often wiped out populations in estuaries.

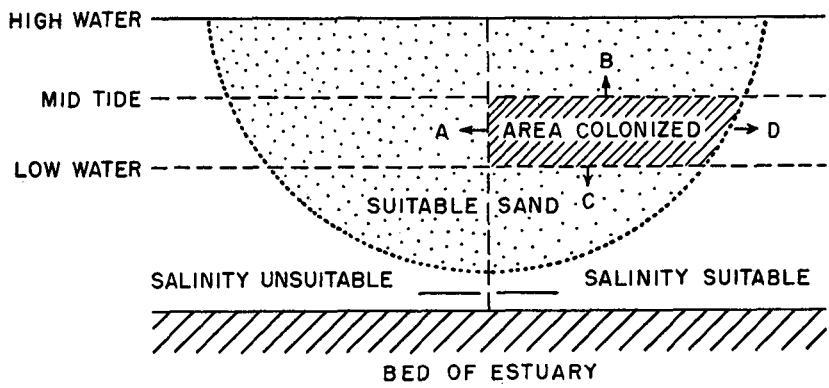

FIGURE 12.—*Diagram of the action of limiting factors in an estuary*
After Day (1951)

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Such a concept of environmental restriction as proposed by Day applies best to recent immigrants to estuaries or to organisms that are still essentially marine in their environmental requirements. In contrast to such organisms are those that seem to require the fluctuations of the estuarine environment for their optimum development; these might be considered the true estuarine organisms. Unfortunately there is little physiological evidence to support this.

Although the variation of environmental factors in estuaries may be large, it is nevertheless a permanent feature of the estuarine environment, and thus the organisms which become adapted to the fluctuations in estuaries have found an environment which may actually be comparatively stable in the geological sense, since the range of environmental factors may be greater than the secular change of an environment without such short-period fluctuations. That is, the aggregate rate of change in the estuarine environment may actually be less than in the geographical province in which it occurs over the same period of time. The significance of this from the viewpoint of maintaining stocks at a low evolutionary rate was recognized by Simpson (1944):

> At one end of the sequence are animals that tolerate almost no alteration of environmental conditions, but live in a virtually unvarying environmental niche, and at the other end are animals that tolerate extreme cyclic variations in temperature, salinity, and so forth, and live on environments characterized by such cycles. Thus, an animal that became adapted to continuous cold during the Pleistocene would either become extinct or rapidly evolve a different physiological adjustment in post-Pleistocene times. But an animal which developed wide temperature tolerance, which is no less an adaptation than is adjustment to a particular part of the temperature range, would tend to continue unchanged.

A diagrammatic presentation of this concept of environmental constancy is suggested in Figure 13.

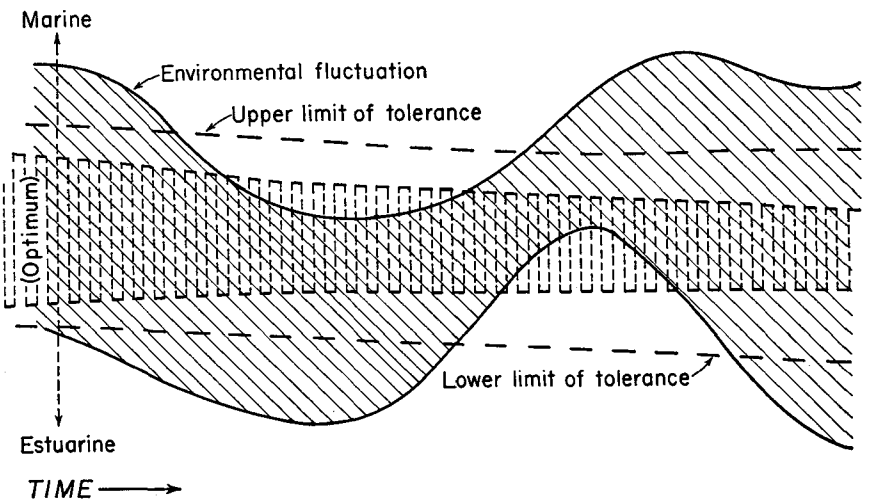

FIGURE 13.—*Diagram showing suggested relationship between optima, range of tolerance, and range of environmental fluctuation in an estuarine environment, trending in this case toward narrowed tolerance*
From Hedgpeth (1953)

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Such a concept of the permanency of estuarine conditions carries with it the idea that the typically estuarine species are conservative forms with a long history. This is certainly true of such organisms as oysters, some of which seem to be estuarine types derived from Cretaceous stocks, and gastropod stocks of the Neritacea which can be traced back to the Triassic. A conspicuous example of the persistence of an estuarine form is that of *Limulus*. However, it might be argued that this concept is invalidated by the small number of truly estuarine species; Monod (1926) considers these species to be recent immigrants or recent descendants of nonestuarine ancestors. Euryhalinity is probably a physiological trait not easily come by and, once attained, is very conservative. This is suggested by the work of Karpevich (1947) with the genus *Dreissena* in the Caspian, as he concluded that the adaptability of these typically brackish-water mollusks to salinity changes "is a characteristic that is constant for a species or even throughout the genus." In a study of the distribution of euryhaline fishes Gunter (1942) found that families of fishes occurring on both sides of North America had euryhaline species on both sides and that "euryhalinity runs in families."

Euryhalinity, then, may be a physiological characteristic not of a species or a genus alone, but of a phyletic stock, and, while Monod's suggestion is to some degree correct (especially for the colonization of small, comparatively recent estuaries), it should be amplified to indicate that this repeated colonization is from the same of similar stocks of organisms. There seems to have been no striking change in the stocks giving rise to estuarine species, although there is some suggestion that the depletion of one such stock is followed by a replacement from a similar stock. Such an example is to be found in the decapod Crustacea in the families Atyidae and Palaemonidae. The atyids appear to be an ancient family, possessing no near-marine relatives and now exclusively fresh water in habit. Ortmann (1902) suggested that the atyids or their progenitors accomplished their migration from the sea possibly in Jurassic time. The palaemonids, on the other hand, occur in fresh-water, estuarine, and marine habitats and appear to be in the process of migration from the sea. Several species of *Palaemonetes* are among that small group of typically estuarine animals, while some species of *Macrobrachium* are characteristically fresh-water inhabitants and, only occasionally invade estuaries (Fig. 14).

The isolation of certain primitive animal types suggests that these forms have left the ocean at remote times. For example, the nearest relatives of the syncaridean crustaceans occur in Carboniferous rocks, while the living species (e.g., *Anaspides*) occur in Tasmania, New Zealand, and eastern Europe. In their migration from the sea they may have been preceded by the ancestors of the present fairy shrimps (Anostraca, Notostraca, and Conchostraca), and the colonization of alkaline waters and inland brines by some of these forms is probably a secondary adaptation.

The wide tolerance of estuarine organisms explains their ability to establish themselves in estuaries all over the world. At the same time, they are probably unable to compete with marine organisms in the sea, so their dispersal via the sea is limited by the ecological competition of marine organisms. Since the advent of man, and especially since rapid means of transportation have been used, many estuarine or euryhaline species have been inadvertedly assisted in their dispersal

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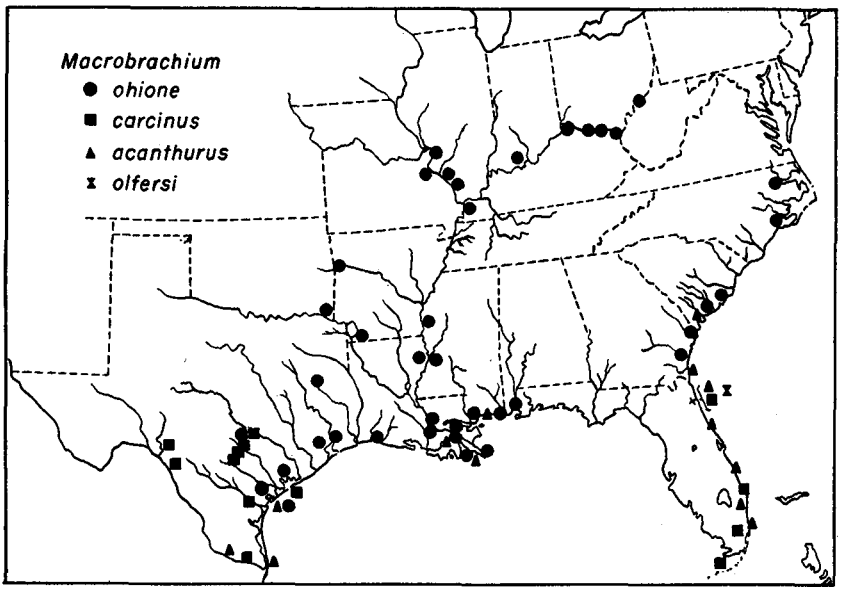

FIGURE 14.—*Distribution of the euryhaline genus* Macrobrachium *in estuarine and fluvial waters of the United States*
From Hedgpeth (1949)

to new estuaries.[1] The factor of ecological competition has also played its part in the development of another characteristically estuarine group, the seasonal migrants. That is, it is not only the food supply of estuaries, but the freedom from competition enjoyed by the juveniles (which seem to be more tolerant of dilutions than their elders—*see* Chapter 7), that enables a species to utilize estuarine waters as nursery grounds. Conversely, the lack of suitable food may keep some highly successful animals from colonizing estuarine waters; Sollas (1884) long ago suggested that this might be the reason that cephalopods have not been able to flourish in estuarine waters or make the transition to fresh water.

A suggestive analogy for the dispersal of estuarine organisms may be drawn from the distribution of fresh-water organisms. Many fresh-water copepods, gastrotrichs, and algae are almost world-wide in occurrence, although the difficulty of dispersal via land or air would seem to be greater than that posed by the sea to a euryhaline organism. But fresh-water organisms have developed spores and resting stages which are more satisfactory vehicles for long distances than are the larval forms of estuarine organisms. Thus, the distribution of fresh-water organisms has been the result of the dispersal of species, whereas that of estuaries has been a matter

[1] Human intervention seems to be the principal cause for the colonization of the Salton Sea in southern California by a suite of marine organisms (Rogers, 1949); some of these were brought over from San Diego in an effort to provide a forage base for food, while the barnacle *Balanus amphitrite* seems to have made its way on seaplane floats. Recent efforts to stock the Salton Sea with more desirable fish have not yet succeeded, perhaps because of the high temperatures of the water. The presence of *Balanus amphitrite*, *Brachidontes minimus*, and *Cardium edule* (among other species) in the isolated Birket el Gessabaia near Siwa Oasis, some 150 miles from the Mediterranean, has been attributed to birds (Omer-Cooper, 1948). For a discussion of other examples *see* Chapter 13.

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of family or generic groups. It is interesting to note how rapidly the Chinese mitten crab, *Eriocheir sinensis*, has spread from Western Europe to the Black Sea, once it was transported from Asia (Panning, 1933; 1939), and the spectacularly successful establishment of the striped bass in the Sacramento River of California from the Atlantic seaboard following an initial plant of 125 individuals. The most recent example of such transference is that of *Elminius modestu* from Australasian waters to Britain, where it has become a serious oyster pest (Allen, 1953). Fishes which are able to travel in the sea as adults have, apparently, a somewhat better chance to disperse than do those groups of organisms whose dispersal is accomplished in juvenile or larval stages. At least three of the groups of fishes recognized by Myers (1949) on the basis of their salt tolerance have evidently managed to attain their present distribution via the sea (and are thus poor indicators of past land connections); these are the vicarious, complementary, and diadromous groups. The fact that these groups are composed of certain families suggests again that we are dealing with euryhaline stocks capable of colonizing estuaries and, eventually, fresh water.

One of the classic hypotheses for the origin of estuarine and fresh-water faunas was proposed by Von Martens (1858), who suggested that migration from the sea occurred in tropical regions where the temperatures of river and sea water were nearly uniform. In the summary of the CHALLENGER Reports, Murray (1895) suggested that estuarine and fresh-water regions were populated as a result of shoreward drifting of pelagic larvae or organisms living in the "mud line" at the edge of the continental shelf. Sollas (1884) had suggested that fresh-water faunas originated by isolation of parts of the sea which subsequently became fresh, and that colonization was successful to the degree that the organism had delayed its development—that is, that organisms that hatched as near-adults rather than as small, feebly swimming larvae which then had to undergo growth and metamorphosis were better adapted to colonize estuaries and fresh water. This was approached somewhat differently by J. Needham (1930) who pointed out that the small, yolkless eggs characteristic of many marine invertebrates were dependent upon the external medium for many of the essentials for their later development and that the production of large eggs with stored nutrients was of great advantage to the organism in the more dilute environment of estuaries and fresh waters.

Such physiological adaptations may be preceded by structural modifications which enhance the survival of an organism in dilute salinities. A case in point may be found among the gastropods. Primitively the gastropods had paired kidneys, and the gonad discharged through one of the kidney ducts. Such an arrangement prevents the development of the sexual apparatus necessary to internal fertilization, and those mollusks which retain both kidneys, and in which fertilization is external, are restricted to the sea. When a kidney has been lost, the mollusk is able to develop the sexual apparatus leading to internal fertilization and the production of large eggs, or a brood chamber, and colonization of estuaries and fresh water becomes possible (Yonge, 1947).

There are several indications that the invasion of estuaries is easier in warmer waters; the most important is the comparative richness of the fauna of tropical and subtropical estuarine waters as compared with those of high latitudes. Panikkar

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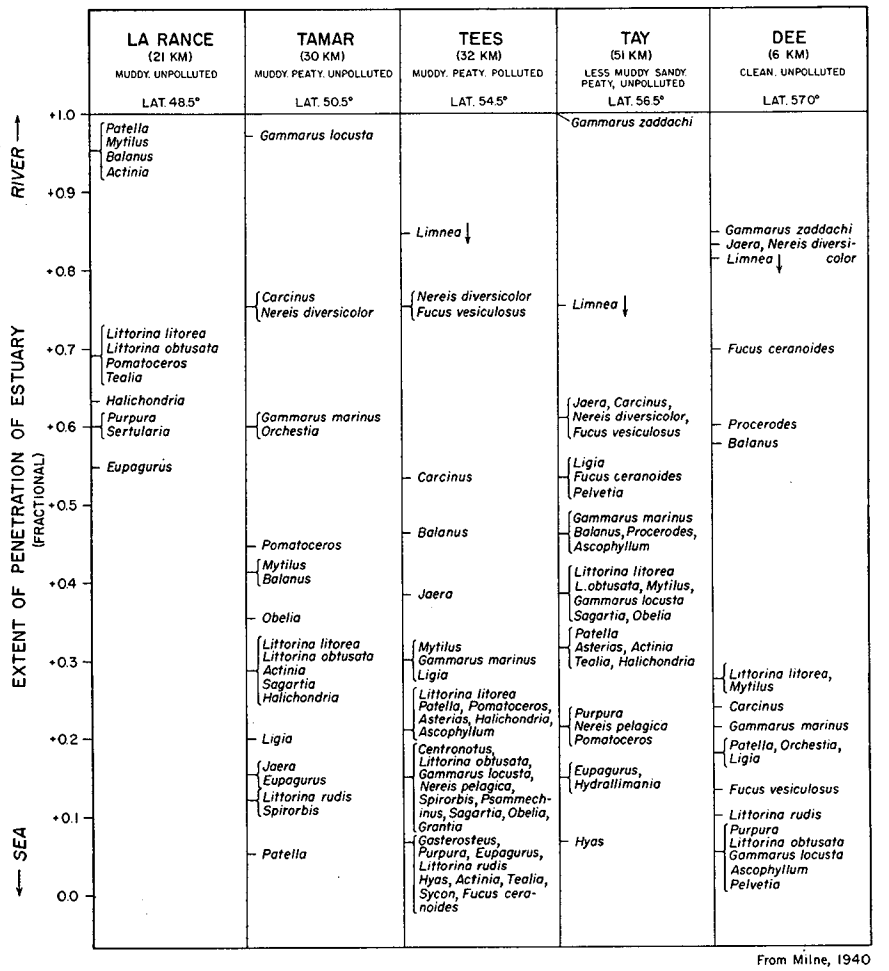

FIGURE 15.—*Extent of penetration of various organisms in various estuaries at different latitudes* After Milne (1940)

(1951) suggests that this may be correlated with an increased osmoregulatory ability in higher temperatures. Another line of evidence is the apparent lower tolerance of certain species for fresh water in the northern parts of their range; Segerstråle (1949; 1950) mentions a number of animals which are not found in fresh water in the Baltic region although they have fresh-water races farther south. In comparing the penetration of the same species in various estuaries in France and England, Milne (1940) found a greater penetration of the same species in the French estuary, suggesting a temperature effect (Fig. 15).

The origin of estuarine organisms by the relict method, the cutting off of arms of the sea, is a hypothesis which must be received with some caution. While such regions as Lake Baikal and the African lakes are classic examples with faunas that

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have evolved in isolation, the striking similarity of some comparatively recent "relict species" in various parts of the world suggests not the production of the same species by isolation in widely separated regions, but the development of a characteristic form associated with environmental conditions, such as the varieties of *Artemia* in different brine concentrations, and of rotifers (*Brachionus*) in silicate concentrations (Whitney, 1916). The example of a possibly postglacial relic, *Mysis relicta*, originating from a marine species, *M. oculata*, may be such a case. It is difficult to agree with Gurney (1914) that the presence of *Mysis relicta* in Europe and the Great Lakes indicates a simultaneous and independent evolution of the two species; Olofson (1918) considered *relicta* to be an ecotype, and Banner (1954) doubts that it can be considered a "good species." Smith (1953) suggests that there may be physiological races of the same species (*Neanthes lighti*) in different parts of the same estuary.

2. THE ESTUARINE FACIES

A. FAUNA

Of the various components of the estuarine facies, that from fresh water is the smallest and most restricted in an estuary. Among the invertebrates, the principal contributions from fresh water consist of various insect larvae (and some adult forms), oligochaetes, and a few pulmonate mollusks. Such limnic elements are more conspicuous in the comparatively stable environment of the Baltic Sea (See Remane, 1950, and Chapter 24.)

In the lower part of an estuary the fauna is predominantly marine; it consists for the most part of species occurring in the neighboring seas. Of these, the littoral (or intertidal) species, already accustomed to daily changes in their environment, are the most obvious. The invasion of estuaries by intertidal animals may be more characteristic of regions where wave action is not so great as, for example, on the south African coast, where Day (1951) found a comparatively limited penetration of such species. Some forms, however, such as littorines and grapsoid crabs, extend well inside the estuary and maintain their usual levels with reference to the tides. Reduced wave action limits the occurrence of many animals even where salinities are not greatly reduced and turbidities are not extreme. In Tomales Bay (California) for example, where fresh water inflow is comparatively small and salinities are relatively stable, such a high intertidal species as *Acmaea scabra* disappears long before *Acmaea limatula*, a species of lower levels.

The opposite effect is evident in estuaries where there are both tidal action and salinity variation. Here the salinity fluctuation is greater in the lower levels of the estuary, since the more saline water is brought in by the tidal prism and for the most part carried out again, and we find that intertidal or high-level species, exposed to less salinity variation, can penetrate farther upstream than the species of deeper waters, with the exception of those living in burrows. This may be due in part to the stronger tidal currents which prevail at the lower stages of the cycle, as suggested by Spooner and Moore (1940).

In general, penetration of estuaries (and also of the Baltic) by marine and, conversely, fresh-water organisms is a function of the rate and magnitude of tidal change rather than of the actual salinity gradient. That is, marine organisms occur much farther upstream, and fresh-water organisms much nearer the sea, in an estuary where tides are small and the gradient relatively stable, than in an estuary with a large tidal range and rapidly changing gradients. This means that the minimum number of species is to be expected in that part of the estuary where the salinity variation is greatest (Fig. 16). A corallary to this is the greater penetration of marine species in estuaries of lower gradient, although the salinity may also be lower, but more constant, as in Randers Fjord (Denmark), where tidal action is greatly reduced (Fig. 17).

Many of the motile invertebrates and vertebrates found in estuaries come in with the tide and leave with it, or at least move downstream from the head of an estuary with the tide. In addition to such wanderers and stragglers, many of which invade the estuaries in pursuit of food, there are

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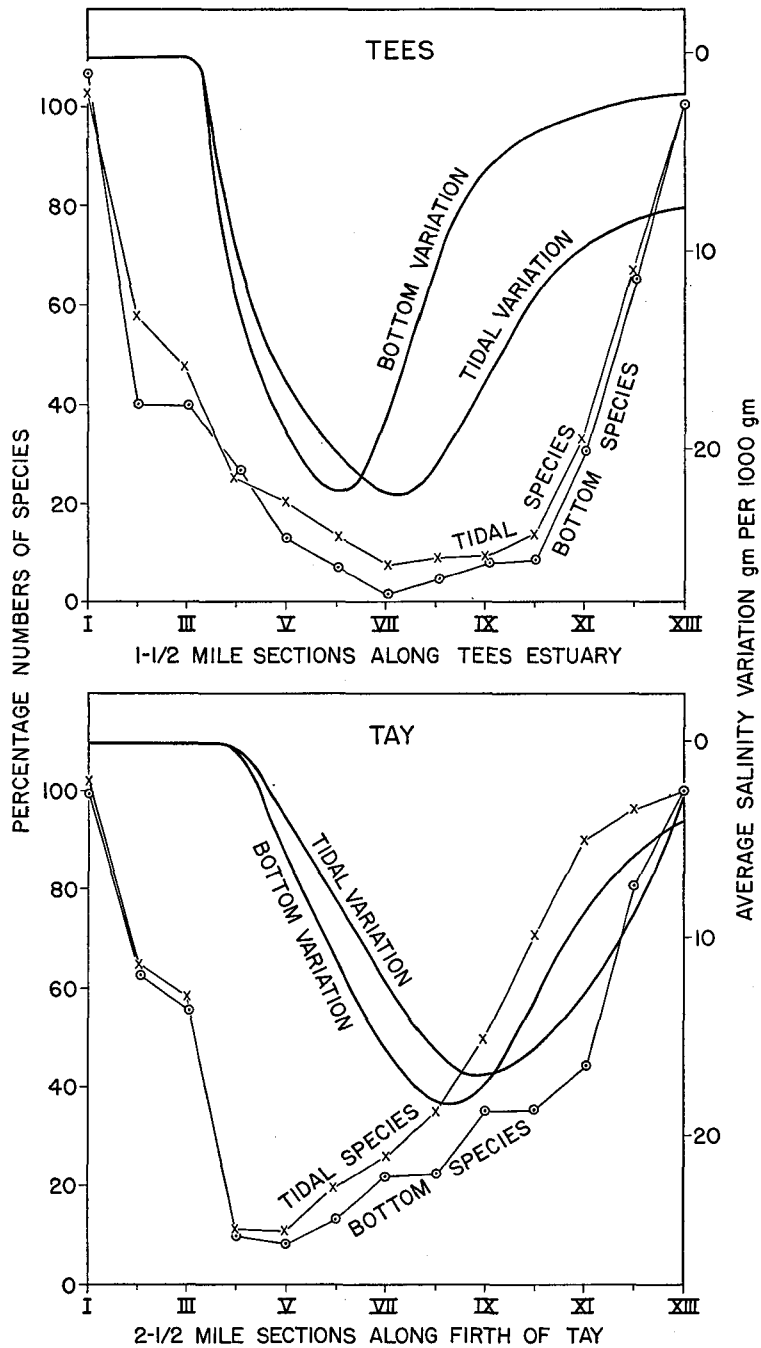

FIGURE 16.—*Average salinity variations and percentages of species along the tidal and bottom areas in the Tees estuary and the Firth of Tay*
After Alexander, Southgate, and Bassindale (1935)

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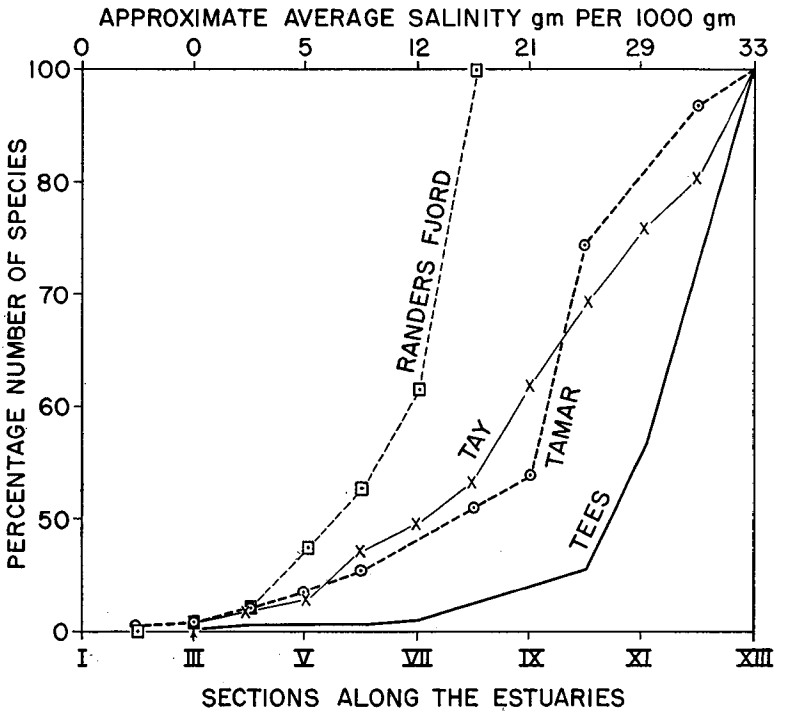

FIGURE 17.—*Distribution of marine animals in Randers Fjord, the Firth of Tay, and the estuaries of the Tamar and the Tees*
After Alexander, Southgate, Bassindale (1935)

the seasonal migrants. The seasonal migrants include those animals entering the estuary to spawn (*e.g.*, certain fish such as the striped bass), those passing through the estuary on the way to spawning grounds in rivers or the sea, and those migrating as young into an estuary to feed.

The utilization of estuaries as nursery grounds is especially pronounced in the middle latitudes, where many fishes and such motile invertebrates as certain species of penaeid shrimp and portunid crabs depend to a large degree upon the resources of the estuary for growth and maintenance of their populations.

It is, however, the estuarine component that determines the estuarine facies. It is possible to recognize the estuarine occurrence of some widely ranging forms by their reduced size or to follow an estuary gradient by the reduction in number of marine-derived species, as Gunter (1947) has suggested, but this is not always certain, as the results of local differences in nutrition or substrate may resemble the effects of temperature, salinity, and turbidity conditions prevailing in an estuary.

It is difficult to express the quantitative relationships of the various faunal components since both numbers of species and their populations should be considered in such an expression. The best-known representation of the quantitative distribution of species in estuarine waters is that of Remane (1934). This famous diagram (Fig. 18A) is, as Hiltermann (1949) said, an idealized abstraction, and it has been criticized (especially by Dahl, 1948) because no scale is placed on the ordinate, and for the arbitrary separation of marine and brackish environments at 18‰. Nevertheless, it does represent the essential distribution within an estuary, and such independent investigations a the Tees River survey have confirmed the general utility of the diagram (Fig. 18B).

This picture of decreased number of species near the transition region of an estuary also appears to be true for the numbers of individuals (populations). The preliminary work by Caspers (1948;

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1954) on the comparative productivity of regions in the Elbe estuary indicates that productivity, like the number of species, is lowest in the transition between marine and fresh-water regions in the same gradient (Table 3). This is also indicated by the composite summary provided by Lundbeck (1926), from which Table 4 has been compiled. However, these conclusions are based upon bottom organisms. Organic production in the overlying waters of an estuary may be rather high in spite of the reduction of photosynthesis by turbidity, as a result of the concentration of elements from the outside. This seems to be the situation in the Bay of Fundy, for example (Huntsman, 1952).

In his summary of the status of brackish-water studies Redeke (1933) listed the characteristic "mesohalinophillic" animals of various European estuaries (Table 5). These he considered to be the indicator species of true brackish-water conditions. Ekman (1953, p. 117-118) has added a few names to the list and attributes the widespread European distribution of these species to a prehistoric, brackish Sarmatic sea. Some of these species, or almost indistinguishable relatives of them, occur in many parts of the world. *Cordylophora lacustris* (or *C. caspia*), for example, occurs at various

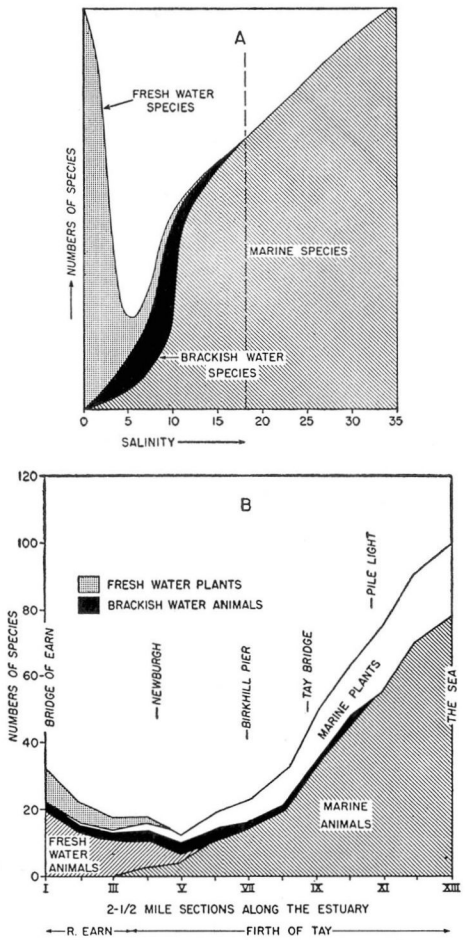

FIGURE 18.—*Composition of estuarine environments*

a. Remane's diagram of the comparative composition of fresh-water, brackish, and marine species in the Bay of Kiel (After Remane, 1934); b. Composition of fauna and flora along the Firth of Tay (From Alexander, Southgate, Bassindale, 1935).

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TABLE 3.—*Comparative numbers of species and weights per square meter as related to the salinity gradient in the Elbe Estuary*

Compiled from Caspers (1958)

	n/m^2	g/m^2
	Sea water	
Mollusks	1,025	5,970
Polychaetes	19,000	78
Crustacea	75	20
Totals	20,100	6,068
	Brackish water	
Corophium	6,500	24
Tubificids	500	
Polychaetes	25	13
Totals	7,025	37
	Fresh water	
Tubificids	55,000	80
Chironomids	27,000	32
Pisidium	4,500	31
Totals	86,500	143

TABLE 4.—*Comparative rough weights of bottom animals (g/m^2) in fresh, brackish, and marine waters*

Compiled from Lundbeck (1926)

Minimum	*Average*	*Maximum*
	Fresh water	
1.23	30.31	128.48
	Brackish water	
1.31	16.03	168.39
	Marine	
9.70	304.24	2878.03

harbors along the Atlantic coast of North America from Gaspe to the Panama Canal, and in San Francisco Bay on the Pacific coast, and in the southern hemisphere. Among the species not included in Redeke's list to be regarded as cosmopolitan estuarine species are the anemone *Diadumene* or *Aiptasiomorpha luciae*, the serpulid worm *Mercierella enigmata*, and the tubiculous amphipod *Corophium acherusicum* (Fig. 19).

In addition to such widely distributed species, there are genera of equally wide distribution; *Palaemonetes* has species in estuaries all over the world (and in fresh waters), and the bryozoan *Membranipora* has cosmopolitan estuarine representatives. Species of Mysids and sphaeromid isopods are also characteristically estuarine, but many have closely related marine species (Table 6). As already suggested in the case of *Mysis oculata* and *M. relicta*, this occurrence of pairs or groups of closely related species in the sea and in estuaries or fresh water may indicate that we are dealing with environmental variations as indeed are recognized for *Gammarus zaddachi*. (*See e.g.*, Segerstråle, 1950.) In many of these cases the taxonomy is difficult, and the specialists are uncertain or disagree as to the proper names to be used.

A somewhat similar diagram, which, however, does not indicate the approximate salinity ranges, has been published by Stock and Mulder (1954), who call such pairs of species "ecological twins".

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TABLE 5.—*Distribution of certain animals in estauries and brackish waters of northern Europe*
From Redeke (1933)

	Firth of Forth	Norfolk	Holland	Elbe-Astuar	Randers Fjord	Schwentine-Mündung	Untere Warnow	Ryck-Mündung	Frisches Haff	Finland
Coelenterata										
Cordylophora caspia (Pall.)	−	+	+	+	+	+	+	+	+	+
Annelida										
Nereis diversicolor Dum	−	+	+	+	+	+	−	+	+	+
Copepoda										
Eurytemora affnis et *hirundoides*	+	+	+	+	−	+	−	[1]	+	+
Acartia bifilosa Giesbr	+	+	+	−	−	+	−	+	+	+
Mesochra lilljeborgi Boeck	+	+	+	−	−	−	−	+	−	−
Nitocra spinipes Boeck	+	+	+	−	−	−	−	+	+	−
Laophonte mohammed Bl. et Rich	−	+	+	−	−	−	−	+	+	−
Tachidius brevicornis Lillj	+	+	+	+	−	+	−	+	+	+
Tachidius littoralis Poppe	+	+	+	+	−	−	−	+	−	+
Ostracoda										
Cyprideis littoralis (Brady)	+	+	+	−	−	−	−	+	−	−
Cirripedia										
Balanus improvisus Darw	+	+	+	[2]	−	+	+	+	+	+
Isopoda										
Heterotanais oerstedti (Kr.)	−	[3]	+	−	−	+	+	+	+	−
Cyathura carinata (Kr.)	−	+	+	−	−	+	−	+	−	−
Sphaeroma rugicauda Leach	+	−	+	+	+	+	+	+	+	+
Idotea viridis (Slabber)	−	+	+	+	+	−	−	+	+	−
Iaera albifrons Leach	+	−	+	+	+	+	+	+	+	+
Amphipoda										
Gammarus locusta (L.)	+	+	+	+	+	+	−	+	+	+
Gammarus duebeni Lillj	+	+	+	+	+	−	−	+	[4]	+
Leptocheirus pilosus Zadd	+	+	+	+	+	+	−	−	+	−
Corophium volutator (Pall.)	+	+	+	+	+	+	−	+	+	+
Corophium lacustre Vanh	−	−	+	+	−	−	+	−	+	+
Mysidacea										
Neomysis vulgaris (J. V. Thomps.)	+	+	+	+	+	+	+	+	+	+
Decapoda										
Palaemonetes varians (Leach)	+	+	+	+	−	−	−	+	−	−
Mollusca										
Embletonia pallida Alder et Hanc	−	−	+	−	−	−	−	+	+	+
Bryozoa										
Membranipora crustulenta Baster	−	−	+	−	−	+	+	+	+	+
Victorella pavida Kent	−	−	+	−	−	−	+	+	+	−

[1] *E. hirundo*?
[2] *B. crenatus*?
[3] *H. gurneyi* Norman
[4] *G. zaddachi* Sexton

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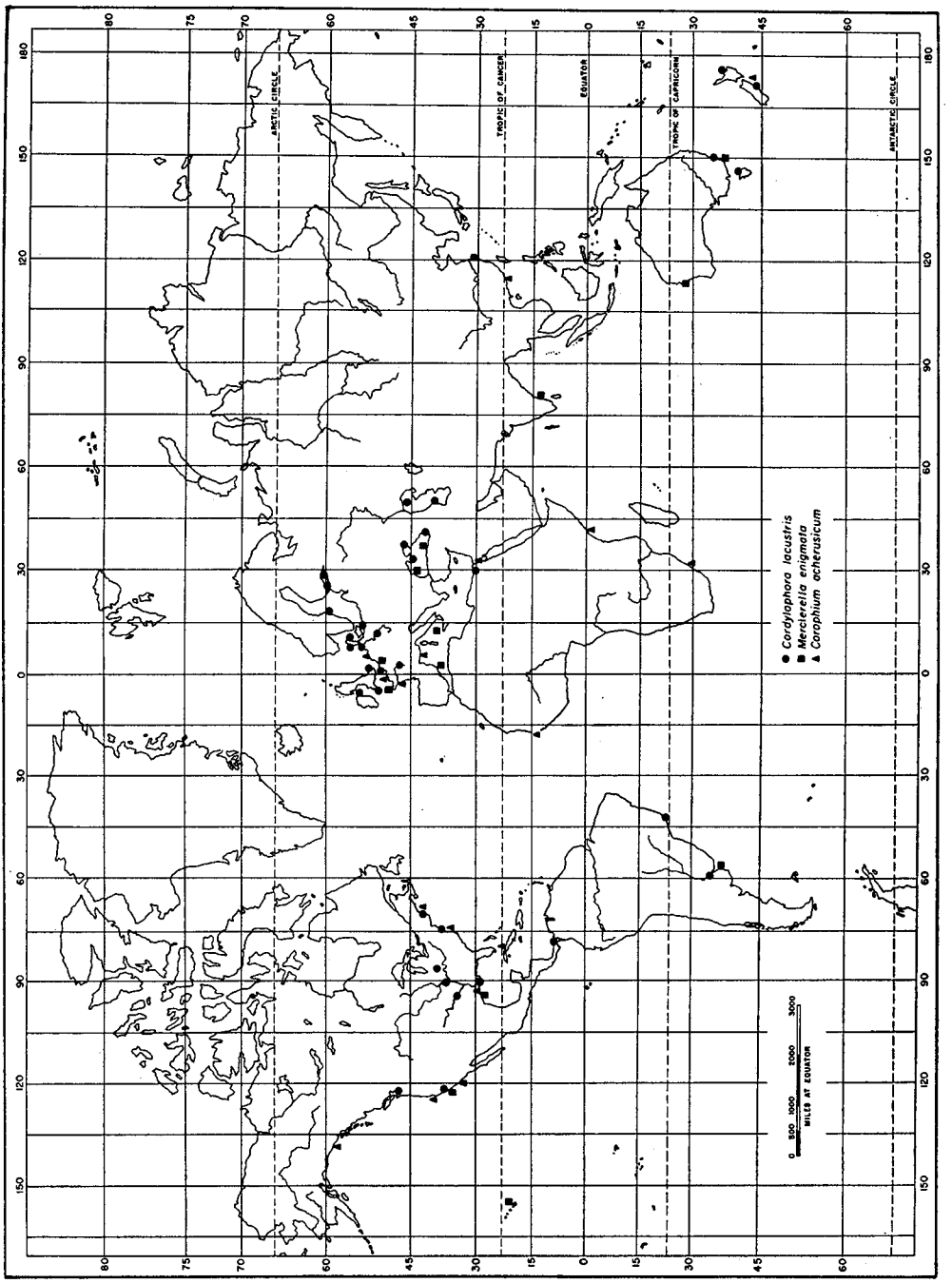

FIGURE 19.—*Occurrence of various widely distributed animals in estuaries and harbors*
Compiled from various sources

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They include, in addition to systematically related forms (single twins), unrelated but ecologically similar forms, which they refer to as double twins.

Various attempts to subdivide estuarine environments on the basis of faunal differences have been made. Redeke's salinity spectrum system is actually based on such faunal differences in the comparatively stable waters of Holland. It has occasionally been applied elsewhere, as by de Oliveira (1950) to the Bahia de Guanabara, with indifferent success.

Paleontologists, seeking to recognize ancient estuarine environments, have examined living and subfossil assemblages in estuaries and have suggested subdivisions of estuaries based on these studies. Most of this work has been done by students of Foraminifera, who propose facies (or, "biofacies") and subfacies on the basis of assemblages of dead tests, fully realizing that such assemblages may be the result of post-mortem accumulations rather than indications of living populations (Phleger and Walton, 1950; Parker *et al.*, 1953). A somewhat similar study, with special reference to mollusks, was made by Ladd, in Texas (Volume 2, Chapter 22). Subsequent field work in this region has demonstrated that studies based on permanent remains (potential fossils) may not adequately indicate the degree of short-term fluctuation in the environment. Similar studies have been undertaken in Europe; Rottgardt's, analysis (1952) of living or recent Foraminifera and ostracods in Kiel Bay is an example of such a detailed attempt to study the paleontological significance of distribution in relation to salinity (Fig. 20).

B. FLORA

We find a similar reduction in the number of species in the flora of estuaries and a correspondingly wide distribution of some of the characteristic genera or species. Most of these widely distributed plants—e.g., *Spartina*, *Salicornia*, and *Scirpus*—are more properly marshland species. The brown and red algae are, on the whole, less adaptable to reductions in salinity than are the green algae, and few of them occur in estuaries, although *Gracilaria* may be abundant enough in some regions to be harvested for its agar content.[2] Such filamentous green algae as *Enteromorpha*, *Chaetomorpha*, and *Cladophora* flourish in estuaries and often form dense growths.

Although tides and the substrate are major factors in the distribution of attached estuarine algae, other factors of importance include turbidity, temperature and salinity (Doty and Newhouse, 1954), pH, methyl orange alkalinity, and access of sea water, as differentiated from static salinity (Wood and Palmatier, 1954), illumination, and wave height.

The vertical distribution of algae in estuaries is comparable to that of marine coasts; green algae tend to predominate in higher zones and near river mouths, whereas the red and brown algae tend to predominate in subtidal and lower zones near the mouths of estuaries and lagoons. Certain algae which are not limited by factors associated with emersion and submersion occur at random throughout the vertical range. Tidal control of algal zonation in estuaries can be complex (Wood and Straughan, 1953) and differs according to locality.

Classified according to substrate, some algae live on soil, such as *Chara*, which forms dense carpets in shallow water (Wood, 1954), or *Microcoleus*, which often binds marsh sand and mud; others are attached to stones or shells, such as *Cladophora*, *Enteromorpha*, *Gracilaria*, *Rhizoclonium*, and *Ulothrix*; a third type is epiphytic on other algae or on phanerogams, including *Cladophora* and *Champia* on *Zostera* and *Ceramium* on *Ruppia*. A very significant flora consists of the masses of algae which break loose from their substrate and continue to grow while accumulating in depths of estuaries, such as *Enteromorpha*, *Chaetomorpha*, *Spyridia*, and *Gracilaria*.

The close dependence of phytoplankton in estuaries and lagoons upon nutrients from the land is shown by the great increases in phytoplankton concentration following natural contribution of nutrients by flooding streams (Nash, 1947) and artificial fertilization of salt-water ponds by commercial nitrates and phosphates (Pratt, 1949; Raymont, 1949). In spite of the seasonal abundance of nutrients, the phytoplankton in estuaries is generally less abundant at the head than nearer the sea or immediately outside, because of the reduction of light penetration by turbidity. (*See, e.g.*, Huntsman, 1952.)

[2] *Gracilaria "confervoides"* is the most important species; the algae recognized under this name may, however, belong to several species.

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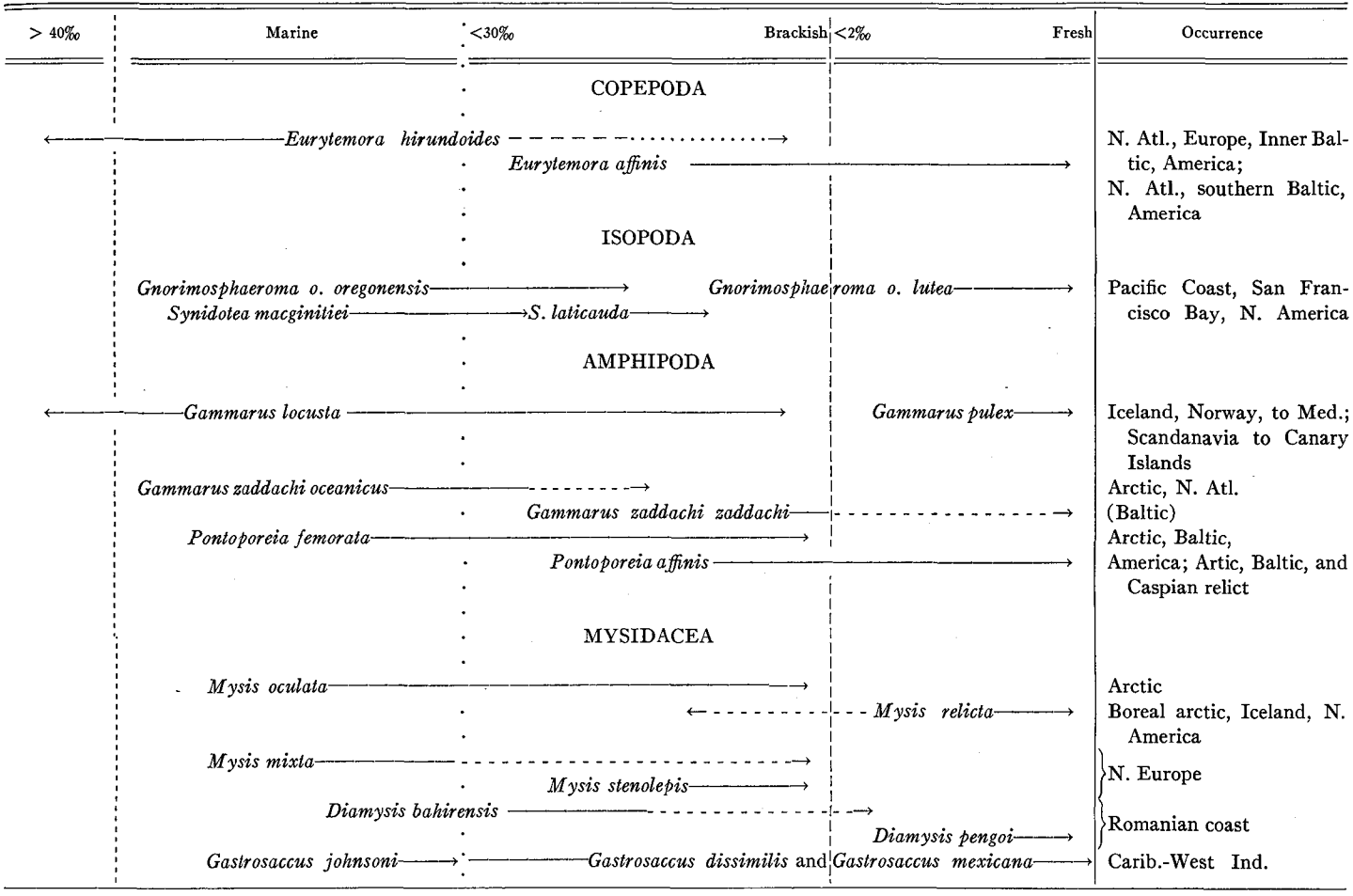
TABLE 6.—*Distribution of geminate pairs in marine and brackish or fresh waters**



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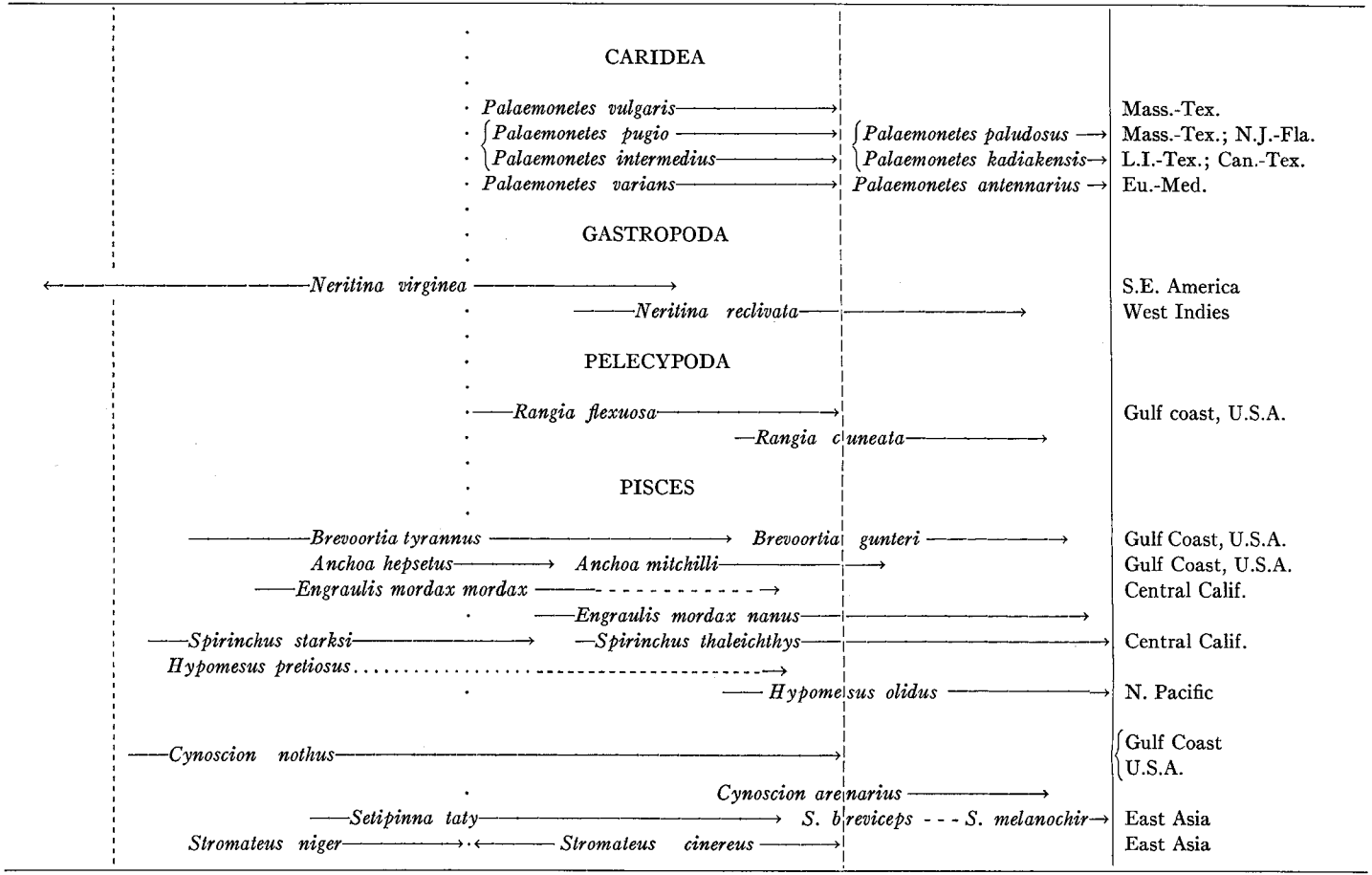

* Compiled with the assistance of G. Gunter, L. B. Holthuis, C. L. Hubbs, R. J. Menzies, and S. G. Segerstråle

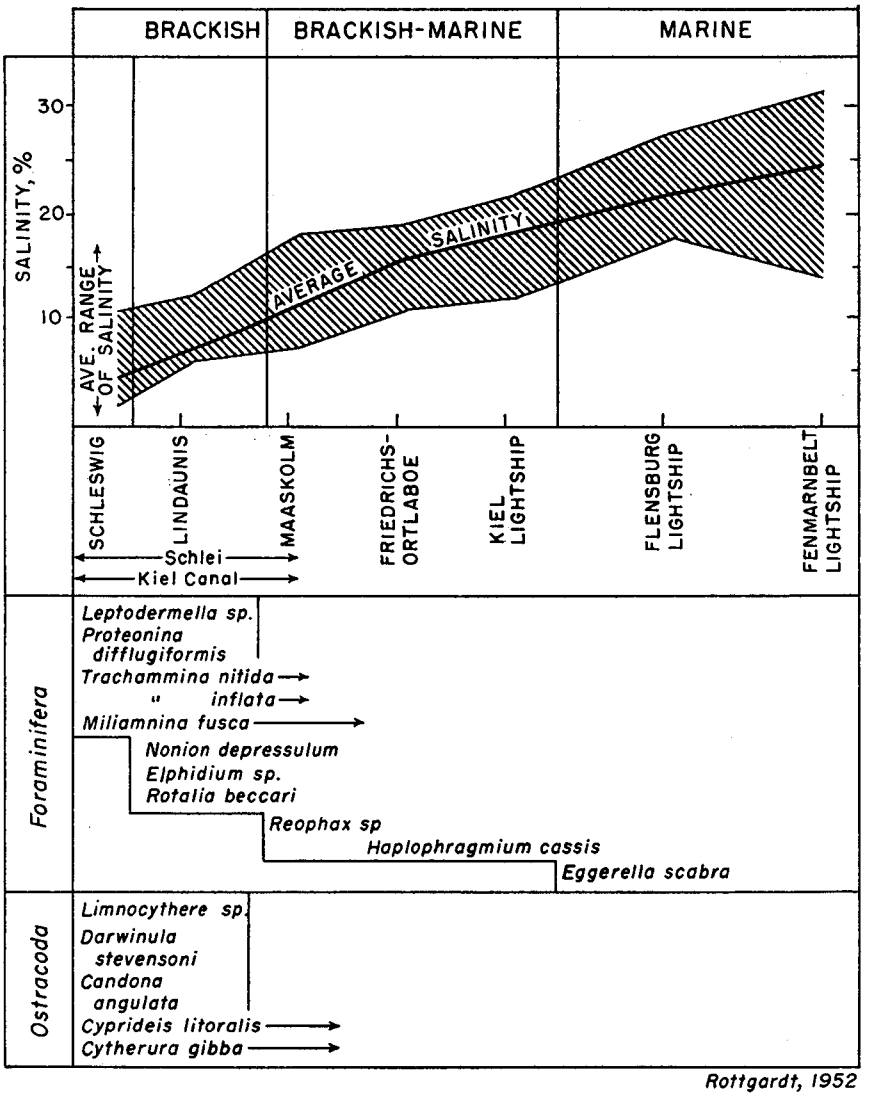

FIGURE 20.—*Relations of microfauna to salinity in Kiel Bay*
After Rottgardt (1952)

Nevertheless, plankton may become so abundant as to color the water and in some way cause mortality to fish. (See Chapter 29.) Various studies have shown that the phytoplankton of estuaries is predominantly marine in origin, with a minor representation of fresh-water forms (Brockmann, 1935; Cowles, 1930).

One of the most important controlling factors of the animals of estuaries and lagoons, and especially of their marshes, is the bacterial flora. Bacteria may have as much influence on the distribution of other plants and animals as has temperature, nutrient concentration, etc. ZoBell and Feltham (1942, p. 71) have noted that a cc of bay water contains many hundred times the number of bacteria that an equal amount of sea water may harbor. The bay mud contains even more; where overlying

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water has thousands of bacteria per cc, the mud may have millions. Both aerobes and anaerobes are abundant in the top few centimeters. As one might expect, aerobic forms are most abundant at the surface, and they occur in greater numbers than anaerobic bacteria to a depth of about 60 cm at Mission Bay, California. This is well below the depth of free oxygen, implying that many of these bacteria are facultative rather than strict aerobes.

The activities of the bacteria are responsible for the reducing conditions in the muds of estuaries and lagoons. Sterilized mud becomes oxidized and light gray, but upon repopulation by bacteria it is slowly reduced again and resumes its dark gray to black color. The various chemical reactions caused by bacteria will be discussed more fully in the section on Sediments.

Another important role of bacteria is that of food supply for the various bottom-dwelling animals (ZoBell, 1946). Many of these animals have special filtering devices for catching bacteria, whereas others merely digest them along with organic detritus; some ciliates (*Euplotes*) and nematodes live in anaerobic bottom sediments and may feed on the associated bacteria. Several grams of bacteria per cubic foot may be produced daily. As well as supplying food for numerous animals, the bacteria release plant nutrients by decomposing dead organic matter. Part of the decomposed material is utilized by the bacteria themselves, but much of it forms the nitrates, phosphates, carbon dioxide, etc., necessary for plant growth.

3. HYPERSALINE LAGOONS

A hypersaline lagoon may be defined as environment more or less directly connected with the sea, in which salinities are concentrated to values greater than 40–50‰ by an excess of evaporation over fresh-water inflow. Such circumstances also imply rather high summer temperatures. The environment so defined is marginal in the ecological as well as the physical sense, since the environmental conditions are such that few of the organisms reproduce naturally in these lagoons, and it is transitory in the geological sense. The hydrographic characteristics of hypersaline lagoons are in some ways the reverse of those of estuaries (Fig. 5). Zernov (1949) recognized five types of maritime salt lakes, ponds, etc., according to their salinity characteristics. Hypersaline lagoons fall into his "ultrahaline" type, which he characterized as having salinities from 47 to 300‰; this scheme thus includes both lagoons and salterns. While the salinity of 47‰ is probably as acceptable as any particular value for the threshold concentration of a hypersaline lagoon, the fact that it is a body of water in some way connected with the sea must also be included in the definition.

Environments of this character occur along the shores in the tropics and subtropics throughout the world, but have yet to be studied in adequate detail. Except for the greater total concentration of salts, the composition of hypersaline lagoons is similar to that of sea water; in contrast, inland brines or alkali waters are much higher in carbonates and have different Ca:Mg ratios (Table 7).

The populations of these lagoons consist of limited aggregations of organisms recruited from the inhabitants of estuaries. Only in exceptional cases are inland-brine or salt-pond organisms found, and, in so far as known, there is no characteristic endemic hypersaline component. The absence of such a characteristic brine-loving form as *Artemia* from such environments as the Laguna Madre and the lakes of the Suez Canal is probably the result of the presence of cyprinodont fishes which eat them—*i.e.*, ecological. The absence of *Ephydra*, the brine fly characteristic of salterns and inland brines, from such situations may also be a result of ecological competition. Blue-green algae are not usually found in marine brines, perhaps because of the lack of carbonates (Baas Becking, 1928), but Taylor (1954) mentions

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TABLE 7.—*Percentage composition of various marine and inland brines*

	Sea water a	Laguna Madre b	Suez Canal c	Salton Sea		Owens Lake c
				1913d	1945e	
CO_3	0.41*	0.23	0.01	1.57	0.29	22.70
SO_4	7.68	2.15	7.67	12.46	18.55	9.89
Cl	55.04	60.5	55.59	47.38	43.70	25.40
Ca	1.15	0.93	1.05	1.97	2.12	—
Mg	3.69	3.68	3.64	1.62	2.41	—
Na	30.62	31.4	31.21	32.30	31.05	37.83
K	1.10		.64	.34		2.09
‰	35.00	64.05	51.03	10.02	ca. 27.0	118.83

* As CO_3^-

a, From Rubey (1951); b, from Hedgpeth (1953); c, from Clarke (1924); d, From MacDougal *et al.* (1914); e, from Imperial Irrigation District, data in files of C. L. Hubbs.

"an enormous development of an almost leathery blue-green algal flora" behind Padre Island (Laguna Madre) where salinities are often 40–50‰. A few organisms apparently can withstand high concentrations of some substances; the most amazing of these is the ability of two small cyprinodont fishes, *Aphanius dispar* and *A. fasciatus*, to live in water containing 12 mgm/H_2S and 2640 ppm free sulfur (Smith, 1952). The presence of fish in such waters also implies an organic source of food.

Within comparatively broad limits, high concentrations of salts in the medium are not a barrier to certain euryhaline organisms, since their range of tolerance includes both environmental extremes. Ferronnière (1901, p. 320–321, 351) seems to have been one of the first to point out that organisms capable of withstanding reductions in salinity can also tolerate hypersaline conditions. He considered hypersaline environments to be an extension of the supralittoral region, which included also brackish waters, since the similar biotic facies of the two environments was composed of the same tolerant organisms. This phenomenon is familiar to many field workers in regions where extreme salinity ranges are encountered; Gunter, for example, on the basis of an extensive field experience on the Texas coast, states that "all of the fishes taken in waters of very low salinity, except for the fresh water species, can also live in waters of high salinity" (1945, p. 112).

Unfortunately there are not many experimental data concerning most of the organisms known to inhabit hypersaline lagoons, and the most we can say of them is that they are known to occur in such environments. We do not have very good field data on the actual salinities and temperatures, especially on a seasonal basis, for most of the environments that have been studied. There have been researches on such organisms as the red green alga *Dunaliella* (*e.g.*, Sciacchitano, 1926), and the famous brine shrimp *Artemia* (*e.g.*, Kuenen, 1939), but these are studies of highly peculiar organisms living in salterns. Some saltern organisms are marine in orgin, but more of them seem to be related to fresh-water forms (*cf.* Florentin, 1899).

While these evaporation ponds or salterns pass through a phase resembling a hypersaline lagoon, this is transitory, and the peculiar biotic complex of the salterns flourishes best when cut off from the sea.

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Five hypersaline environments have received particular attention: the Bitter Lakes of the Suez Canal (Fox *et al.*, 1927; 1929), the Sivash, on the western side of the Sea of Azov (Vorob'ev, 1940; Zenkevich, 1947), the Laguna Madre of Texas (Collier and Hedgpeth, 1950; Hedgpeth, 1953), a Bulgarian liman (Caspers, 1952), and the Santa Lucia estuary in South Africa (Day *et al.*, 1954). The Bitter Lakes are not, strictly speaking, hypersaline lagoons, as they are old saline basins rejuvenated by the opening of the Suez Canal in 1869 and since gradually decreasing in salinity. Nevertheless, they provide some interesting information on the tolerance of certain organisms to high salinities; Tortonese (1952) mentions concentrations as high as 75‰. A large variety of animals was collected in the Bitter Lakes by the Cambridge Suez Canal Expedition in 1924, when salinities were from about 43 to 57‰. Of the 326 species tabulated by Fox as occurring in the canal, 145 were found in the Bitter Lakes; most of these may be traced to the Red Sea, where salinities are about 40‰. With the exception of a peculiar variety of *Balanus amphitrite*, no particular modifications, especially no "stunting of growth", were mentioned in relation to the high salinities of the Bitter Lakes. To the contrary, a holothurian, *Synapticula reciprocans*, was "considerably larger" than those observed in the sea.

A number of organisms have been able to pass through the Bitter Lakes, especially from the Red Sea into the Mediterranean, and many of the records of occurrence in this part of the Suez Canal are the result of such dispersal or migrations and do not necessarily indicate that the species concerned can complete their life cycles in this environment. A number of larval forms, especially of Crustacea, have been observed in the Bitter Lakes, however.

THE SIVASH: The Sivash, or Putrid Sea, is a true hypersaline lagoon, remarkably similar in some of its physiographic and biological characteristics to the lagoons on the coast of Texas and northeastern Mexico (Fig. 21). Summer temperatures up to 30–35°C are recorded for both environments, but minimum temperatures are much lower in the Sivash, as it freezes over in severe winters. Both are shallow, with maximum depths of about 9–12 feet (3.2 m is the greatest depth in the Sivash). Both regions are considered highly productive and can support commercial fisheries, although this productivity depends upon the continued migration of fishes or their young from the neighboring seas. In both environments high summer temperatures and salinities bring about mass mortalities, and winter kills also occur.

According to the investigations of Vorob'ev (1940, as summarized by Zenkevich, 1947) the most abundant benthic organisms in the northern part of the Sivash, in order of their relative biomasses, are *Cardium edule*, *Chironomus salinarius*, *Syndesmya ovata*, *Gammarus locusta*, *Nephthys hombergi*, *Mytilaster lineatus*, *Hydrobia ventrosa*, and *Nereis zonata*. This complex thins out toward the south as the salinity increases. The maximum penetration of many of the forms in the Sivash in relation to salinity is indicated in Figure 22. When it is remembered that the average salinity of the Sea of Azov is about 11 ‰, the wide range of salinities under which most of these species can live is apparent.

There is some relationship between salinity and the production of plant life, principally because of dense growth of *Cladophora* in the waters of higher salinity; Zernov (1949, p. 165—apparently from Vorob'ev) gives a table of the comparative production of zoobenthos and phytobenthos as related to salinity in the Sivash:

Salinity, ‰	18–36	36–54	54–72	72–90	90–108	108–126	126–144
Zoobenthos, g/m²	277	137	48	21	16	14	3
Phytobenthos, g/m²	180	498	478	17	110	214	833

Vorob'ev estimated the total plant production (both benthos and plankton) to be 1,322,000

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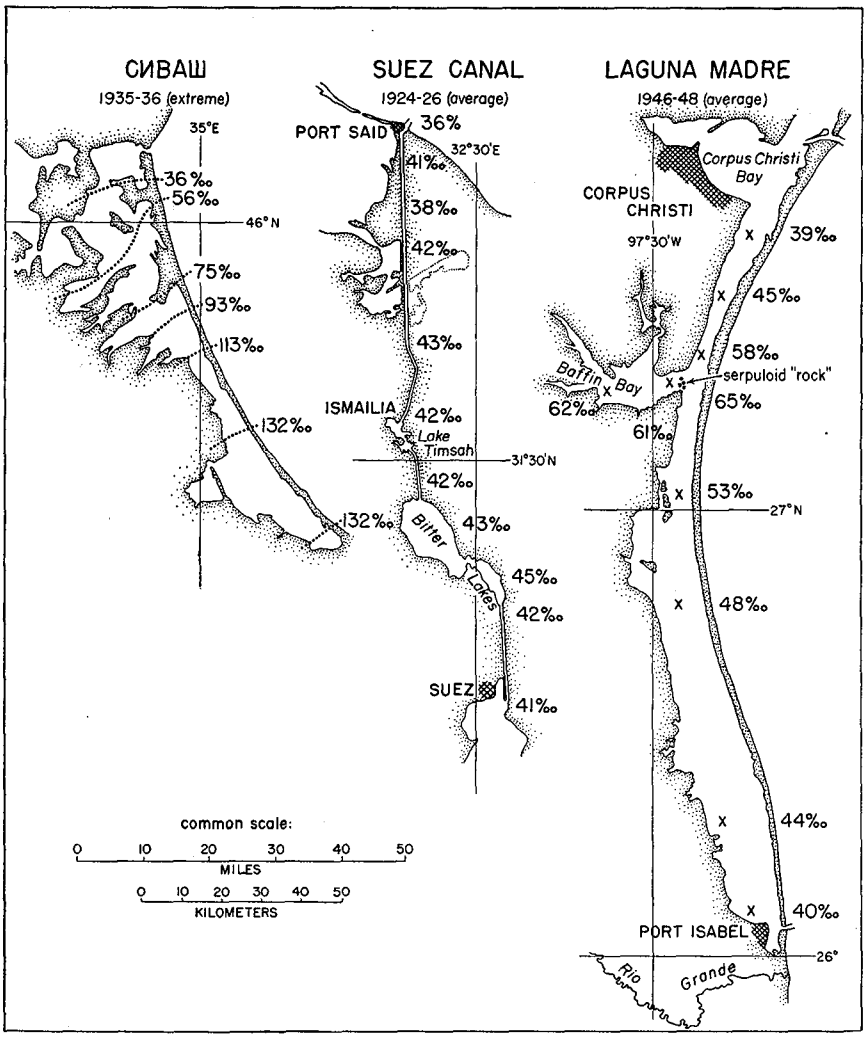

FIGURE 21.—*Sketch maps of the Sivash, the Suez Canal, and the Laguna Madre to the same scale* Showing comparative salinity conditions. Compiled from various sources.

metric tons per year; most of this is not used by animals. He estimated the biomass of fish in the northern part of the Sivash to be approximately 21,000 tons if complete utilization of the food supply is assumed; in some years the mullet catch alone has been about 500 tons, but the average for 20 years was 80–90 tons. The actual and potential fish resources of the Sivash have inspired Russian fisheries workers to recommend attempts to alleviate the extreme salinity conditions in the Sivash by damming the more extreme regions and cutting channels through the Arabastkaia Spit which separates it from the Sea of Azov.

The relations between the populations of the Sivash and the Sea of Azov suggest conditions in other hypersaline lagoons: "Along with Azov waters an enormous quantity of plankton and larval benthos forms are constantly carried into the Sivash, and we have what might be called a forced colonization of the Sivash. A majority of the larvae and adult organism entering the Sivash quickly

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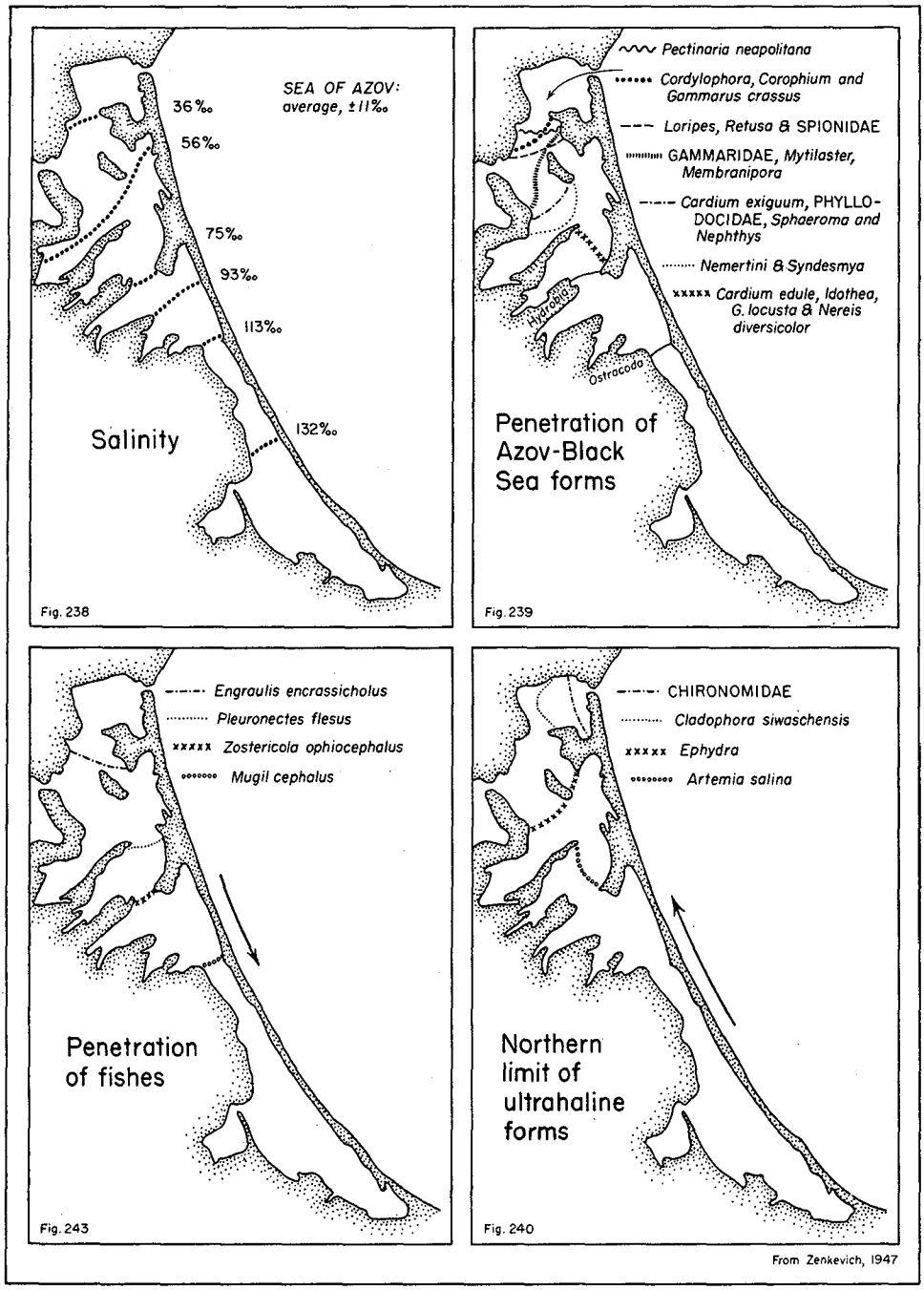

FIGURE 22.—*Distribution of various organisms in the Sivash as related to maximum salinity conditions*
After Zenkevich (1947)

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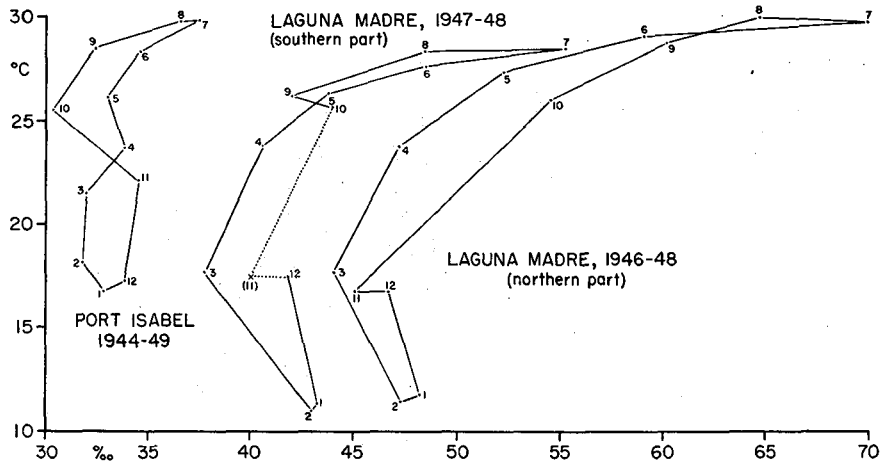

FIGURE 23.—*Temperature-salinity conditions in the Laguna Madre*, 1947-1948
After Hedgpeth (1953)

die, or do not live for a prolonged period, or settle in the northern part of the Sivash. We have every basis to assume that, were it not for the steady influx of forms from the Sea of Azov, the population of the Sivash would be considerably poorer in number of species and in biomass; in spite of the great abundance of species in the Sivash they produce very little and there is a marked dimunition of their biomass throughout the course of almost the entire year" (Zenkevich, 1947, p. 394–395).

LAGUNA MADRE: Studies of the organic life and productivity of the waters of the Laguna Madre comparable in scope to Vorob'ev's work in the Sivash are yet to be made, and the faunal composition, especially in Baffin Bay (not to be confused with the Baffin Bay west of Greenland; *see* Fig. 2) region, is not yet well known, although the fish catch in the Laguna Madre has been as high as 2,000,000 pounds (900 metric tons) in some years (Hedgpeth, 1947). While the fauna of the southern part of the Laguna Madre, near Port Isabel, is not greatly different from that of the neighboring Gulf of Mexico (Hedgpeth, 1953), the average salinity in 1947–1948 was 40 ‰, and salinities as high as 60 ‰ have been recorded in that region (Fig. 23). In the Baffin Bay area salinities average 60 ‰ and range from 50 to 80 ‰.

An interesting feature of the Laguna Madre region is the occurrence of reeflike serpuloid masses at the mouth of Baffin Bay, where it joins the Laguna Madre proper. No evidence has been found in recent years of living serpulids in these rocklike clumps of tubes, some of which are several feet in diameter and rise 3–4 feet above the sandy bottom of the lagoon. The occurrence of these serpulid masses, and of oyster shells in Indian middens on near-by shores, suggests that lower-salinity conditions prevailed there within perhaps the last 2000–3000 years. At this time, the only living oysters in the Laguna Madre are found near Port Isabel, where they appear to be making their last stand against the increasing salinities (Hedgpeth, 1953). The nearest known living serpuloid reefs are a Vera Cruz, Mexico, where they exist in sea water or almost maring conditions not far from the harbor. (*Cf.* Heilprin, 1890.)

The fauna of Baffin Bay, where salinities are as high as 80 ‰ and seldom below 50 or 60 ‰ except for brief periods following occasional cloudbursts, includes at least two polychaetes, *Nereis pelagica occidentalis* and *Polydora ligni*, the amphipods *Podocerus brasiliensis* and *Grandidierella bonnieroides*, and a copepod, *Acartia tonsa*. A barnacle, apparently *Balanus eburneus*, is common. The most abundant mollusk species are *Anomalocardia cuneimeris*, *Mulinia lateralis*, and *Polymesoda floridana*; these clams, especially *Anomalocardia*, which seems to be very abundant, do not appear to grow as large in these waters as they do in less saline environments (Hedgpeth, 1953). A small gastropod, *Acteon candens*, is also common. The fish fauna includes *Cyprinodon variegatus*, *Menidia beryllina peninsulae*, and the ubiquitous mullet *Mugil cephalus*. *Artemia* and insect larvae have not

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been observed, and, while green algae (*e.g., Chaetophora*) are present, they do not form the dense growths that must occur in the Sivash. The shores of Baffin Bay have, in fact, a barren, desolate appearance, and the water is usually a dull yellowish.

While the more conspicuous elements of the fauna of hypersaline lagoons are fairly well known, little attention has been paid to smaller organisms, and often no salinity data are given in the references to the occurrence of organisms in high salinities, except as "concentrated brine," "saturated with salts," or some such circumstantial statement as "the water was so dense with salt and alkali that a good swimmer could not put his hands on bottom in water five feet deep, except by climbing down the lead line of the net." (Weed, 1925). Hence it is difficult to assemble a list of organisms according to their known salinity tolerances, and Table 8 is little more than a preliminary compilation. To make the data comparable, all readings, whether density, degrees Beaumé, or chlorinity, have been converted to "salinity". This is simply intended to be a rough index of the total concentration of salts in the environment, without reference to the proportion of salts.

In summarizing our still incomplete knowledge of the fauna of marine-derived brines, we can say that this fauna is recruited principally from groups or organisms already well represented in the sea, and at the same time from species adapted to estuaries and brackish waters. Copepods, polychaetes, mollusks, and fishes are particularly abundant, but several other highly successful groups, including sponges, hydroids, and echinoderms, are absent or represented by only a few species. Thus it appears that the same faunal elements that have not been able to penetrate fresh water successfully are also limited from hypersaline environments. The most pronounced ecological peculiarity of these hypersaline lagoons, apart from their high salinities, is the allochthonous nature of a large part of the fauna. Few species reproduce successfully, and the bulk of the populations, especially of the larger forms, is maintained by continuous migration or is carried by water movements from the neighboring sea. The high summer temperatures of such environments, as well as the high salinities, probably inhibit the reproduction of many of the species. There also seems to be a tendency toward dwarfing of species in these environments. When the lagoons are cut off from the sea the difficulties of maintaining natural

TABLE 8.—*Upper tolerances of organisms*

Protozoa	50–60 ‰	Ostracoda	60–100 ‰
Hydromedusae	60	Cirripedia	60–80
Turbellaria	139	Isopoda	70
Nemertea	60	Amphipoda	90
Rotifera	60	Macrura	60
Nematoda	70	Brachyura	70
Oligochaeta	60	Pelecypoda	60–80
Polychaeta	139	Gastropoda	80
Copepoda	80	Echinoderma	75

Pisces 75–85

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populations are even greater, and the fauna is reduced to a very few species, usually consisting of entomostracans, mollusks, and cyprinodont fishes.

4. THE BORDERS OF ESTUARIES

Along the borders of estuaries there is a variety of environments in the transition zones between land and water. Since these environments are influenced as much by terrestrial as by aquatic factors, their character varies with climatic conditions. In cool temperate regions of abundant rainfall there may be extensive marshlands grading into meadowlands or lowland shrubs, and in warmer regions there may be a gradation into cypress swamps or cane thickets or into sandy lowlands with a mixed cover of shrub oak and cactus. In the tropics and subtropics the borderland between land and estuary may be occupied by a mangrove swamp.

In this region between water and land there is an accumulation of sediments by physical action and by plants, and the features of zonation and plant succession are similar, at least in the middle and tropical latitudes. First there is a zone of bare mud, which grades at its lower limit near 0.0 tide or mean low water into subaqueous beds of marine and brackish phanerogams. In regions where the red mangrove (*Rhizophora*) flourishes, the muddy zone is colonized down to low-tide level by the viviparous seedlings of this plant, and the mud is sheltered from the sun by the thickets of prop roots[3]. The mangrove is thus the pioneer in colonizing the tidal margin of the estuary. In temperate regions, various species of *Salicornia* or *Spartina* are among the pioneer colonizers, although they are often associated with algal mats or felts, principally of blue greens or greens (see the general review by Uphof, 1941, and the section of tidal marshes, below).

BAY SHORES: Too often ecologists study the tidal flats bordering bays and estuaries in terms of the organisms living in or upon the substrate and exposed at low tide, although admittedly this region is entirely different at high tide. When viewed from the water, these flats can be seen as regions of shelter for smaller motile organisms as well as areas where nutrients and plankton may become concentrated to the advantage of the numerous burrowing and slowly moving benthic forms. The physical conditions—temperature and salinity in particular—are more variable in the shallow flats bordering estuaries than anywhere else, and this range of conditions is reflected in the wide variation of plant and animal assemblages in rather small areas; such variation, especially in the animal assemblages, is indeed characteristic of all estuaries and fjords where there are also intricate patterns of currents, resulting in wide local differences in sediments and food supply. As a result, the close mingling of assemblages makes bottom-community studies difficult. The criteria for determining bottom communities presented in Chapter 17 are difficult to apply, and such a study as that by Dexter (1947), in which the communities are indicated as "fragments of faciations", emphasizes these difficulties. Such studies do indicate that the paleontologist may accept as one of his criteria for identifying assemblages of estuaries and inlets (especially where the salinities are near those of sea water) the variations in assemblages over comparatively short distances. Figures 24 and 25 present two examples of community studies in estuaries, that of Figure 24 without reference to substrate conditions, and that of Figure 25 an example of a very detailed study of sediment types as well as of the communities.

The shallows on the edge of coastal bays in Texas have been likened to a miniature continental shelf (Hedgpeth, 1953). These bays are shaped like a bowl with a flared edge, and the steeper slope

[3] "Mangrove" has two meanings: as a general term it is applied to those plants (*Rhizophora*, *Avicennia*, *Laguncularia*, etc.) adapted to living in loose wet soils in saline tide-waters ("maritime swamps"); botanically, the term is restricted to the Rhizophoraceae (Davis, 1940).

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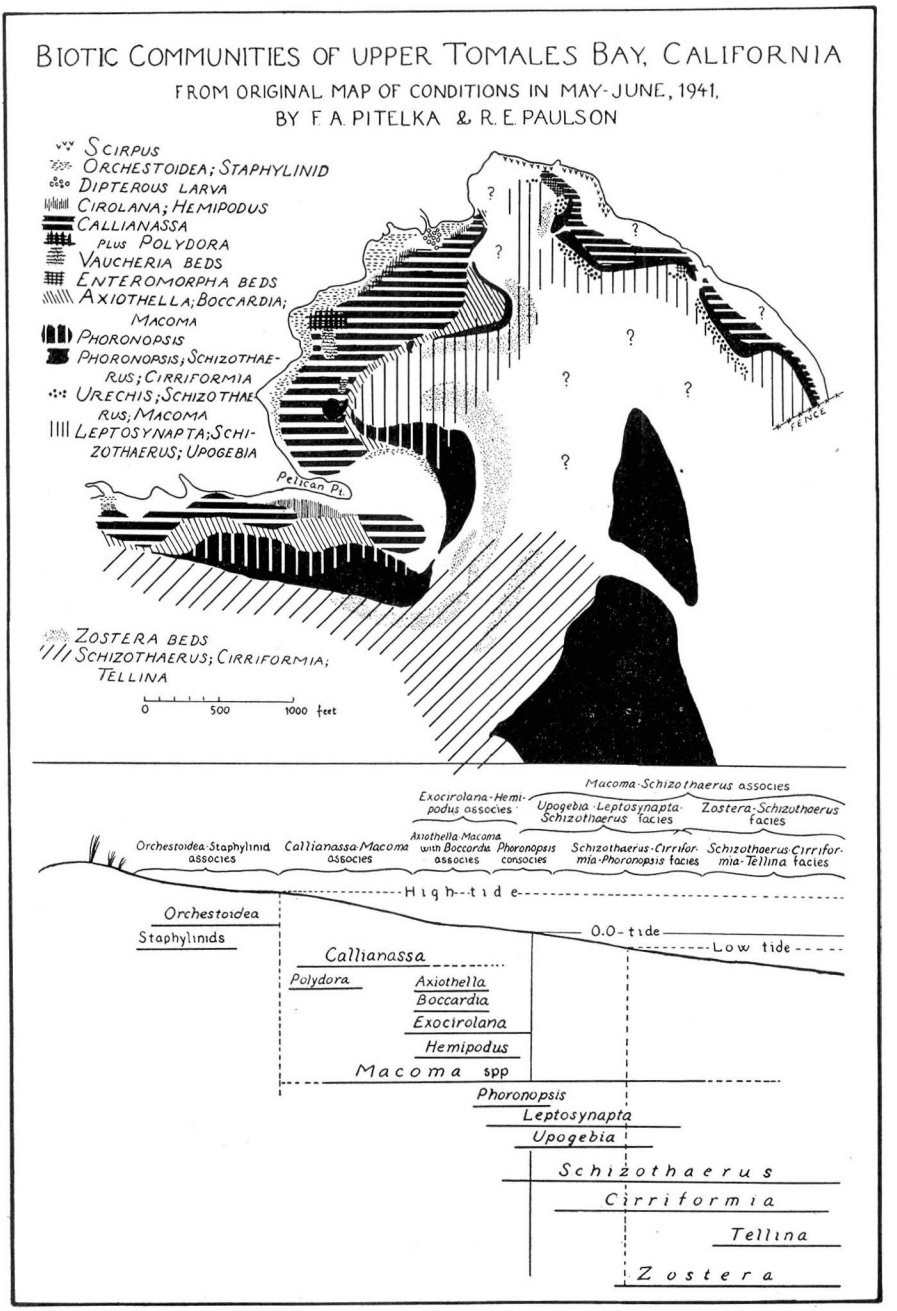

FIGURE 24.—*Areal and vertical extent of bottom communities near mouth of Tomales Bay, California*
From *Between Pacific tides*, courtesy Frank A. Pitelka and the Stanford University Press

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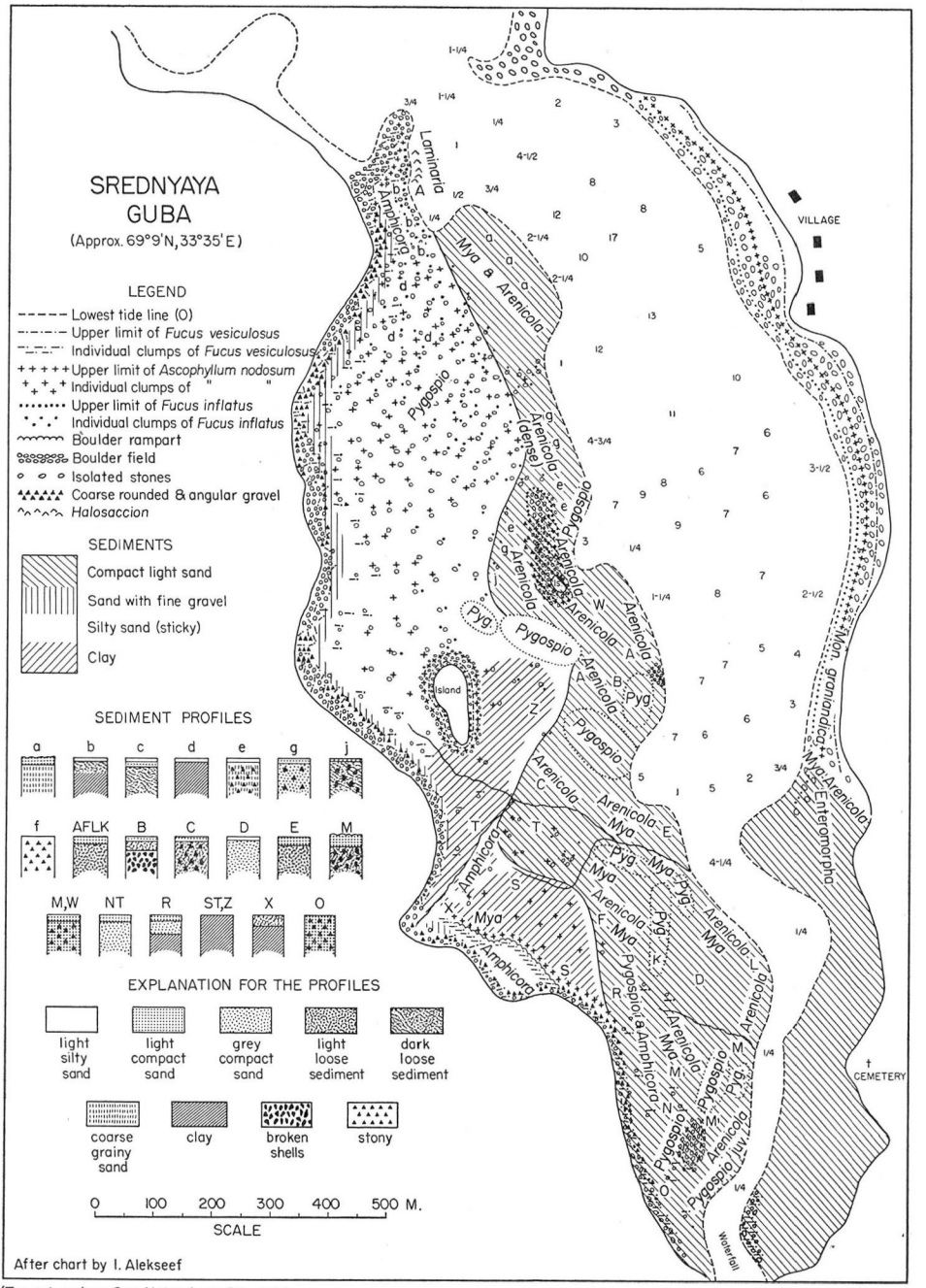

(Trans. Lenningr. Soc. Natural, vol. 59, pt. 2.)

FIGURE 25.—*Distribution of bottom organisms and sediment types in Middle Bay, near Murmansk*
After Guryanova, Zachs, Ushakov (1929)

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separating the flats from the basin proper might be regarded as being analogous to the continental slope of an ocean basin although the magnitude is only a hundredth. The shallow inshore region is often occupied by extensive beds of turtle grass (*Thalassia testudinum*), various bushy algae, especially *Gracilaria confervoides*, and stands of *Spartina*. The bottom material varies from sand to fairly firm mud, or soft mud covered with plant detritus. Often there are oyster shells which afford shelter for small crabs and pistol shrimp. The characteristic inhabitants of this bay-shelf region are cyprinodont fishes and grass shrimp, *Palaemonetes* spp. (Gunter, 1945, p. 93). This *Cyprindontes-Palaemonetes* community also occurs in estuaries and grassy flats along the Tunisian coast (Seurat, 1929); the primary requisite for these animals seems to be shelter, as they are seldom found away from the shallows or some sort of plant growth, although the temperature and salinity variations in such shallows are extreme (Gunter, 1945, p. 94). The extent of these flats varies with season, as only a few inches in change in bay level may considerably increase or decrease the area under water. A similar relation between rooted vegetation and fishes has been recognized in fresh water (Dansereau, 1945).

In such areas as the semi-arid to subhumid Texas coast with its pronounced seasonal differences in sea level the estuary edge or border may be extended well above average sea level in shallow saline ponds, and the effective border between land and sea may actually be nearly 3 feet above "sea level" (Hedgpeth, 1950). Conditions are more extreme in such flats, and the aquatic plant cover is greatly reduced, but, since predatory fish are also scarce or absent, the environment still offers shelter to small fishes and shrimp. The variety of the fauna is reduced, but the populations are abundant, and the ponds are important feeding grounds for aquatic birds. The shallow ponds are also the habitat of various burrowing polychaetes and anomurans (*Upogebia* and *Callianassa*), small gastropods, and crabs. Clams are scarce in such environments, perhaps because of the seasonal fluctuation of water level. The organisms constituting this assemblage are resistant to salinity variations or are able to remain in their burrows with saltier water during periods of rainfall when the ponds are nearly fresh. The marshy or grassy borders of the ponds are occupied by large colonies of fiddler crabs (*Uca*) and marsh crabs (*Sesarma*), the salt-marsh periwinkle (*Littorina irrorata*), and the pulmonate *Melampus coffeus*.

The various burrowing crabs, which are often very abundant in such environments in the middle latitudes and on coasts where the water-temperature requirements for their larval stages are met in the summertime (as on the Atlantic coast of the United States), constitute an active factor in turning over the sediments. Thus they occupy the role of the clams and the anomuran burrowers at the lower levels, and, like these organisms, they occur in characteristic aggregations and patterns. There may, for example, be two or three species of fiddler crabs (*Uca*) and a marsh crab in the same region, but the distribution of their colonies is governed by the consistency of the substrate and the distance from the water line. Some species of fiddlers prefer wet mud, others burrow in damp sand. Farthest from the sea are found the very large burrows of the land crabs (*Cardisoma, Ucides*). All these burrowing crustaceans lead semiterrestrial lives as adults but must return to the bay or lagoon waters to release their eggs. Most of the gregarious species are vegetarians or feeders on micro-organisms and exhibit pronounced territorial preferences (Crane, 1947). In the East Indies mangrove regions Verwey (1930) distinguished five zones on the basis of the distribution of the crustacean fauna (Fig. 26).

THE WADDENS: Although tidal flats are characteristically associated with the sheltered conditions in estuaries, they reach their greatest development in the waddens or Watten of the North Sea. The waddens extend along this subsiding and essentialy deltaic coast from Denmark to Holland, protected by the outlying Friesian Islands (Pl. 1). They are composed principally of sand or mixed sand and mud, with areas of soft mud in sheltered locations and in the lee of islands where marshlands have been freshly eroded. The waddens are dissected by permanently flooded tidal channels and smaller branching and meandering channels which are exposed by the tide (Pl. 2). On mixed bottoms, especially in the northern waddens, there are extensive fields and patches of eel grass (*Zostera*). Many of the mussel beds in the German and Dutch waddens are overgrown with *Fucus*, which seems to stabilize the mussels.

In the northern parts of the waddens, salinities are not much lower than the ocean (*ca.* 30 ‰) but are reduced near the rivers, and in the Dutch wadden sea they are not much above 18 ‰. At the

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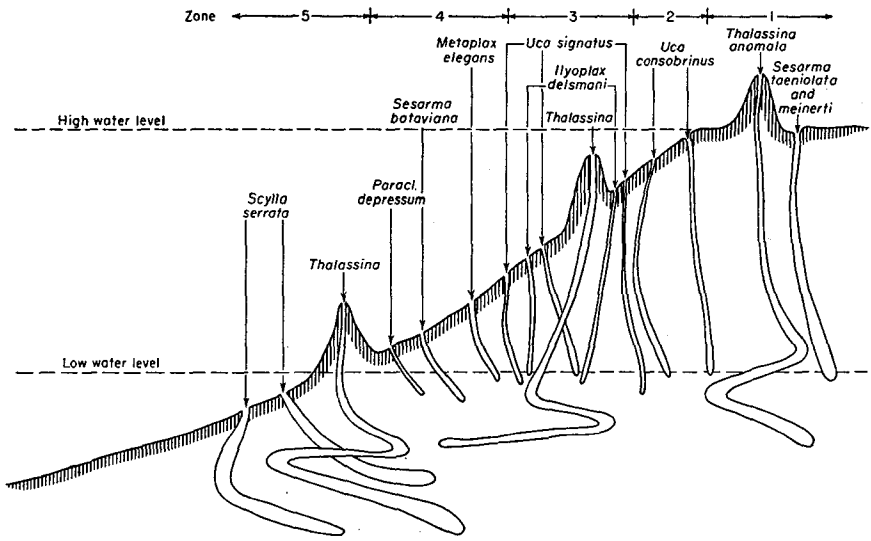

FIGURE 26.—*Idealized cross section of a mudbank in the East Indies* Showing zonation of various crustacean burrowers. After Verwey (1930)

southern part of the waddens is the Zuider Zee, now closed off from the sea in the process of reclamation, and in itself a large-scale experiment in the acclimation of euryhaline organisms to fresh water. At the time of its closure, the Zuider Zee was studied by Dutch biologists, and a careful catalogue of its flora and fauna was prepared (Redeke, 1922). Subsequent events have been reported in a series of reports by the Zuider Zee Commission, *De Biologie van de Zuiderzee tijdens haar Drooglegging.*

The animal life of the waddens consists of clam beds (Petersen considered the flats to fall in the *Macoma baltica* community; *see* Chapter 17), mussel banks, and colonies of such worms as *Pygospio* and *Arenicola.* The characteristic habits of these various common animals of the waddens are represented in Figure 27. It is from the aggregations of benthic organisms on the waddens that some of our ideas of marine communities have been derived, and from the ecological viewpoint the waddens are probably the most intensively studied region of the seas. The scope of the major papers dealing with the waddens is indicated on Plate 1. Many of these reports, especially those of Thamdrup (1935), Wohlenberg (1937), and Linke (1939), are illustrated with well-reproduced photographs showing the aspects of the waddens and the animal communities. The waddens are also intensively studied by geologists interested in problems of sedimentation. Because of the apparent similarity of conditions on the waddens to those which may have prevailed in ancient sedimentary environments, they have been of particular interest to paleontologists, and both Dutch and German paleontologists have made studies of the waddens which are essentially paleoecological. The active centers of this research are the research institute of the Senckenberg Museum (Frankfort a/M) at Wilhemshaven ("Senckenberg am Meer") and the Geologisch Institute at Groningen.

Although many of the higher parts of the waddens are sparsely populated sand, the lower parts, especially the regions of mud and mixed sand and mud, support large populations of organisms. Their productivity, in terms of fish food, is estimated by Smidt (1952) to be higher than many shallow-bottom communities.

MUSSEL BEDS AND OYSTER REEFS: The most significant aggregations in estuaries are those formed by oysters and mussels. Oyster reefs in particular are a major factor in altering patterns of sedimentation in bay bottoms and may on occasion cause segmentation of bays into smaller units. Further, the shells of oysters and mussels provide habitats for a variety of smaller organisms, and the resulting assemblages are of course the classic types of the biocoenosis.

In its manner of forming reefs or banks the European oyster *Ostrea edulis* resembles the common

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mussel, *Mytilus edulis*. The latter tends to form elongate reefs on suitable substrates along the margins of deeper channels in tidal flats near the low-tide level where the currents are of intermediate strength (Kuenen, 1942), and the few indications we have of the shape of "wild" banks of *O. edulis* suggest that it forms reefs in a similar manner. Lack of food, stronger currents, and predominantly sandy substrate prevent *M. edulis* from establishing beds on the higher parts of the tidal flat; at lower levels, where currents are weaker, the food supply is also less (Kuenen, 1942). The mussel not only forms beds parallel to currents but may also form them across tidal channels or "creeks" so that they resemble crescent-shaped dams; in such situations the currents in the creek appear to be opti-

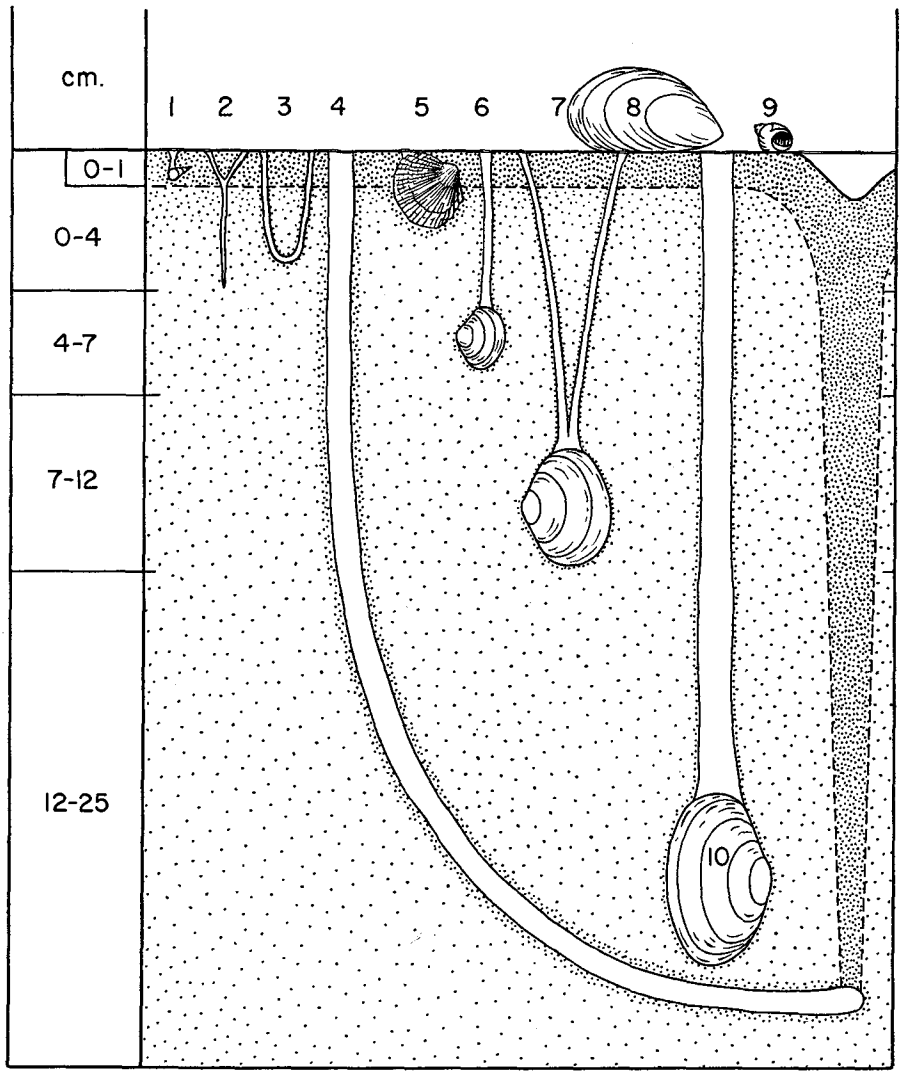

FIGURE 27.—*Living positions of certain benthos organisms of the waddens*
(1) *Hydrobia*, (2) Burrow of *Pygospio*, (3) Burrow of *Corophium*, (4) Burrow of *Arenicola*, (5) *Cardium*, (6) *Macoma*, (7) *Scrobicularia*, (8) *Mytilus*, (9) *Littorina*, (10)*Mya*. The oxidized sediment is closely stippled, the other material sparsely. After Thamdrup (1935)

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mal for the mussel (Verwey, 1952). While the distribution of larvae may be more or less general in the comparatively restricted area of an estuary or even of the Waddens of Europe, so that the larvae are universally distributed by the water masses (the old view of Hoek that mussel larvae were selected by water masses and other factors so that they settled only in the right places is denied by Maas Geesteranus [1942]), the larvae of mussels, like those of oysters, have rather rigid substrate requirements. The activity of such larvae, especially of the oyster, in actively searching out a suitable spot before fixing themselves has been studied in some detail (Korringa, 1941). Once settled, the oyster cannot abandon its site, but mussels often do, and small mussels (and sometimes up to perhaps 5 cm) can detach themselves and, with the assistance of the current, seek a more favorable site (Maas Geesteranus, 1942).

The origin and manner of formation of oyster reefs by the American oyster *Crassostrea virginica* was studied by Grave (1905), who developed a hypothesis to explain how oysters could build bars transversely across the currents. He considered that the first oysters settled near the shore, and later generations settled on them but nearer the current where feeding is better, thus gradually building out into the main channel until the structure altered the current pattern, which usually resulted in cutting the reef away from the adjacent shore. This oyster also builds reefs parallel to the main-current axis, or along the banks of tidal streams where current and feeding conditions are satisfactory. These reefs are often loaf-shaped in cross section, rising to the surface of the water to form islands, and may represent the accumulations of thousands of years (Norris, 1953). In mangrove regions other species of oysters, some of them with peculiar hooklike processes which grip the mangrove stems, may develop massive loaf-shaped banks around the prop roots. (*See*, for example, Saville-Kent, 1893, Pl. 39.)

Oysters and mussels do not necessarily form massive reefs or banks, and under certain conditions, possibly where back eddies provide adequate food and where the bottom is of firm mud or offers suitable hard objects for the spat to settle on, oysters in particular will establish a rather level aggregation (as opposed to the loaf-shaped reefs found in mid-bay regions) of scattered clusters (Pl. 3). It is possible that access by predators to such shallows prevents the oysters from forming more massive aggregations in these situations. In waters of lower salinity, mussels settle on oysters, sometimes winning out in the competition for food. While clam beds are not so conspicuous, the aggregate mass of living organic matter in a large clam bed is at least as large as that of an oyster reef of comparable dimensions.

TIDAL MARSHES: One of the most characteristic aspects of the meeting of land and sea in temperate and warm-temperate latitudes is the salt or tidal marsh. Only on rocky shores are there no marshlands, but every small creek subject to tidal influences and every lagoon and slough protected from the surf is bordered by marshlands. Some of the plants, at least the genera, that grow in tidal marshes are worldwide in distribution. Since some of the same genera and species occur on inland salt marshes, it is best to refer to the marine marsh as a tidal marsh in order to emphasize the different characteristics and environmental modifications that prevail in the region subject to the periodic fluctuations in level and seasonal storms associated with the border of the sea.

Although not an integral part of a tidal marsh, the submersed growths of such marine phanerogams as *Zostera*, *Posidonia*, *Cymodocea*, or *Thalassia* may, under certain circumstances, prepare the way for the formation of a marsh by the trapping and accumulation of sediments. Some of these marine pondweeds or "eel grasses", especially species of *Posidonia* and *Phyllospadix*, grow on rocky bottoms. The reeflike accumulates or "mattes" of plant material and sediments formed by *Posidonia oceanica* on the Mediterranean coast of France are described in some detail by Molinier and Picard (1952); similiar formations along the Egyptian coast are discussed by Aleem (1955). These authors consider *Posidonia* to be a major biogenous agent, similar to the algae of tropical reefs in its effects on the environment. The lagoon floors of tropical reefs are often occupied by fields or patches

PLATE 2.—VIEWS OF DUTCH WADDENS

FIGURE 1.—Exposed tidal channel, showing laminations and other minor features. (Photograph courtesy L. M. J. U. van Straaten)

FIGURE 2.—Tidal creek bordered by mussel beds. (Photograph by D. Kreger, courtesy L. M. J. U. van Straaten)

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FIGURE 1. Exposed tidal channel, showing laminations and other minor features. (Photograph courtesy L. M. J. U. van Straaten)

FIGURE 2. Tidal creek bordered by mussel beds. (Photograph by D. Kreger, courtesy L. M. J. U. van Straaten)

VIEWS OF DUTCH WADDENS

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VIEW OF A NATURAL OYSTER REEF, ISLE DERNIERES, LOUISIANA

(Photograph by Davis Aerial Photographic Service, Houma, Louisiana, courtesy of Texas A. and M. Research Foundation)

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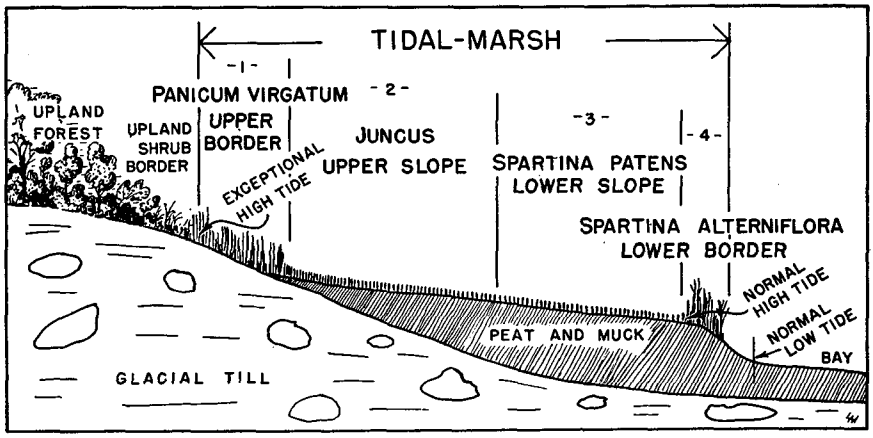

FIGURE 28.—*Diagrammatic cross section of the upland-to-bay sequence in a New England tidal marsh*

Showing the characteristics of the major vegetational units. Vertical scale much exaggerated. From Miller and Egler (1950)

of *Thalassia* (turtle grass), which is also the genus occupying sheltered bay environments on the Gulf Coast of the United States and in the Caribbean region. *Zostera* seems to be chracteristic of temperate and warm-temperate latitudes and is widespread in cooler regions of the northern and southern hemispheres, where it occupies bay bottoms and the deeper sloughs of marshlands. Shaler (1886) postulated that a growth of *Zostera* was the initial stage in the development of a marsh on a subsiding coast, but subsequent studies have indicated that it is not a necessary stage in marsh development.

Between the low-tide level and the marsh proper there is a barren zone, where erosion and wave action prevent the establishment of vegetation, but where such action is not great there are felts or mats of blue-green or green algae. As Taylor (1954, p. 179) observes,

When sediments become stabilized, a different situation is presented. If the tidal rise and fall is considerable, broad zones of beach which were immersed at high water of spring tides are exposed at times of neap tide and such zones may show an algal flora. If they receive enough moisture from salt-marsh pools by percolation, or from rain or by other means, they may support a considerable and recognizable vegetation of such Myxophyceae as *Lyngbya aestuarii* and *Microcoleus chthonoplastes*, or on the surface mats of *Rhizoclonium riparium*. Such a vegetation may even be able to survive a little gentle wave action undisturbed. Where silt transported by stream movement is left stable by recession, it, likewise, may develop similar colonies in brackish estuaries."

Above this zone, at about mid-tide level, are found the first (or last) plants of the tidal marsh. In many parts of the northern hemisphere the sea-most plant ("first colonizer" or "pioneer") is usually a species of *Spartina*, forming a narrow zone between the bare mud and the next vegetation type, which on many marshes may be another species of *Spartina*. On the New England marshes this sequence is represented by *Spartina alterniflora* and *S. patens* (Fig. 28). In many parts of the southern hemisphere—*e.g.*, New Zealand and western South America—*Spartina* is absent, and the pioneer stage is occupied by species of pickle-weed, *Salicornia*, or even *Scirpus* (as in New Zealand; *see* Evans, 1953), a genus characteristic of higher levels in North America.

In Australia the transition is from *Zostera* or *Ruppia* to *Navicula* or blue-green felts that hold the muds together, preventing erosion and turbulence. Through this mat grows the *Salicornia* or *Juncus*, followed by *Atriplex* and then *Casuarina* or one of the ti trees, *Melaluca*.

It is not safe to say, even for the northern hemisphere, that a given species of *Spartina* is the

PLATE 3.—VIEW OF A NATURAL OYSTER REEF, ISLE DERNIERES, LOUISIANA

(Photograph by Davis Aerial Photographic Service, Houma, Louisiana, courtesy of Texas A. and M. Research Foundation)

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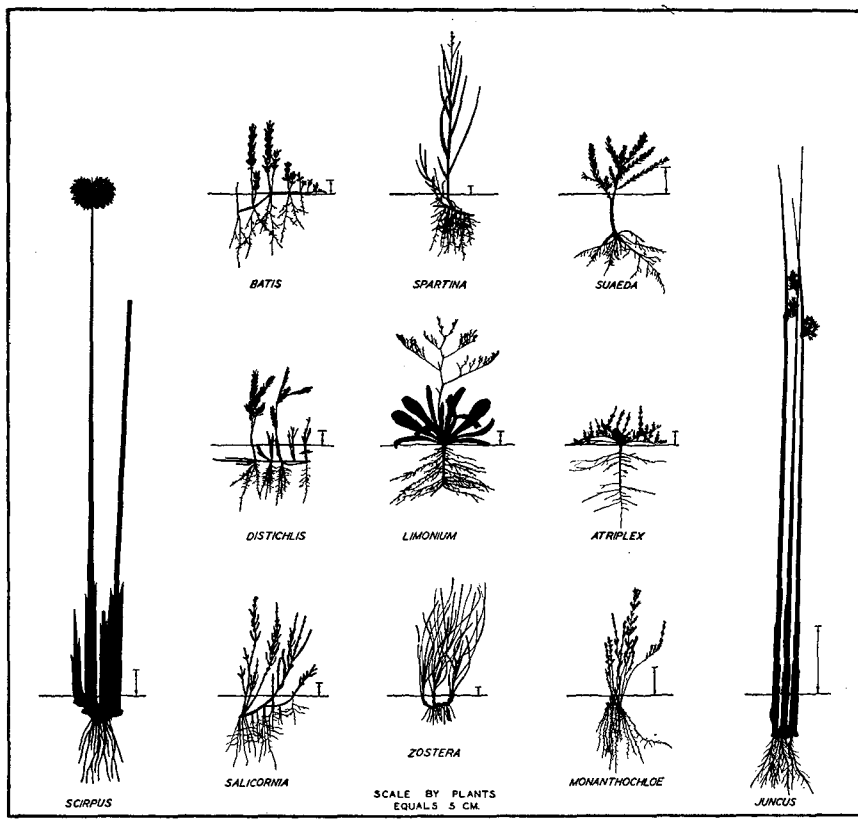

FIGURE 29.—*Silhouettes of several typical genera of marsh phanerogams, especially as represented in California*

"pioneer," in view of the example of *Spartina townsendii* in Europe. This species was apparently unknown before about 1870 and is now considered to be a comparatively recent hybrid between *Spartina stricta* and *S. alterniflora* (Jacquet, 1949; Perraton, 1953), but it is nevertheless the dominant species of tidal marshes in southern England and the French channel coast.

The intermediate zone, whether of *Spartina*, *Salicornia*, or some other plant, gives way, near (or somewhat above) the high-tide line, to a zone characterized in New England marshes by *Juncus*, and in some regions by the "general salt marsh" of Chapman (1938), consisting of several (six or more) species. *Distichlis* is a characteristic genera of the middle or intermediate tidal marsh zones; in New England it occurs throughout the *Spartina patens* zone, tends to form nearly pure stands (in places with *Borrichia*) on the Texas coast, and is missing from the flora of many localities (*e.g.*, New Zealand, England). *Plantago*, considered characteristic of higher zones in English tidal marshes, is found, with *Limonium*, from the *Spartina alterniflora* zone to the *Juncus* zone in eastern North America. The upper border of the tidal marsh, inundated only by the highest seasonal tides, is characterized by *Panicum virgatum* in New England, by *Batis maritima* in England, and by *Distichlis* in southern California. Some of these characteristic marsh genera are illustrated in Figure 29.

While the zonation of phanerogams on a given marsh or series of marshes in a particular region may be well marked and constant, the arrangement, at least in generic constitution, may be quite different in another locality. A general summary of the distribution of halophytes up to 1940 is given by Uphof (1941), although without reference to specific tidal levels. Some recent papers are by Bourn

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and Cottam, (1950), Chesapeake Bay; Boyce (1954), N. Carolina; Chapman (1938–1941), England, NE. America; Dansereau (1947), Brasil; Davis (1948), Florida; Evans (1953), New Zealand; Gillner (1950), Sweden; Jacquet (1949), France; Mikkelsen (1949), Denmark; Miller and Egler (1950), Connecticut; O'Neill (1949), Louisiana; Patton (1942), Australia; Penfound and Hathaway (1938), Louisiana; Perraton (1953), England; Purer (1942), S. California. (*See* the annotated bibliography under phanerogams for further details.)

The more important factors controlling the zonation of phanerogams on tidal marshes are the height of the marsh, the salinity of the soil, and the texture and bulk density of the soil. Of these, perhaps the height of the marsh is the most important factor, since this determines the level to which tidal waters may reach and the percentage of coverage by the water. This tidal coverage, combined with inflowing fresh water, determines the salinity conditions in each community. The bare zone between the edge of the marsh and the low-tide level is an unstable region where the greatest runoff during ebb occurs, and erosion prevents the establishment of rooted vegetation. In those parts of the marsh where the water table is sustained by tidal action, and the fine-grained nature of the soil and its low permeability assist in the retention of moisture, salinities are high. Curves of salinity across a marsh are approximately equal to sea water on the lower and middle zones; they rise to a peak during the dry season in the upper zone and fall to nearly zero in the supralittoral zone.

The question has occasionally been raised whether the salt-marsh plants grow where they do because of preference for saline or brackish conditions or because these plants have a higher tolerance for such conditions. Taylor (1939) attempted to answer this question by growing certain salt-marsh plants under various conditions of controlled salinity. He found that 10 common species grew best in nearly fresh water and that only *Salicornia europaea* and possibly *Distichlis spicata* of this series were true halophytes. Oosting (1945) conducted a somewhat similar experiment; he subjected marsh and dune plants to salt spraying and found a graded series of tolerances to this treatment, corresponding to the zonation of the plants. The question of what a halophyte is appears to be somewhat a matter of degree. (*Cf.* Uphof, 1941.) The best example of a halophyte is probably *Salicornia*; Patton (1942) found a greater osmotic pressure in the cell sap of *S. australis* than in the surrounding water, and plants of this genus are characteristic of marshes bordering highly saline waters, including the salt pans of marshes, which they often invade as the first pioneers.

All the characteristics of the sediments essential for the growth of the salt-marsh plants are closely interconnected. One factor is the bulk density and porosity of the mud. Measurements made at Newport Bay, California indicate a trend toward lower bulk densities in area of finer-grain sizes (Stevenson, 1954). In the *Zostera* bed with a sandy soil, the average bulk density was 1.72. In the *Salicornia* zone, however, it was 1.10. A low bulk density may be one factor in the tolerance of the various species of *Spartina* and *Salicornia* because neither plant is found in areas where grain sizes are large and densities high. With the lowest bulk densities, the sediments in the *Salicornia* zone are not commonly saturated with water, whereas those where *Spartina* grow are nearly always saturated. Under normal conditions the mud in the latter zone is very loose and fluid and cannot support weight. Plants of *Spartina leiantha* are thus readily pulled up with their roots, and storms accompanying high tides often uproot scores of them.

Rate of deposition of sediment also influences the vegetation, for in areas of rapid accretion most of the energy of the plants is required for upward growth of the main stem, with little development of branches (Richards, 1934). Still faster deposition would overwhelm the plant and leave a barren surface, as on parts of the Dutch waddens.

A detailed description of the animal life of tidal marshes is beyond the scope of this work. The marshlands, teeming with bird life, the breeding grounds of mosquitoes and muskrats, with their sloughs frequented by fish, have excited the interest and attention of ornithologists, mosquito-abatement committees, and economic zoologists, to say nothing of the sportsman with rod and gun. Hence, there is a vast literature on all aspects of life on marshlands. (*See* McAtee, 1941, for a typical example.) Comparatively little of this literature is of use to the paleoecologist who requires field correlates for his studies. An example of the use of fossil and subfossil mollusks in interpreting the history of a marsh is the often-overlooked study by Knight (1934). In recent years students of Foraminifera have demonstrated that the foraminiferal facies of tidal marshes are surprisingly uniform throughout

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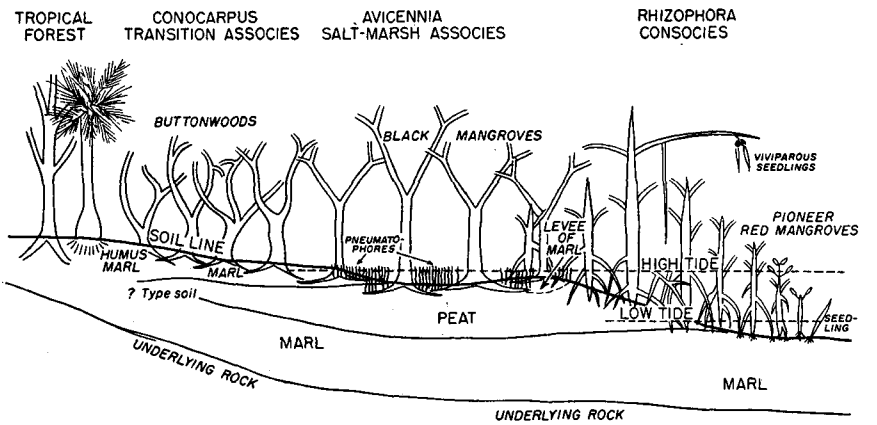

FIGURE 30.—*Diagrammatic transect of the mangrove communities from the pioneer Rhizophora family to the tropical hammock forest*

Showing approximate tide levels and soil conditions usually found in marl soil regions (*e.g.*, Florida). After Davis (1940)

the world and a number of papers describing such facies have appeared. (*See* especially Phleger and Walton, 1950, and Rottgardt, 1952).

MANGROVE SWAMPS: The pioneer role of the mangroves in colonizing the muddy estuarine shore and initiating the succession leading toward the establishment of the tropical forest is presented diagramatically in Figure 30 (for further details, *see* Davis, 1940; Dansereau, 1947). Some students consider that the importance of mangroves as land builders has been overemphasized (Thorne, 1954). When fully developed a mangrove swamp is an impenetrable thicket of roots over the tidal flat affording shelter to a host of semi-aquatic organisms such as various mollusks and crustaceans and providing access from the near-by land to birds, reptiles, and even monkeys (Hesse *et al.*, 1951, p. 240–241).

Although the black mangrove *Avicennia* (actually a laurel) occupies the next position landward where the red mangrove *Rhizophora* is well developed, there are places where *Avicennia* grows in the absence of *Rhizophora*, and in such places it is the pioneer plant. Such a situation can be seen on the coast of Louisiana west of the Mississippi Delta (and in the lower part of the Laguna Madre of Texas) where dense thickets of *Avicennia* grow along the bayous on the coastal islands. Such growth is evidently on the margin of the range for this plant, as it is severely damaged by frost in this region. In Australia *Avicennia* occurs from about 28°S to 37°S. E. J. Ferguson Wood reports that in Australia *Avicennia* is commonly known as the gray mangrove and "black mangrove" is a species of *Ageciras*.

Mangrove swamps are not peculiar to estuarine situations but may be developed in shallow oceanic lagoons. Such a mangrove swamp on the Great Barrier reef is described by Yonge (1930) and by Stephenson *et al.* (1931). Where the mangroves grow on sandy ground there may be dense "fields" of *Thalassia* and sandy-bottom pools inhabited by typically marine assemblges. Within the swamp itself are muddy glades, frequented by such gastropods as *Telescopium telescopium* and *Pyrazus palustris*, the hermit crab *Clibanarius striolatus*, and the skipping fish *Periophthalmus koelreuteri*. The burrowing red crustcean *Thalassina anomala* and the large black lamellibranch, *Cyrena coaxanus*, also occur.

Oysters are more abundant in estuarine mangrove swamps, where the typical "mangrove facies" is best developed. This "facies" is a curious mixture of marine, estuarine fresh-water, and terrestrial forms. The mudskipper, *Periophthalmus*, feeds on crabs, mollusks, and insects (which invade the mud flats beneath the mangroves during low water), and the mud itself harbors many worms, including a sipunculid which seems well on the way to becoming a terrestrial animal (Harms and Drag-

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endorff, 1933). Indeed the environment of the mangrove swamp seems to be one of the most favorable of existing environments for the transition from sea to land (Gislén, 1947).

There is some doubt, however, that it was available as a migration route during the first transitions to terrestrial life, for mangroves, as we know them today, do not appear until mid-Cretaceous time, although they may have developed earlier (Axelrod, 1952). While mangrove swamps may therefore be of comparatively late origin, geologically speaking, they were probably preceded by similar tidal communities, made up of lycopods, arthrophytes, and ferns.

DELTAS: The great river deltas present another aspect of the estuarine environment, in which depositional forces are either in balance with or stronger than erosional forces. Where the coast line is sinking, the delta may be built into the sea, as that of the Mississippi, or fill up a former estuary, as in the case of the Danube (Antipa, 1937). Deltas are not well developed in regions of subsidence where tidal action is strong, but instead we have environments like the waddens and the deeply incised estuaries of England. Reduced tidal action is not a necessary requirement for a development of a delta; the Niger has a well-developed delta where the tidal range is about 6 feet (but the Congo does not). A delta is essentially a complex of estuaries between marshlands; even in the Mississippi delta a wedge of saline water creeps upstream against the fresh-water flow.

In spite of the great economic importance of deltas (many of which are valuable fishing areas), there are few comprehensive studies of the physiography and ecology. The work of Antipa (1937; 1941) on the delta of the Danube is a classic study that is yet to be approached for other deltas, although Schachter's researches on the Camargue (the delta of the Rhone) lack only a survey of historical changes to compare with Antipa's work in comprehensiveness. Some preliminary studies of the delta of Nile have been published by Faouzi (1937), and the productivity of the Volga delta has been analyzed by Chugunov (1923).

The great delta of the Mississippi River has also been neglected from the viewpoint of comprehensive ecology, although there is a considerable body of information concerning its physical processes, the adjacent marshlands, and the associated fisheries. The papers of O'Neill (1949) and Penfound and Hathaway (1938) provide some information on the marshlands, the general physiography has been described by Russell *et al.* (1936), and the history of changes in the lower river system is presented in some detail by Fisk (1944). The effects of such changes on the fauna, and especially on the oyster fishery, have been outlined by Gunter (1952), and the zoogeographical aspects have been briefly reviewed by Hedgpeth (1953). All this information remains to be synthesized as a comprehensive monograph.

III. Sedimentation in Estuaries, Tidal Flats and Marshes

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Many fairly detailed reports on certain minor aspects of the sediment in individual estuaries and lagoons have been published, but only a few general summaries of sedimentary conditions in contemporaneous environments are available. Two good but brief ones were prepared by Andree (1920) and Twenhofel (1932) as parts of more general textbooks.

GRAIN SIZE: The distribution of grain sizes in estuaries and lagoons is fairly well known from studies made at a number of places throughout the world. The coarsest sediment in most estuaries and lagoons is on the barrier or baymouth beach or bar. This consists of sand or even cobbles (in many estuaries of southern California, New England, and Britain). In some instances the material is too coarse to have been transported across or through the tidal flats and has been derived from erosion of a sea cliff followed by longshore transportation by waves. The excellent sorting and the absence

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of much silt and clay may also be ascribed to the turbulence of the waves. Some estuaries have an entrance that was originally narrow because of the submergence of very irregular topography. Tidal currents in such entrances are great enough so that the bottom has been scoured out locally, leaving rocky or gravelly bottom. Examples are San Francisco Bay (Louderback, 1939) and many bays or estuaries of Japan (Shepard, Emery, and Gould, 1949; Hishida, 1950) and Britain (Allen and Todd, 1900).

In general, conditions in an estuary are the reverse of those in a river. In the river proper the coarser sediments are generally in the channel, and the finer sediments are along the shore. In the tidal section of a fresh-water river a transition takes place, and the distribution of sediments is quite variable and confused. However, as soon as the estuary proper is reached, where there is some admixture of sea salts, and were the net up-stream flow of the lower layers occurs, there is a distinct change in sediment distribution. Near the mouth of the estuary coarser sediments are frequently again found in the channel as a result of the action of larger waves from the ocean and because much of the silt load of the stream has already dropped into the channel farther up the estuary.

Flat portions of the floors of estuaries and lagoons that are deeper than about 3 fathoms are generally covered by a blanket of sediment that becomes progressively finer with depth of water. One of the best examples is the Thau Lagoon on the Gulf of Lions in southern France, where Sudry (1910) found a smooth concentric pattern of sediments ranging from sand along shore to fine mud at depth. Other examples are Tvärminne Storfjärd in Finland (Segerstråle, 1934) and Chesapeake Bay (D. W. Pritchard, personal communication). Such an ideal distribution of sediments occurs only where the bottom is relatively flat and wave and current conditions are mild. The net up-stream flow in the lower-water layers of an estuary is an important factor in keeping the finer materials in the channel. Where the area is more open to waves and currents, such as Ensenada Bay in Baja California, Mexico, the sediments are less regularly distributed. Finally, where the deeper areas are extremely irregular, mud occurs only in the lower areas, and coarser sediments, such as calcareous sand, residual sand, and even residual gravel characterize the shallower banklike areas. Examples are common in Japan (Niino, 1943; Shepard *et al.*, 1949) and have been reported in the United States at Buzzard's Bay (Hough, 1940).

The sediment distribution in the shallower areas of estuaries and lagoons (mostly the tidal flats) is more complex but usually follows a systematic pattern. Most of the flow of water is naturally confined to well-defined channels (Plate 2) that slowly change and migrate over the tidal flat, as shown by remapping at intervals of several years (Lüders, 1934; Van Veen, 1950). The velocity of the water is such that the finer grains are swept out, and a residual concentration of coarse sediment is left in the channels. This sediment is slowly shifted, replaced by new sediment brought in during floods, and buried. Perhaps the most comprehensive studies of the relationship of the coarse sands to tidal channels were made at Jade Bay, Wilhelmshaven, Germany (Linke, 1939), the Wadden Zee off the Netherlands (Koning, 1950), Barataria Bay, an estuary on the Mississippi River delta (Krumbein, 1939), and Newport Bay, California (Stevenson, 1954).

The tidal-flat areas between the channels, in contrast, consist of poorly sorted mud that generally becomes finer with distance from the tidal channels. This distribution is much the same as that noted by Russell and Russell (1939) between distributaries of the Mississippi delta.

ORGANIC CONSTITUENTS: In addition to their mineral content, the sediments contain a host of animal and plant remains. Remains of all phyla of animals are buried in the sediment, but not all may be preserved as fossils. So much organic debris is contributed from the fresh water of rivers, the salt water of the open sea, and the overlying brackish water that Bourcart (1942) has termed the mud a biological milieu. The organisms, even if their remains become scattered by scavenging, decomposition, and diagenesis, still have enriched the sediments in organic matter, calcium carbonate, silica, nutrients, and other constituents.

Possibly the most interesting of these is organic matter. Trask (1932, p. 151–162) made many analyses of organic nitrogen in sediments of estuaries and lagoons throughout the world. Study of his results shows that, in general, the deep floors of areas where evaporation is less than runoff and precipitation have organic nitrogen from 0.2 to 0.6 per cent, and hypersaline areas, below 0.2 per cent. The dividing percentage, 0.2 organic nitrogen, corresponds to about 1.7 per cent organic carbon, or 2.9 per cent total organic matter.

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The muds of the floor of Laguna Madre, a hypersaline lagoon complex on the Texas coast, have only 0.04 per cent organic nitrogen according to Trask, about 0.6 per cent total organic matter. Those of San Pedro Bay, a marine environment in California, have 0.1 to 0.2 per cent organic nitrogen. In contrast, Barataria Bay, an estuary in Louisiana, has up to 2.3 per cent organic carbon, about 4 per cent total organic matter (Krumbein and Caldwell, 1939). Much lower values characterize the coarser sediments of the tidal channels and the beaches of Barataria Bay. In general, one would expect the highly organic sediments of normal estuaries and lagoons to be black (Yoshimura, 1938; Hishida, 1950) or at least darker than those of lower organic content belonging to the hypersaline environment.

Phosphorus, like nitrogen, is abundant in sediment of normal environments—0.1–0.4 per cent in the Clyde Estuary (Moore, 1930) and about 0.1 per cent in some Australian estuaries with highest values in the tidal zone (Rochford, 1951b). Rochford made a very thorough study of phosphates in estuary muds in order to determine their productivity; he found an inverse relation of released phosphate and oxygen in the water.

Calcium carbonate in the sediments is highly variable because of the presence or absence of shells and because of solution induced by low pH. This solution is probably much more active in normal than in hypersaline areas. Trask (1932, p. 99) found that the median calcium carbonate content in sediments of brackish environments is very low (0–2 per cent). In deeper sediments of coastal bays of temperate and arctic regions he found that calcium carbonate ranges between 0 and 6 per cent, whereas in bays of tropical regions it is 10–47 per cent.

MANNER OF DEPOSITION: The organic constituents of the sediment come from organisms living in the water or the bottom of the rivers, the sea, or the brackish parts of the estuaries and lagoons. Because of the wide range of habitats represented, the burial assemblage can be a most complex one (Miyadi and Habe, 1947).

The inorganic sediments are also of complex origin; they were derived in varying proportion from entering rivers, bordering sea cliffs, the outside sea floor, and from reworking of marsh and other recent deposits (Sollas, 1883; Brockmann, 1935). The bulk of the sediment of most estuaries and lagoons is contributed by rivers. In the main distributaries, usually continuous with tidal channels, the sediments are coarse. Most deposition normally takes place at or beyond the end of the distributaries, prograding the tidal flats. At all river stages, much of the fresh water flows out atop the dense salt water and carries with it a load of suspended sediment. Probably in most streams the bulk of the suspended sediment is silt which is deposited directly out of suspension. Clay sizes, however, may be deposited through flocculation. On flocculation, the clays fall through the water and are added to the deeper floors of the estuaries and lagoons. Bourcart (1939; Bourcart *et al.*, 1941) has shown that much sediment also travels down the Seine River at or near the surface in large floccules containing much organic debris. When these settle to the bottom or are stranded by lowering water level they stick and are held there by capillary action.

Sediments derived from erosion of sea cliffs are most abundant around the periphery of estuaries, where cliffs are occasionally attacked at high tide by the relatively small waves. Additional cliff-derived material moves along the offshore or baymouth beach or bar. Some of this material, plus other sediment from the sea floor, is swept into the entrances of the estuaries and lagoons by flooding tidal currents, and probably most of it remains near the tidal inlets (Lucke, 1934). During storms additional material is transported across the bar into the quiet water behind it. Thus there is a continuous loss of sediment from the seaward side of the barrier that results in a landward shift of the beach unless there is a compensating resupply of new sediment. Off the North Carolina coast repeated surveys (Beach Erosion Board, 1935) have shown an average rate of erosion of the bar of 18 feet per year between 1852 and 1917. Mixed with the sediment that is carried into the lagoon or estuary are numerous shells of animals that live only in the open sea and that therefore serve as criteria of seaward derivation of the sediment.

Regardless of the source of the sediment, much reworking occurs within the estuaries and lagoons. Probably most, but not all, reworking takes place on the shallow tidal flats where the ebbing and flooding currents erode and redeposit the sediment. Erosion is well shown by the migration of the tidal channels and by the muddy color of the water when no inflow of river water is taking place. Newport Bay is a good example of reworking because the original river course was diverted from

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the bay years ago, and yet the marshes still receive sediment, evidently at the expense of other portions of the marsh. Most of the sediment that is eroded at flood current is deposited on the wide flat marsh during the slack at high tide. Probably only a minor amount of sediment is eroded by the ebbing current, and most of it must be carried into the deeper areas nearer the entrance, or even out to sea.

One of the best studies of reworking was made by Hunter (1912) in the Chesapeake Bay near the mouth of the Choptank River, by comparing maps made in 1848, 1900, and 1910. He found that erosion on low cliffed shores of clay and marl amounted to as much as 110 feet per year. Three islands were removed. The bottom in depths of 30 feet was deepened or shoaled by as much as 6 feet. Because a much greater area was deepened than was shoaled, Hunter considered that at least that part of the bay was then in a cycle of erosion.

The prevailing condition within estuaries and lagoons must, of course, be deposition. The average rate of deposition is far greater than that of the open sea because most of the sediment deposited in the open sea is contributed by rivers, many of which have to first pass through the quiet settling basins provided by estuaries and lagoons. Probably the fastest rate is at the end of a prograding tidal flat. The rate atop a tidal flat is a function of the supply, the height of the flat, and of the rate of subsidence due to compaction and diastrophism. As long as deposition exceeds compaction, the tidal flat can be built up, but where deposition is prevented by diversion of streams and by building of retaining dikes and walls the surface must slowly sink. Recent studies of the bays along the Texas coast by F. P. Shepard (1953) indicate an average shoaling of the order of 9 inches from 1875 to 1936 in spite of general subsidence of the region of about 1 foot during the same period.

INTERSTITIAL WATER: The amount of interstitial water in sediments of estuaries and lagoons depends on their porosity and the percentage of saturation. Sediments below low tide can be expected to be fully saturated, with a water content by per cent wet weight ranging between 12 per cent for sand and about 70 per cent for the finest mud. The soupy top layer of mud may have an even higher water content.

The salinity of the interstitial water is dependent on that of the overlying water and thus in an estuarine environment can be much higher or much lower than normal sea water. Reid (1932) has shown that there is only slow interchange between the interstitial water and the overlying water; accordingly, the salinity of the interstitial water probably represents a rough median value of the salinity of the overlying water which flows past the point during the year. Because the salinity of the interstitial water is subject to a smaller range and variation than is the overlying water, it provides a fairly stable environment for burrowing organisms and for the roots of plants. Where the sediments are exposed for long periods above sea level, however, the surface layer has a great change of salinity, ranging from complete leaching by rain water to development of a salt crust by prolonged evaporation (Chapman, 1939). A smaller range in salinity is presented by sediments at greater depth below the surface.

Direct measurements of oxygen content of the interstitial water are difficult, and there are few recorded. Thamdrup (1935) found that concentrations of oxygen in the water of the surface mud of the Danish Waddensea were less than 10 per cent saturation, and in surface muds below mid-tide there was no oxygen. These muds were black and contained up to 5 mg/L of hydrogen sulfide. This condition is also present in the mud flats of Germany (Linke, 1939) and the Netherlands (Van Straaten, 1950b; 1951b). The muds covering the bottom of normal estuaries and lagoons are also high in hydrogen sulfide. Many other examples are known from the Baltic Sea (Segerstråle, 1933; Strøm, 1939; Brattström, 1941) and elsewhere. Locally, the hydrogen sulfide even becomes so abundant that gaseous outbursts of muddy sediment occur (Copenhagen, 1934). In other areas the oxidation-reduction potential (Eh) tells much of the story. Muds of San Pedro Bay estuary (Emery and Rittenberg, 1952) and Mission Bay marshes (ZoBell and Feltham, 1942) have a negative Eh, indicating that they are reducing, and that no free oxygen is present. Under such conditions, these and other similar muds have an odor of hydrogen sulfide, produced by anaerobic bacteria that extract their oxygen supply from sulfates of the interstitial water. The hydrogen-sulfide concentration is also reflected in a black color resulting from formation of ferrous sulfide (Doss, 1912; Häntzschel, 1939b). At San Pedro Bay and Newport Bay in California, this deposit was considered to be melnikovite; no pyrite was present. However, in the Dutch waddens pyrite is present below the zone of

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iron monosulfides (Van Straaten, 1950b; 1951b). On a mud flat at Newport Bay an area of crystalline sulfur was discovered. This may be due to local oxidation of hydrogen sulfide following penetration of air into the sediment in a manner analogous to that reported for some lake-floor sediments by Lohammar (1939). Other gases such as methane (marsh gas) are not uncommon (Schütte, 1914) and during their escape may produce gas pits and domes (Klippel, 1939).

The oxygen consumed by bacteria is of prime importance in the distribution of animals. Bacterial consumption causes a deficiency of oxygen below the top few centimeters of mud. This, coupled with the presence of hydrogen sulfide, discourages most animal life below the mud surface. A few species make temporary excursions, and others may inhabit the mud and feed or respire with siphons or introverts. Protozoa (*e.g., Euplotes*) and nematodes may be abundant in certain conditions. Most bottom dwellers must, however, restrict their activities to the top layers of mud. Even on the mud surface, the rate of oxygen consumption by bacteria may reduce the supply so much that the oxygen tension of the overlying water is noticeably lowered. Other processes in the mud also consume oxygen, but ZoBell and Feltham (1942, p. 74) have determined that the bacteria are the principal users.

Bacteria are also responsible for the formation of organic acids that may bring the pH well below the values of about 7.5 that are produced by high carbon dioxide from animal respiration. Although the pH of the waters varies greatly with locality, climate, depth of water, and other factors, a reasonable average is between 7.8 and 8.0. The pH of muds, however, usually ranges from 7.3 in sandy mud to 5.7 in very clayey mud of Newport Bay (Stevenson, 1954). In Australian estuaries the range is usually 6.8 to 7.8 (E. J. Ferguson Wood, personal communication). Marshes of Newport Bay and others along the Pacific coast contain low concentrations of calcium carbonate. The same situation exists on marshes and mud-floored estuaries and lagoons elsewhere in the world (Sudry, 1910) and even on mud flats (Van Straaten, 1950b).

That estuarine sediments have low values of pH and calcium carbonate could be significant when dealing with black shales which have primarily chitinous fossils. Also it is quite possible that ancient estuarine deposits may be barren. It seems important, therefore, that means other than paleontologic should be devised to identify ancient brackish-water sediments.

In addition to its areal variation, the pH may present a decrease from the mud surface to depths of a few inches followed by an increase at greater depth (Debyser, 1949a). In a mud flat near La-Rochelle, France, Debyser (1949b) also found a diurnal variation of pH from about 8.0 at night to 8.4 in the day that evidently is produced by photosynthetic activity.

CHARACTERISTIC MINOR FEATURES: In discussing the characteristic minor features of the sediments, such as cross bedding, laminations, slump structures, mud cracks, erratic inclusions (shells, etc.), and traces of burrowing organisms, it is convenient to divide the environment into several sections: beaches, subaqueous areas, and tidal flats. The beaches along the seaward side of the offshore or the baymouth bars or islands are not materially different from others facing the open sea. Those around the periphery of the marshes differ from seaward beaches only in a minor degree, in having steeper slope, poorer sorting, and greater entrapment of air, all resulting from the presence of only small waves. Shells included in the sand also are different because most of them are derived from the tidal flats, instead of from the floor of the open sea. The minor features of these beaches are similar to those of other beaches.

Little is known about the minor features of the submerged portions of estuaries and lagoons, except that cross-bedding must be common in shallower areas having continuous erosion and redeposition by tidal currents. For the same reason, the coarser debris must tend to work its way downward, so that one would expect the common presence of coarse debris covered by finer materials throughout the shallower part of the subaqueous area. Examination of the surface of this area by diving and by underwater photography is impeded by the turbidity of the water.

The third portion of the environment is the tidal flats; considerable information about them is available, and many sedimentary features occur only in that environment. The presence of these features in ancient sediments can serve as adequate criteria for identification of tidal flats. For convenience, we might divide the features of tidal flats into two main categories: those of mechanical-chemical and those of organic origin. The mechanical-chemical category includes general sediment characteristics such as fine grain size, poor sorting, high organic matter, presence of hydrogen sulfide

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and iron sulfides, black color, and low calcium carbonate. Perhaps more interesting, however, are the minor structural features.

In the study of these features, the workers at Senckenberg-am-Meer at Wilhelmshaven, Germany, have done most outstanding work. Brockmann, Häntzschel, Krejci-Graf, Lüders, Richter, Schäfer, and Schwarz have devoted much time and energy to the description and evaluation of the characteristic features found on the extensive waddens bordering the mouths of the Elbe, Weser, and Ems rivers. Their work has been well summarized by Richter (1929) and by Bucher (1938) who gave an extensive bibliography. Schäfer (1953) published a historical review of Senckenberg-am-Meer.

ANCIENT DEPOSITS: Estuarine and lagoonal deposits, especially their marshes, are formed so near sea level they should easily be destroyed if uplift follows deposition. However, there must have been many times when the site of deposition became downwarped, giving the deposits a good chance of preservation. If the region were submerged fairly continuously one would expect to find the deposit atop eroded land topography and below neritic marine deposits. It is, of course, obvious that there may be some examples of formation of the deposits during a short period of emergence, as a result of which they may be found atop marine sediments and below nonmarine ones. In addition, during a long time of stability after submergence the deposits may form on eroded land topography, build up to sea level, and then be covered by flood-plain and other nonmarine beds. The more general relationship of the estuarine and lagoonal deposits to the supposed sequence of deposits and environments of geosynclines has been attempted by Krumbein, Sloss, and Dapples (1949) and others.

The estuarine and lagoonal deposits themselves appear to contain sufficient criteria to permit their proper identification at least in many instances. If preserved, the fauna and flora may contain many characteristic species as outlined above, though in general the ratio of number of species to number of individuals is lower than in most other environments. These characteristics permitted Hiltermann (1949) to recognize brackish-water environments in rocks of Mesozoic and Cenozoic age in Europe. In addition, there should commonly be present some mingling of fresh, brackish, and salt-water species. Even if the fossils are not preserved in recognizable form, one should expect a high content of organic matter, in normal environments with sediments characteristically black with abundant iron sulfides. Extreme examples of hypersaline environments may contain beds of salt or gypsum formed by excessive evaporation. Minor features of the sediments in both types should include tracks, borings, laminae, and rarely mud cracks. In some instances all shells and tests originally deposited in black muds may have been dissolved during diagenesis; the chitinous parts would remain the longest. In other muds the remains may be partially dissolved. Richter (1931), for example, presents photographs of half-dissolved trilobite and mollusk remains from the Paleozoic Hunsrück shales.

The black shales and underclays interbedded with marine and non-marine beds that constitute the cyclothems of the Pennsylvanian and other periods are certainly transitional. As suggested by Wanless and Shepard (1936) and others, they may well be lagoonal marsh deposits.

The lithologic and organic characteristics of many black shales and graptolitic black shales suggest estuarine or lagoonal origin, though published beliefs regarding their environments of deposition have been clouded by much misinformation about marine processes. An excellent review of the various opinions has been presented by Twenhofel (1932, p. 258–265).

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Chapter 24

Baltic Sea*

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INTRODUCTION

Separated from the Atlantic by the Scandinavian Peninsula, the Baltic Sea penetrates far into the northern part of the European Continent, extending over an area of about 420,000 sq km (distance from Copenhagen, at the entrance, to the inner end of the Gulf of Bothnia, *ca.* 1500 km, greatest width *ca.* 300 km).

The Baltic can be regarded as a northern equivalent of the Mediterranean in that it is enclosed by land and communicates with the Atlantic by narrow outlets at its western end. In many other respects, however, the Baltic is just the opposite of the Mediterranean Sea—*e.g.*, regarding depth and temperature conditions. The main part of the Mediterranean basin lies more than 2000 m below the surface (maximum depth more than 4000 m), while the Baltic is a shallow area, where depths less than 100 m predominate (maximum depth 459 m). The temperature in the Mediterranean is fairly stable and high (never below 12°–13°C.), whereas in the Baltic, the northern end of which extends almost to the Arctic Circle, there are strong seasonal fluctuations, and in winter the inner parts are regularly covered with ice. However, the most striking difference between the basins concerns the salinity conditions. In the Mediterranean the strong evaporation balances the fresh-water influx and even increases the saltiness of the water in comparison with that of the Atlantic (to more than 39‰); the much lower evaporation from the Baltic, in combination with the great volume of fresh-water delivered by about 250 rivers, causes a high dilution. By far the greater part of this area has a salinity less than 8 ‰, and farthest inward, at the end of the Gulf of Bothnia and the Gulf of Finland, the water is almost fresh. Thus the Baltic belongs to the ecologically interesting brackish-water areas and, in the main, even to the highly diluted "brackish-waters par excellence" (Redeke), characterized by special plants and animals and by a peculiar mixture of marine and lacustrine organisms. The Baltic is by far the largest marine area of this type in the world.

The ecological interest offered by the brackish Baltic is augmented by the fact that the salinity is strikingly stable in comparison with conditions in estuaries off open oceanic coasts, caused mainly by the absence of tides. Furthermore, the salinity decreases slowly and gradually toward the inner end of the long, narrow basin. Thus, the Baltic forms, as it were, a gigantic experimental aquarium for studies of the bio-

* As the author of this chapter is a zoologist, more stress is laid upon the fauna than upon the flora. The author's thanks are due to the following specialists, who have critically read the manuscript or parts of it: the zoologists, Prof. Dr. A. Remane (Kiel), Dr. B. Forsman (Kalmar), and Dr. K. Purasjaki (Helsingfors): the botanists, Prof. Dr. E. Häyrén (Helsingfors), Dr. M. Wærn (Uppsala), and Dr. H. Luther (Helsingfors). The literature is considered up to June 1953, when the manuscript was completed.

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logical significance of salinity, one of the main factors controlling the distribution of aquatic organisms. The impression of an experiment is accentuated by the late- and post-Glacial history of the Baltic, which has included periods with fresh and with fairly salty water. In other respects, also, the Baltic offers remarkably favorable conditions for ecological research, owing to the very varied nature of the area. Its extension in a north-south direction involves a fairly wide temperature range; the coastal types vary from sands to rocks, and from open shores to sheltered labyrinths of archipelagos, more extensive than anywhere else in the world; the existence of a series of basins causes marked differences in such factors as bottom deposits, supply of oxygen and nutrient salts, etc.

Finally, the composition of the Baltic flora and fauna is of unusual interest; there is not only the typical mixture of marine, lacustrine, and genuine brackish-water forms normally characterizing diluted areas, but, there is in addition a special faunistic element, which is lacking on oceanic coasts: the Arctic relicts, introduced during the Glacial Age. The area harbors a series of them, mostly animals, of which some are even a conspicuous element in the fauna, especially in the inner parts of the Baltic, where the low temperature in winter favors organisms at home in polar waters.

The challenge to research offered by the Baltic has largely been accepted by biologists in the surrounding countries; in fact, the Baltic is one of the best-known waters of the world and, with the former Zuider Zee in Holland, classical in the annals of brackish-water research. Among Baltic areas especially thoroughly studied, the Sound (Öresund), the Kiel waters in the south, and the archipelago near the Zoological Station of Tvärminne off the southwestern Finnish coast may be mentioned. The biological work has been greatly assisted by the ready access to hydrographic data mainly collected as part of the work stimulated by the International Council for the Exploration of the Sea. These data refer mainly to open waters, whereas the coastal zone and the archipelagos are considerably less well known hydrographically.

LIMITS OF THE BALTIC, BASINS AND DEPTHS

The western geographic limit of the Baltic may be regarded as that between the Kattegat and the Danish Sounds: the Little Belt (Lillebaelt), the Great Belt (Storebaelt), and the Sound (Öresund) (Fig. 1). From a hydrographic and biological point of view the question is, however, more complicated. The low and stable salinity and the appearance in the flora and fauna of numerous lacustrine and genuine brackish-water elements and relicts—*i.e.*, the real characteristics of the Baltic—begin to form only inside the Sound and the threshold between Darsser Ort (on the German coast west of Rügen) and Gjedser (on the Danish Isle of Falster), whereas the Danish Sounds and the area south of the Belts show rapid and great variations in the salinity and are inhabited by a practically marine, even though reduced, flora and fauna. On the other hand, the outflow of diluted Baltic water causes a lowering of the salinity in the whole of the Kattegat. Therefore it has been suggested, on the one hand, that the Baltic should be biologically defined as the area east of the line Darsser Ort-Gjedser—inner end of the Sound (Brattström, 1941)—and, on the other, that it should be enlarged to include the "Transition Area" (outer limit between Skagen

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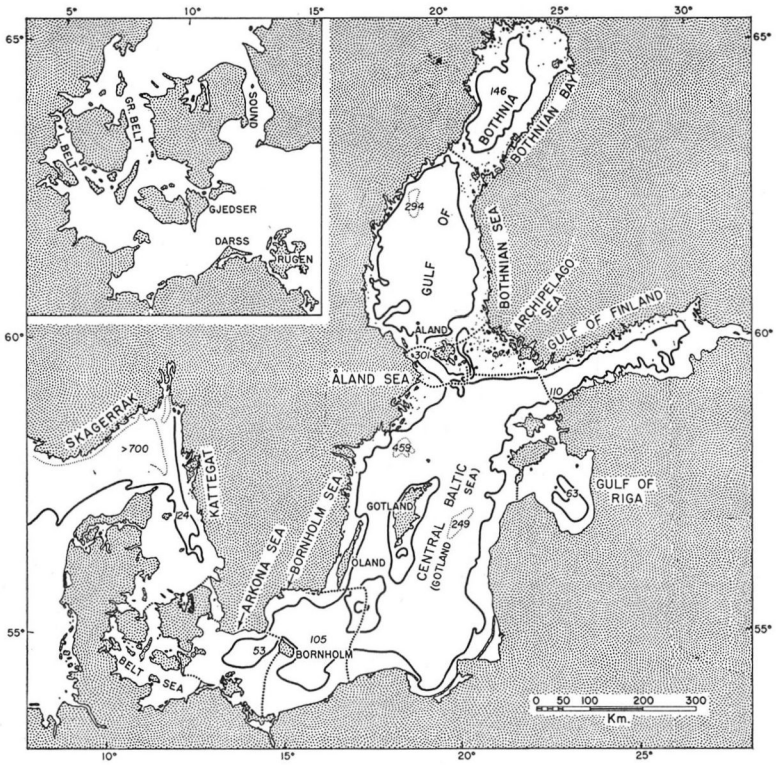

FIGURE 1.—*Chart of the Baltic with subareas*

Dotted line: 200 m, continuous line: 40 m. Figures indicate maximum depths. Combined mainly from Witting (1912), Ekman (1931), Brattström (1941), and Wattenberg (1949).

at the northern end of Jutland and the opposite Swedish coast, Wattenberg, 1949). For practical reasons it seems advisable, however, to retain the traditional geographic limit. The area inside Darss-Gjedser and the Sound, the Baltic proper, is here regarded as including the Gulf of Bothnia and the Gulf of Finland.

The Baltic may be divided into the following parts (Fig. 1): *The Belt Sea* with the Sound between the outer limit of the Baltic and the limits of the Baltic proper. These waters, the inlets to the Baltic, are comparatively shallow, especially at their inner border, where the threshold between Darsser Ort and Gjedser lies maximally 16–18 m below the surface; the corresponding value for the southern end of the Sound is 7–8 m. In the Baltic proper a number of sea areas are distinguishable over submarine basins separated by shallower ridges and rises: the *Arkona Sea*, the *Bornholm Sea*, the *Central Baltic* (the *Gotland Sea*), the *Gulf of Riga*, the *Åland Sea*, and the *Gulf of Bothnia;* this is divided by a central rise, Kvarken (in Finnish Merenkurkku), into the *Bothnian Sea* in the south and the *Bothnian Bay* in the north. The *Archipelago Sea* between the Åland Isles and the Finnish mainland is a transitional shallow area, the uppermost parts of which form innumerable rocky islands and skerries. The *Gulf of Finland* belongs topographically to the same submarine basin as the Central Baltic.

The depth within the basins may be considerable as compared with conditions at the entrances to the Baltic. The southernmost basins are shallower, at most 50–100 m deep, but considerable parts of the Central Baltic lie more than 100 m below the surface, and east of Gotland a depression, the Gotland Deep, reaches about 250 m; north of Gotland another, smaller depression, the Landsort

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Deep, descends to 459 m, the maximal depth of the Baltic. An extensive area of the Åland Sea has a depth of more than 200 m (max. 301 m), and in large parts of the Bothnian Sea depth exceeds 100 m (max. 294 m). In contrast to the Gulf of Finland, the last two basins are largely separated from the central Baltic basin: the threshold limiting the Åland Sea in the south has a maximal depth of 40–50 m only, and in the Archipelago Sea the threshold depth is only 30 m. Owing to the land elevation in the northern Baltic area the marine influence inside the thresholds is slowly decreasing (maximal rate of elevation of the land observed at Kvarken: 0.9 m per century).

CIRCULATION OF WATER: SALINITY

The dilution of the Baltic is due to: (1) its narrow and shallow connection with the ocean, (2) the great influx of fresh water from a widespread land area and precipitation into the Baltic itself, and (3) the comparatively small loss of water through evaporation. In addition to the lowering of the salinity these factors result in a constant outflow of water from the Baltic through the Belts and the Sound. The main outlet, the Great Belt, is, however, too wide and too deep (up to 23 m) to be completely occupied by the outflowing water, and thus salt water from the Kattegat penetrates along the bottom into the Belt Sea. There the bulk mixes with the Baltic water, flowing out on the surface, but the rest is, more or less irregularly, pressed over the Darss threshold into the Baltic proper. Occasionally, a marine influx may, in addition, occur through the shallow Sound (threshold depth 7–8 m). The main gate into the Baltic is, consequently, the strait of Darss. Owing to its shallow depth, 16–18 m, the most saline—*i.e.*, densest—water of the Belt Sea, however, cannot pass into the Baltic proper; the salinity of the intruding bottom water does not exceed 15–20 ‰. This leads to the striking decrease of the salt concentration inside the Darss threshold pointed out above. Whereas in the Belt Sea at the surface average salinities of about 15–20 ‰ are found, the values at the threshold drop to 10–12 and by Rügen to about 8 ‰. Farther inward the decrease is exceedingly slow: at the entrances to the Gulf of Finland and the Gulf of Bothnia—*i.e.*, about 900 km from the Darss threshold—the salinity still equals about 6 ‰, and in the middle of the Gulfs about 5 ‰; then the drop is again accelerated, and at the very ends of the Gulfs 2 ‰ and less is measured (Fig. 5).

In the Belt Sea, the "estuary" of the Baltic, salinity conditions vary greatly; in the Fehmarn Belt, for instance, the average annual range, at the surface, is about 15–30 ‰. This characteristic of the Belt Sea is due to the meeting and turbulent mixing of the outflowing diluted Baltic water with incoming water of high salt concentration and, further, to striking fluctuations in the volume of both components. These fluctuations are principally due to variations in the wind and water-level con-

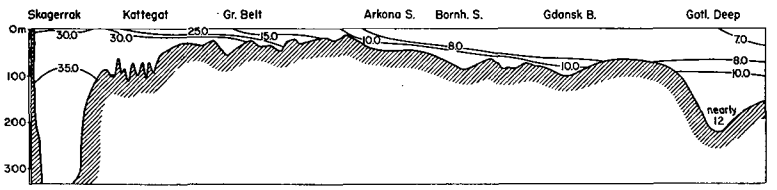

FIGURE 2.—*Schematic cross section from the Skagerrak to the Gotland Deep (November)* Figures denote salinity in ‰. From the Deutsche Seewarte Atlas, 1927; simplified.

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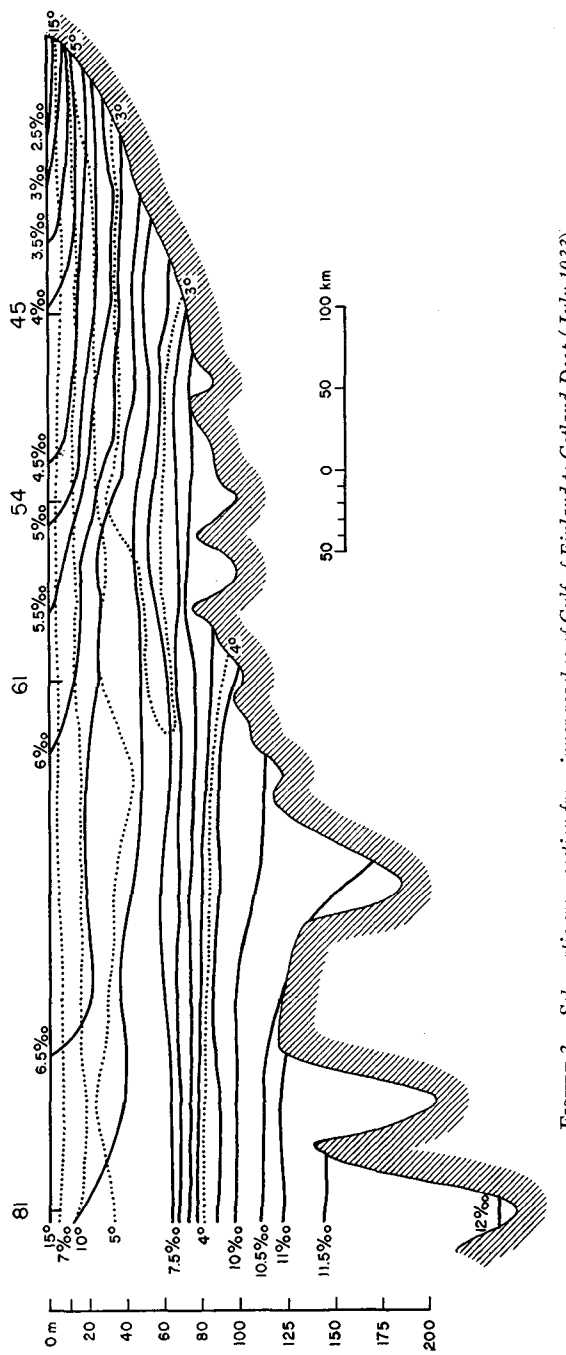

FIGURE 3.—*Schematic cross section from inner reaches of Gulf of Finland to Gotland Deep (July 1933)*

Point 45: Suursaari (Hogland) island; 54: middle part of the Gulf of Finland off Helsingfors; 61: same, but off Hangö, 81: east of Gotland. From Jurva (1952).

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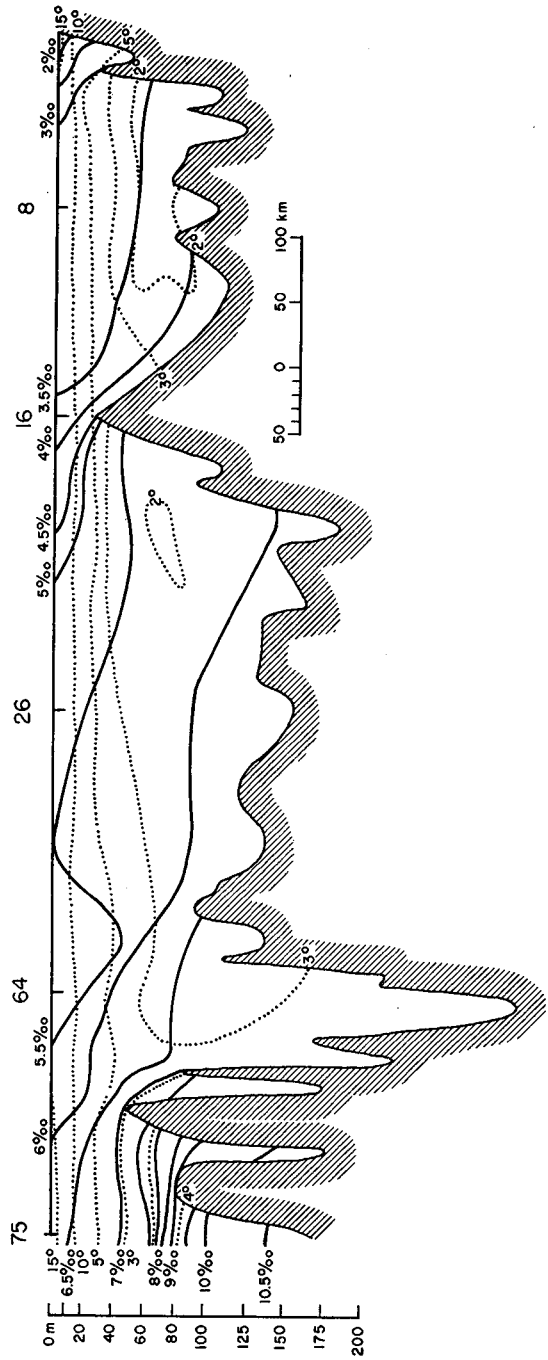

FIGURE 4.—*Schematic cross section from the Bothnian Bay to the northern part of the central Baltic (July 1933)*
Point 8: middle of the Bothnian Bay; 16: Kvarken; 64: Åland Sea; 75: northern part of the central Baltic. From the same source as Figure 3.

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ditions. The great and often rapid changes in salinity contribute considerably to the impoverishment of the marine flora and fauna of the Belt Sea. Under extreme circumstances the influx of salt water into the Belt Sea may be great enough to affect the whole of the water volume above the Darss and Sound thresholds and cause a turning of even the superficial layers to flow into the Baltic proper. Hydrographers assume that the salty water occupying the depth of the basins east of the thresholds is renewed mainly by such irregular but powerful "piston strokes".

With the outflowing Baltic water, on the one hand, and the marine influx, on the other, organisms are constantly transported into areas outside their normal range (Jensen *et al.*, 1937; Kändler and Wattenberg, 1940).

This transport is illustrated by the following example, well known on account of its economic consequences (Schulz, 1932). In the spring of 1923, unusually large quantities of water of more than 34‰ salinity penetrated into the Kattegat, enabling the haddock, *Gadus aeglefinus*, to spawn there. The fry, developed from the eggs, were carried, with the bottom current, into the Belt Sea and even into the Arkona Sea of the Baltic proper, where, in 1925 and the winter 1925–1926, a haddock fishery of previously unknown intensity developed. The big catches ceased, however, by the spring of 1926, owing to the migration of the full-grown fish into the saltier Skagerrak to spawn.

Besides the above-mentioned "piston strokes", fluctuations in the influx of water into the Baltic may also be observed over longer periods. In the last few decades more oceanic water than usual has entered, probably as a consequence of altered wind conditions in connection with the recent change in climate in Northern Europe, causing an increase in salinity even in the innermost parts of the Baltic (salinity in the Gulf of Finland at 5 m depth in 1945–1949 10–20 per cent higher than normal) and favoring the marine component of the fauna (increase of the stock of cod, turbot, and sprat, extension of the reproductive area of *Aurelia aurita*, etc., Fig. 9 (Brattström, 1941; Segerstråle, 1951b; 1953; Purasjoki, 1953).

While the superficially outflowing Baltic water meets no obstacles in its path and hence exhibits a continuous increase in salinity, the rises separating the basins form barriers to the oceanic water flowing in along the bottom. Thus the saltiest bottom layers are successively prevented from entering the following basin (Figs. 2, 4). As a

TABLE 1.—*Annual salinity range (‰, means) at surface and bottom in different parts of the Baltic (in the Basins of the Baltic proper the values for the bottom refer to the deepest part)*

Mainly after the Atlas of the Deutsche Seewarte (1927)

Area	Surface	Bottom
Belt Sea	10–16‰	14–30‰
Arkona Sea	7–10	13–17
Bornholm Sea	7.5	15–16
Gotland Deep	*ca.* 7	11–12
Gulf of Finland (center)	*ca.* 5	8–9
Åland Sea	5–6	6.5–7
Bothnian Sea	5–5.5	6–6.5
Bothnian Bay	3–4	4

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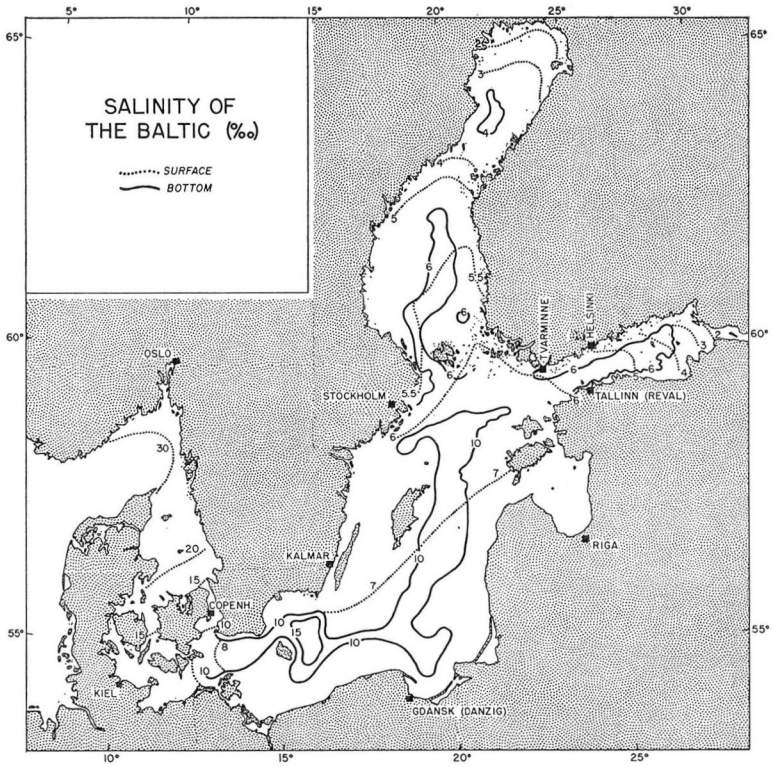

FIGURE 5.—*Salinity (‰) of the Baltic with adjacent areas*

The surface isohalines reflect average conditions (isohalines of 2–6‰ taken from the Atlas of Finland, 1925, those of 7‰ and onward interpolated from the isohalines given by Schulz, 1932, for February and August). The isohalines for the bottom (omitted outside the Baltic) refer to November (from the Deutsche Seewarte Atlas, 1927). The recent increase in the salinity of the Baltic has altered, to some extent, the course of the isohalines given in the chart; for instance, in the Gulf of Finland the surface isohaline of 6‰ has advanced from Hangö to the neighborhood of Helsingfors.

result the inward decrease in salinity at the bottom is discontinuous and much more rapid (Table 1). The dense water occupying the outer basins is also more or less subjected to stagnation with ensuing effects on its content of oxygen, carbon dioxide, etc. Similar features have also been observed in local, topographically isolated depressions in the coastal region of the Baltic (Witting, 1914; Hessle and Vallin, 1934). On the other hand, the irregular "piston strokes" may lead to unexpected and rapid renewal of the water. On the whole, the hydrographical conditions in the depth of the Baltic are much less regular than at the surface.

The salinity variations in the superficial layers of the Baltic proper (Figs. 6, 7) are mainly seasonally conditioned; the highest values are reached in autumn and winter, the lowest, because of the melting of the snow, in spring and summer (Segerstråle, 1951a). The dilution in spring, of course, first affects the coastal waters and later the open sea.

The stability of the salt concentration in upper layers is generally confined to

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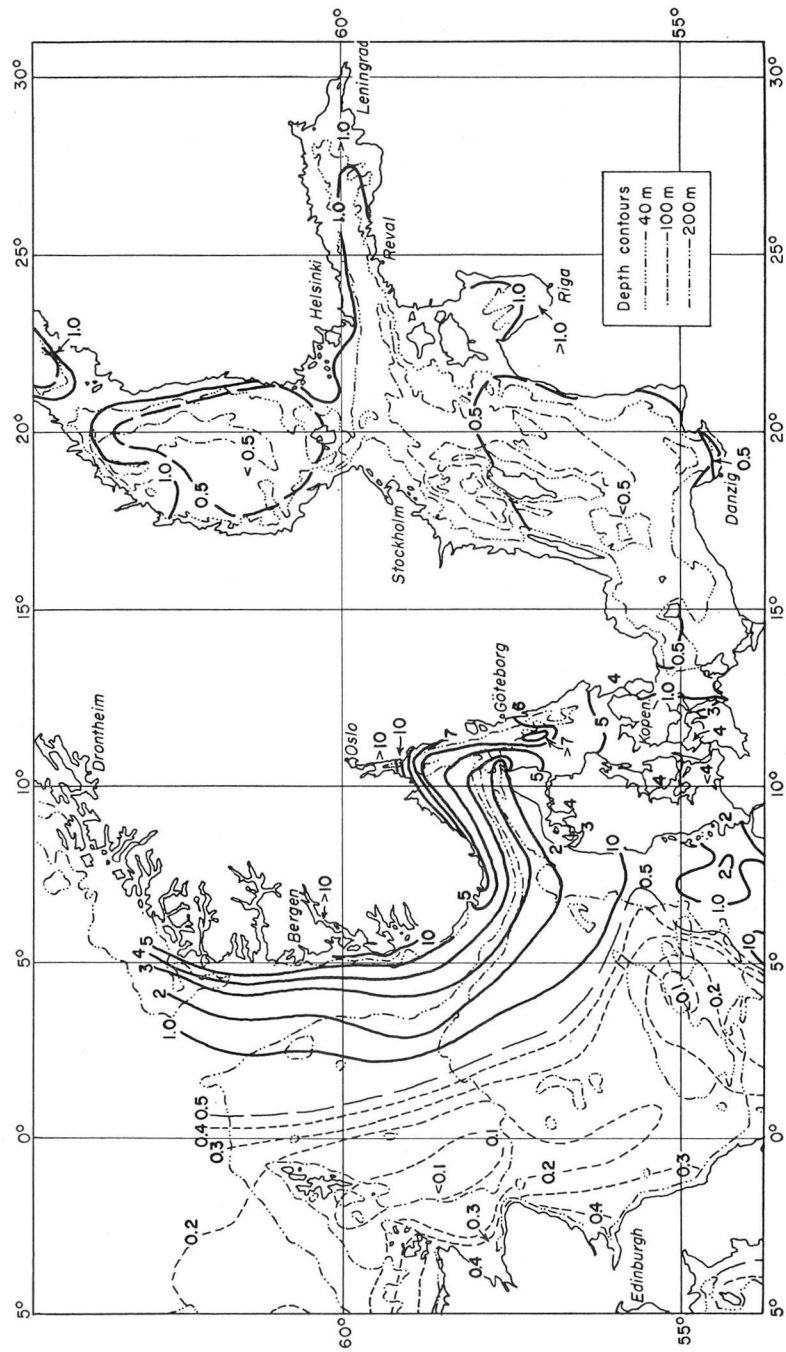

FIGURE 6.—*Annual salinity fluctuations, in ‰, in the Baltic and adjacent waters*

The stable salinity conditions characterizing the Baltic proper and the much wider range in the transition area are clearly seen. From Dietrich (1950).

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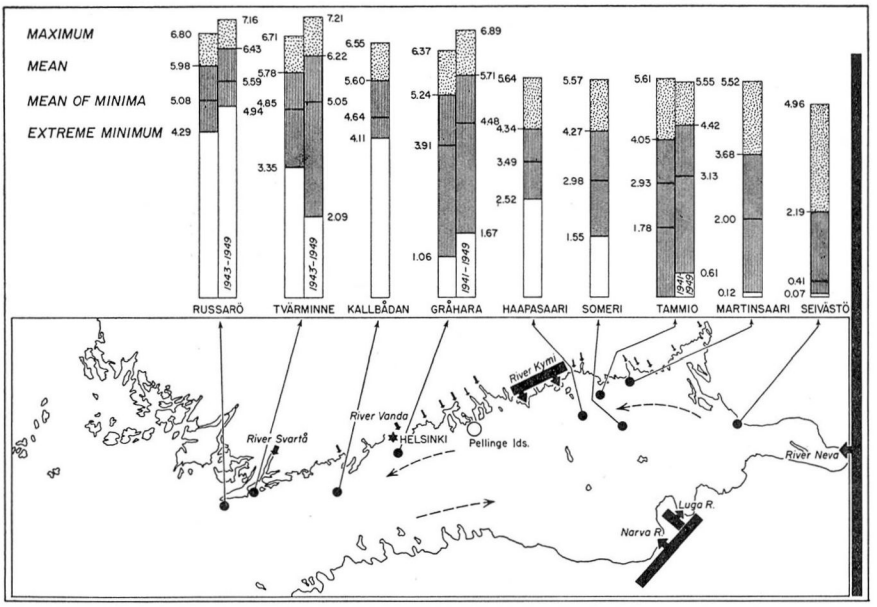

FIGURE 7.—*Chart and diagrams illustrating the range of salinity fluctuations (5 m depth, ‰) in the Gulf of Finland during the period 1927–1949*

According to data collected by the Institute of Marine Research of Finland. Diagrams in which the years are not given refer to the period 1927–1939 (1927–1938 in the case of Someri and Seivästö). Samples normally taken three times a month. Arrows indicate rivers; their width corresponds to the relative volume of outflowing water (on the south coast of the Gulf of Finland, only the largest rivers are given). H = Helsingfors. R.S. = River Svartå, emptying ca. 40 km northeast of Tvärminne and influencing this area in winter, owing to the ice. Arrows in the open sea indicate main direction of currents. The low-salinity minimum near the coast in the east (Martinsaari) is mainly due to the enormous outflow from the Neva, which is diverted to the right; the low minimum at Gråhara is caused by a local river. The stations in the open sea exhibit strikingly stable salinity conditions. From Segerstråle (1951a).

open waters; near the coast, especially in the neighborhood of rivers, the lowering of the salinity in spring is considerably more marked (Fig. 7) (Segerstråle, 1951a). This phenomenon is of great importance to the ecologist studying the fauna and flora of the coastal waters, but has not been much investigated; as was mentioned previously, most of the hydrographic records from the Baltic refer to the open sea. The ice covering in winter contributes to the deterioration of the living conditions for marine organisms near the coast, as a layer of highly diluted water, up to some meters thick, may form under the ice and influence even fairly distant regions (Segerstråle, 1951a).

The last-mentioned feature explains, for instance, the unexpected distribution of *Gammarus* forms observed off the south coast of Finland, at Tvärminne, where the water layers under the ice may be periodically highly diluted by the outflow from a river which discharges in a distance of 40 km (Fig. 7) (Segerstråle, 1951a). In sheltered waters of the archipelago which in winter are permanently covered by ice, the marine *Gammarus zaddachi oceanicus* is outnumbered by the brackish-water forms, *G. zaddachi salinus* and *G. zaddachi zaddachi*, whereas it predominates in the open sea. As the mean sa-

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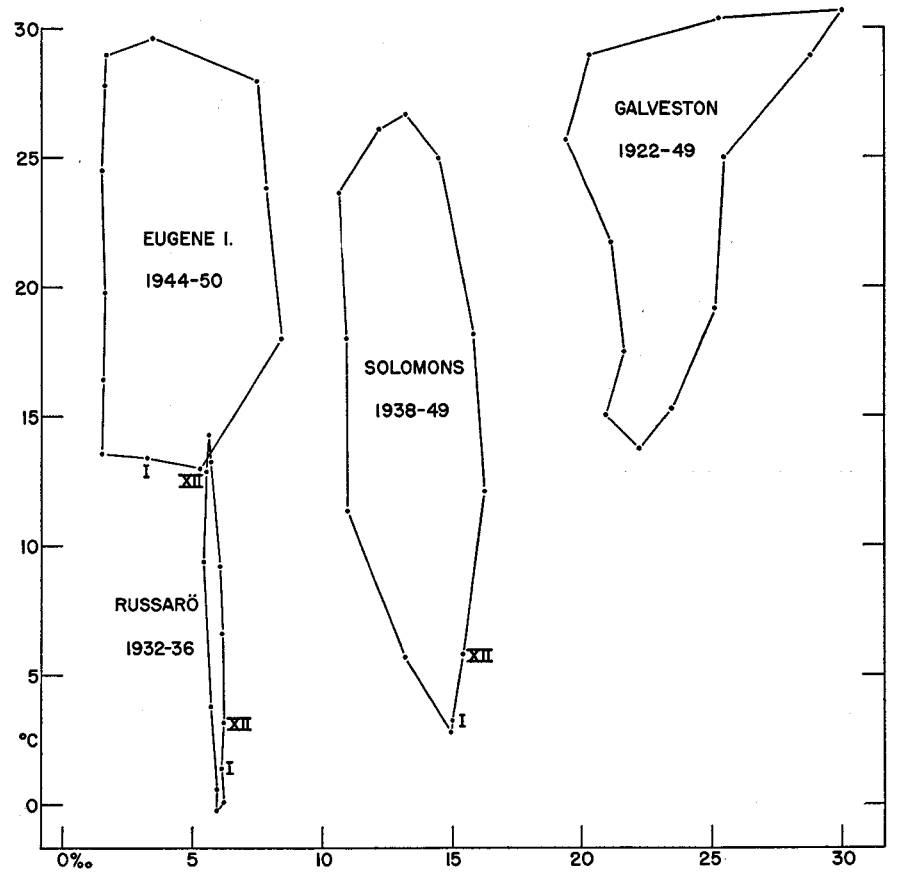

FIGURE 8.—*Hydroclimagraphs*

Showing the annual cycle of salinity and temperature (means) in the inner Baltic (Russarö, off the Finnish southwest coast, for location, *see* Fig. 7; the values, calculated from data published by the Institute of Marine Research of Finland, refer to 5-m depth) and in some brackish areas off the coast of North America (according to Hedgpeth, 1951). Eugene Island and Galveston are on the coast of the Gulf of Mexico, Solomons in Chesapeake Bay on the Atlantic coast. The characteristics of the Baltic brackish area—*i.e.*, the stable salinity and the low temperature in winter—are clearly seen.

linity in the archipelago is higher than in more easterly open waters where *G. zaddachi oceanicus* occurs abundantly, the scarcity of this form in the Tvärminne archipelago is evidently a consequence of the dilution under the ice in spring. Marine plants of the region concerned may also show signs of suffering from the periodic dilution of the upper layers: for instance, *Zostera marina* is generally absent from shallow water (H. Luther, 1951).

In the easternmost part of the Gulf of Finland conditions are unfavorable not only for marine species, which have to endure the outflow from the big Neva River, but also for lacustrine forms, owing to upwelling of salt bottom water (Segerstråle, 1951a).

On account of the earth's rotation the currents in the Baltic are diverted to the right, with a resultant oblique course of the isohalines (Fig. 5) and thus also of the distribution limits of plants and animals (Figs. 15, 17). Regarding the isohalines of

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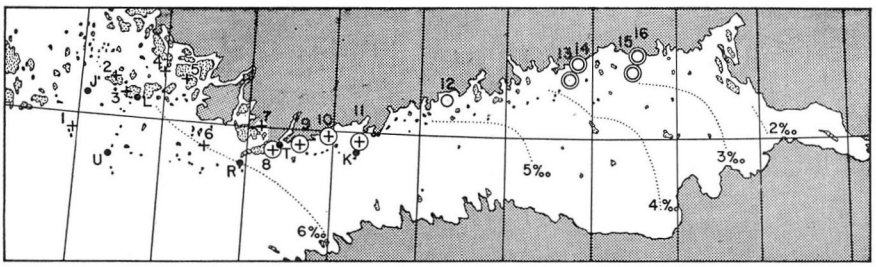

FIGURE 9.—*Example of the biological consequences of the recent increase in salinity of the Baltic*
Extension of the area of occurrence and reproduction of the jellyfish, *Aurelia aurita*, on the south coast of Finland. +, signs of reproduction observed before 1939; ⊕ same, observed since 1939; ○ easternmost finds of adult medusae before 1940; ◎ same, since 1940. *See* Segerstråle (1951b).

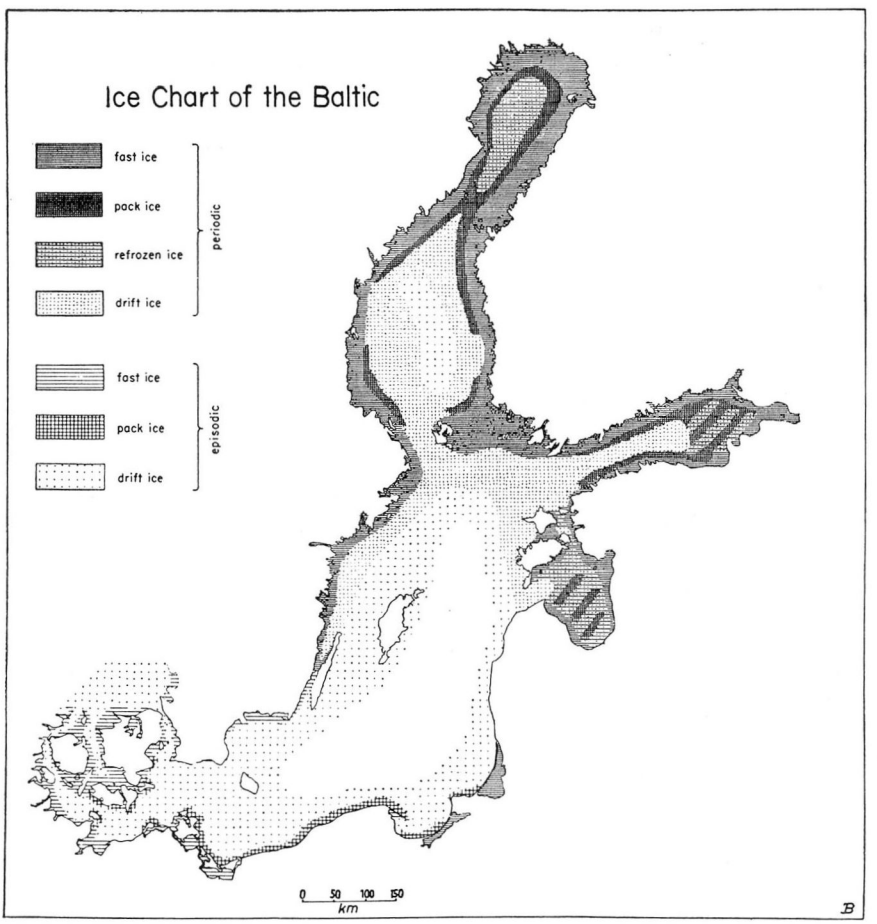

FIGURE 10.—*Ice chart of the Baltic*
Showing average distribution of different kinds of ice. From Blüthgen (1938)

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the Baltic given in Figure 5 and in other maps, we must remember that they reflect conditions in the open sea. Near the coast we have to reckon with considerably lower salinity means than are indicated by the isohalines, and there may be great differences locally, owing to river influence, etc. (Segerstråle, 1951a). Lagoons and other more or less isolated coastal waters receiving river outflow—*e.g.*, the Haffs on the south coast of the Central Baltic Sea, the bays Slätbaken in Sweden, and Pojoviken in Finland—may exhibit almost lacustrine conditions.

The salinities discussed refer mainly to the surface. Conditions in the saltier bottom layers are seen from Table 1 and Figures 2–5. Table 1 shows, *inter alia*, that water of a mean salinity of 11–12 ‰ penetrates along the bottom as far inward as the area east of Gotland and that in the middle part of the Gulf of Finland there is still 8–9 ‰ in the depths. The difference between the surface and bottom layers is thus very marked in most parts of the Baltic. An important exception is the Åland Sea and the Bothnian Sea where salinity in the depths (maximally about 300 m in both seas) is comparatively small and differs little from that of the upper layers. This is due to the shallow sills limiting the Gotland Sea in the north; they prevent the salty bottom water of this sea from entering the Åland Sea and Gulf of Bothnia (Fig. 4).

In depths down to about 70 m a salinity minimum of the bottom layers is observed in autumn, when convectional processes cause homogenizing in this water column. Currents may bring about complications: at Tvärminne, at the mouth of Gulf of Finland, the depth minima are seemingly due to water coming from eastern, more freshened areas and are correspondingly delayed. In addition, owing to special wind conditions the strongly diluted surface water may occasionally reach considerable depths (at least 20 m) (Segerstråle, 1951a).

SALINITY CLASSIFICATIONS

Somewhat different salinity systems, proposed by Välikangas (1933), Remane (1940), and, more recently, Ekman (1953), have been applied to the Baltic; they are all based upon that advanced in 1922 by the Dutch hydrobiologist Redeke, who was the first to give a classification of the water according to its salt concentration. Välikangas' system is as follows:

	Salt concentration ‰
Fresh water	<0.5
Oligohaline brackish water	0.5–3
Meiomesohaline brackish water	3–8(10)
Pleiomesohaline brackish water	8(10)–16.5
Polyhaline brackish water	16.5–30
Seawater	>30

Remane's main objection to this system concerned the inclusion of waters with a salinity of 16.5–30‰ within the brackish zone; in his opinion they are of a clearly marine type. This view was, in turn, criticized by Dahl, who, on the basis of studies off the Swedish west coast, claimed the existence of a special fauna in Välikangas' (and Redeke's) polyhaline brackish-water zone (Dahl, 1948). In spite of Dahl's criticism, Ekman (1953) follows Remane in the point just mentioned and adds some other minor modifications to the system of Välikangas; his system is as follows:

	Salt concentration ‰
Fresh water	<0.5
Oligohaline brackish water	0.5–3

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Mesohaline brackish water	3–10
Polyhaline brackish water	10–17 (20?)
Oligohaline sea water	17 (20?)–30
Mesohaline sea water	30–34 (?)
Polyhaline sea water	>34 (?)

Ekman gives the following motivation for his modifications: "One must agree with Remane that 'polyhaline brackish-water' (above called oligohaline sea water) is not brackish as far as its fauna and flora are concerned. It is a mixed zone with a predominating element of euryhaline sea animals. Välikangas and Brattström strongly emphasize the fact that the most important boundary in the Baltic is at 8–10‰ salinity—that is, between Darsser Ort and Gjedser, which represents the southwestern boundary of the Baltic proper. The change proposed above gives the term "polyhaline brackish water" a new meaning, of course, but we are thus able to avoid the division of the mesohaline fauna into two subdivisions, which Välikangas' system entails, *i.e.*, the meiomesohaline and pleiomesohaline. This division is logically unsatisfactory since the subdivisions show more marked differences between themselves than the main divisions mesohaline and polyhaline."

According to Ekman's system, by far the major part of the Baltic proper belongs to the mesohaline brackish-water zone. The innermost parts of both Gulfs are oligohaline brackish, as are highly diluted coastal waters elsewhere in the area, while the deepest layers up into the region of Gotland are polyhaline brackish. The Belt Sea is mainly a polyhaline brackish area, which may at times be dominated by oligohaline sea water. It goes without saying that the increase of the salt concentration with depth causes a corresponding increase of the marine element of the fauna and flora downwards. In addition, as usual in brackish areas, the upper limit of the vertical range of marine species normally falls toward more-diluted waters. As examples of this phenomenon (brackish-water submergence) may be mentioned the amphipod, *Pontoporeia femorata*, which in the southern Baltic is also found in shallow shore waters, but off the southern Finnish coast is confined to a depth below the 30-m line (Segerstråle, 1937) and, among plants, *Laminaria*. On the west coast of Sweden it extends upward to less than 1 m., in the middle part of the Sound it is absent above the 10-m. line.

OTHER ECOLOGICAL FACTORS

Of the other factors influencing the Baltic fauna and flora, attention will first be given to those which, like the salinity, are connected with the water itself.

TEMPERATURE, BALTIC

The strong continental influence upon the hydrography of the Baltic is seen not only in the dilution of the water but also in the temperature, which is characterized by striking fluctuations, from subtropical conditions in summer to polar conditions in winter. In August the surface layers are warmed to 16–17° C. in large parts of the Baltic, and in shallow waters, even on the coast of the Gulfs, values of more than 20° may be observed in hot summers, whereas in corresponding latitudes of the Atlantic, outside the continental shelf, the surface temperature measures 12°–14° only; in February the opposite deviation from oceanic conditions is still greater: in the Gulf of Bothnia, the Gulf of Finland, Riga Bay, and locally even farther southwards the freezing point is reached, while the Atlantic water of corresponding latitudes still registers 8°–10°.

In autumn, owing to convectional processes, the surface temperature is enabled to influence deeper layers also, in the central Baltic down to about 70 m; deeper down, there is a constant temperature of 4°–5° in this area. In the Åland Sea and the Gulf of Bothnia the slight difference in salinity between surface and bottom layers allows the convection to affect the whole water column, in spite of its considerable

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depth, and the annual temperature range of the bottom layers is about 1°–4°. In the Gulfs in winter, for a period of 2–3 months (mainly February–March), the water is cooled to *ca.* 0°–1° to a depth of 20–50 m (Granqvist, 1938). The warming of the upper layers in spring and summer renders mixing with deeper layers difficult, especially in hot summers (for instance observed at Tvärminne in August 1927: near the bottom at 30 m depth *ca.* 3° against *ca.* 22° at the surface (Segerstråle, 1933a). As a consequence, the temperature curve rises slowly in the deeper layers and reaches its maximum at the time of homogenizing in autumn (mainly October); in the layers at 20°–50° m, which are cooled to 0°–1° in winter, this temperature maximum is about 7°–10°. Thus the "summer" of organisms living there is much delayed and is followed in a few months by the period of minimal temperature.

The low winter temperature, even at considerable depths, in the inner parts of the Baltic offers good conditions for the glacial relict animal, all of which, like most other Arctic species, seem to breed, at least mainly, at this season. The upper layers, which are strongly warmed in summer, are avoided by them (in winter pelagic forms may invade such layers, too).

On the other hand, the exclusion of other animals and plants from this area may, of course, be due to the low winter temperature. (In the case of marine and brackish-water animals, the osmoregulatory factor may be decisive; as is well known, toleration of dilution of sea water seems to be facilitated at higher temperatures.)

Owing to the low winter temperature, large parts of the inner Baltic are covered by ice during this season (Fig. 10). The coastal waters of Finland are frozen over for an average of 2–5 months; in the inner end of the Gulf of Finland the ice period lasts 3–6 months and in the northernmost end of the Gulf of Bothnia 5–7. Great fluctuations occur: in very severe winters the whole of the Baltic is covered by ice, while in exceptionally mild winters ice is not found in the Gulf of Bothnia south of Kvarken or in the Gulf of Finland west of Suursaari (Hogland). The ice sheet covering the coastal waters may locally much increase the vertical and horizontal influence of the fresh-water outflow from rivers and thus be a negative ecological factor for marine organisms. Directly, the ice may damage frozen-in plants and animals: (1) by its low temperature; (2) by tearing off plants and fixed or sessile animals. Large mats of *Phragmites* rhizomes, frozen in at low water, may be detached from the bottom by the rising water etc. (H. Luther, 1951); (3) by suffocating, through lack of oxygen, animals living in shallow water in cases where the ice covering has formed at low water (A. Luther, 1923). Furthermore, the shaving effect of drifting ice may be devastating for plant and animal life. Especially to be mentioned are the accumulations of pack-ice circulating in the sea during the spring and grinding the shores several meters down (Wærn, 1952). Sheltered localites, for instance, in the archipelagos, offer much more favorable conditions for plants and animals in this respect than do exposed shores.

DISSOLVED GASES AND OTHER CHEMICAL FACTORS

The oxygen content of the Baltic water has proved to be markedly low only locally, mainly in the depths of basins where the water is comparatively stagnant owing to high salinity (*cf.* the Black Sea). In the Arkona and Bornholm seas oxygen

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is often almost lacking at the bottom, and in the depths of the Gotland Sea, which receives water already deprived of a part of its oxygen, very low values, at most about 3 cc per liter, are practically always found. Corresponding features are known from local depressions in the coastal zone (Hessle, 1924). Since the salty deep layers of the Gotland Sea cannot penetrate the Åland Sea and the Gulf of Bothnia, and owing to the thorough mixing of the water in these areas, the oxygen supply in these basins is fairly good even near the bottom. Like most of the data from other areas, the O_2 values recorded in the Baltic reflect conditions at some distance from the surface of the bottom; in immediately overlying layers one has to reckon with considerably lower values ("microstratification") (Brundin, 1951). In stagnant deep layers the low-oxygen content, owing mainly to the respiration of animals and other oxidation processes, contrasts, as is to be expected, with the high values for the carbon-dioxide content and the acidity of the water; this feature is typical of deep water as a whole. The pH values in the Baltic, about 8.0 at the surface (as in the ocean), may decrease to ca. 7.0 in the deeps. Another drop occurs parallel with the dilution; in the innermost parts of the Gulf of Bothnia, which receive water very poor in calcium, the pH measures less than 7. All the values recorded so far refer to the open sea; near the coast they are no doubt lower.

The acidity and other chemical properties of the fresh-water outflow from Fennoscandian rivers are obviously unfavorable for a number of lacustrine plants and animals occurring in coastal waters.

The acidity conditions of deeper Baltic waters cause dissolution of mollusk shells (Gripenberg, 1934; A. Luther, 1909). In this respect conditions have obviously altered since the Littorina Age, from which shellbanks, up to several meters thick, are found on the uplifted coasts of the inner Baltic.

As to the humus compounds transported into the Gulf of Bothnia by the rivers coming from large peat-bog districts, mainly in Finland, and which give the coastal waters, and even the adjacent sea, a brownish color, their possible negative influence upon the flora and fauna is not known; after precipitation they are, it seems, of positive significance as a source of food for animals inhabiting the depth.

Investigations in the Baltic into the supply of the major nutrient salts, phosphates, and nitrogen salts, the basis for the production of phytoplankton and other vegetation and thus also for animal life, have revealed clear local differences; some parts are rich, and others are poor in these substances (Buch, 1932; Gessner, 1933a; Rothe, 1941). This variation is due to the nature of the water circulation in the Baltic.

The nutrient salts accumulated in the deep salty layers of the open Baltic are transported inward with the bottom current and, with the upwelling of the water, reach the surface along the coasts and in the inner end of the Gulf of Finland. This leads to a high production of plankton in these waters, which is especially striking in spring, immediately after the melting of the ice, when diatoms develop in enormous quantities (in March-April 1935 up to 1.6 million cells per liter was established near Hango in southwestern Finland, (Buch and Halme, 1947.) From the area concerned the plankton is carried, with the superficial outflow, into the open Baltic, where, after death, it sinks to the bottom, disintegrates, and, through bacterial mineralization, gives rise to nitrogen salts and phosphates, which in their turn begin the same circulation. The open Baltic waters therefore are comparatively sterile.

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The Åland Sea and the Gulf of Bothnia are cut off from this system of circulation by the southern thresholds, which do not allow the nutrient-rich bottom water of the Gotland Sea to enter them. Thus both seas depend mostly on their own vertical circulation for their supply of phosphates and nitrogen salts; furthermore, these areas are fed by surface waters coming largely from the extensive peat bogs in North Finland, which are poor in nitrates and especially in phosphates. The consequence is a very low plankton production, especially in the Bothnian Sea. Poor nutritional conditions seem also to contribute considerably to the depauperization of the vegetation of marine algae in the Gulf of Bothnia (Wærn, 1952); a striking example of this depauperization is the scarcity and reduced size of *Fucus vesiculosus* even in the southern Bothnian Sea, especially off the Swedish coast under the influence of the outgoing current, in salinities in which, in the Gulf of Finland, the species still exhibits luxuriant growth (Fig. 17). The humus substances, carried in great quantity into the Gulf of Bothnia by its affluents, and after precipitation forming loose layers on the bottom in the deeper parts of the Gulf, possibly explain the abundance of the relict crustaceans, *Mysis relicta* and *Limnocalanus grimaldii*, in these localities, as it is assumed that these animals are able to utilize this peculiar source of food, derived from the peat bogs of neighboring land areas (Hessle and Vallin, 1934).

In the Baltic, as in other areas, manuring by rivers from cultivated areas or by waste water from towns has proved an influence on the plankton and benthic vegetation locally in coastal areas and has increased their productivity (Häyrén, 1944; Gessner, 1938; Halme, 1944; Välikangas, 1926).

WATER LEVEL

The tides, which on oceanic coasts so greatly influence the life of the shore, are of small importance even in the Belt Sea and in the Baltic proper are negligible from an ecological point of view. On the other hand, irregular oscillations of the water level, of a duration from hours to weeks and months, are caused by winds and changes in the atmospheric pressure. In the innermost parts of the Gulfs the mean maximum of the deviations above and below the normal level equals about 1–1.3 m, on the southwest coast of Finland about 0.5 m. In the spring the water is usually low, a phenomenon which, in combination with the calm weather and sunshine of this season, has disastrous consequences for the exposed algal vegetation by drying it out and killing it. During summer the lower part of this zone is again submerged and colonized anew by threadlike algae which form a continuous and dense vegetation on the rocks. The upper border of this algal vegetation of the summer is ecologically a fundamental limit between terrestrial and aquatic life and is used as the basis for modern systems of zoning vegetation in the Baltic. In recent works the zonation, of importance to the zoologist also, is as follows (DuRietz, 1950; Wærn, 1952):

Above the limit of summer algal vegetation:

1. The geolittoral or geoamphibiontic belt: the more terrestrial part of the littoral s. lat., comprising the zone submerged by high water and, on exposed shores, by the waves.

Below the limit of summer algal vegetation:

2. The hydrolittoral or the hydroamphibiontic belt, laid bare (to about 0.5 m.) at spring low water; the zone of summer-annual filiform algae (Pl. 3).
3. The sublittoral, the permanently submerged belt.

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COASTAL GEOMORPHOLOGY

In the south of the Baltic the coasts are open and sandy, rocks are very scarce, and the flora and fauna are unprotected by skerries. Northward, rocky shores begin to predominate, and at the same time the specific Baltic archipelagos, with numberless, mostly small, skerries and wooded islets, are encountered; the largest occur in the Archipelago Sea between the Finnish mainland and Åland and off the Swedish coast west and southwest of Åland (Pl. 1).

Besides the nature of the coast itself, as a substratum for plants and animals, the degree of exposure of this is, of course, significant—directly, through the factors of swell and ice, and, together with topographical factors, indirectly in many ways. In the archipelagos, bottoms composed mainly of organic mud may, in places with strong currents, abruptly change into sand and rocky bottoms, whereas in the open sea mud areas are restricted to deeper waters; the transparency of the water mostly measures a few meters only against about 10 m in the open sea, and rocks and vegetation are covered with detritus to a much greater extent than on exposed shores; the salinity generally decreases toward inner parts of the archipelago, the temperature, again rising in the same direction, etc.

In broad archipelagos different successive zones may be distinguished, from the narrow waters near the mainland, exhibiting a more or less "lacustrine" type, to the outermost naked skerries, exposed to the open sea with its higher salinity (Häyrén, 1940). As in such broad archipelagos the different ecological factors are varied and combined in numberless ways, these areas offer excellent opportunities for studies on the influence of the single factors. Botanical investigations in the Tvärminne district, devoted especially to this topic, have, in fact, yielded valuable results (H. Luther, 1951).

In topographically varied areas with homogeneous salinity, sheltered localities as a rule harbor a flora and fauna of a more lacustrine type than do exposed shores, owing to the lack of swell in the former places and the loose, organic sediments which allow many aquatic phanerogams and insects to flourish there.

SEDIMENTS

The question of the sediments of the Baltic was already touched upon. Depths below about 50 m contrast in general with the shallow coastal waters. The latter often have very varied bottoms, while the former are almost everywhere covered by a clayey mud with sand which changes into black mud, rich in organic detritus, in the deeps of the Central Baltic as well as in those of the Bornholm and Arkona seas. In all regions the superficial mud layer contains abundant fecal pellets derived from the benthic fauna. Shell fragments of the planktonic crustacean, *Bosmina maritima*, constitute a characteristic element in the mud of the central and inner Baltic (Apstein, 1916). Pure clay occurs only locally. Above the 50-m line the mineral elements become increasingly predominant, and the bottom changes to predominantly sand and gravel, locally with stones. In the shallow Belt Sea mineral bottoms predominate. The rises between the Arkona and the Bornholm basins and between the latter and the Central Baltic bear banks of moraine boulders covered with algal vegetation in their uppermost parts, which in places lie less than 10 m below the surface. In the

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Bothnian Bay the upper sediment layers are colored brownish red by hydrated iron oxides, which occur regularly on the bottom of both Gulfs and in the Åland Sea and often form small concretions.

Observations in the Finnish archipelago showed that the organic mud of sheltered shallow waters is considerably coarser than at a greater depth between the islets, and it was concluded that the latter type is of less value as food for the benthic animals (Segerstråle, 1933b). Thorough biological investigations into the bottom deposits of the Baltic, along modern lines, considering such food sources as bacteria and other microbenthic forms, are so far lacking.

HISTORY OF THE BALTIC AND OF ITS FAUNA AND FLORA

Knowledge of the late-Glacial and post-Glacial history of the Baltic, consisting of alternating salt-water and fresh-water epochs, and covering a wide climatic range, is indispensable for the understanding of the origin and immigration of its different faunal and floral components. Many geologic problems are still open and under discussion.

At the end of the last glaciation, about 15,000 years B.C., where the southern margin of the shrinking ice sheet retreated from the end moraines in northern Germany and western Denmark, the outermost part of the Baltic depression became filled with meltwater. For a short time there was a narrow connection between this region and the ocean across western Scania in southern Sweden. When this connection was cut off, owing to the general crustal uplift, the so-called Baltic Ice Lake began to form. This fresh-water stage ended, about 8000 B.C., when the ice sheet had reached a part of central Sweden low enough to allow draining of the lake to the level of the ocean.

When salt water entered the Baltic basin across Sweden, the Yoldia Sea came into existence; it is named for the marine bivalve, *Yoldia* (*Portlandia*) *arctica*, which is found in sediments eastward as far as the neighborhood of Stockholm (the greater part of the Baltic had a low salinity at that time) (Fig. 11).

The communication between the Yoldia Sea and the ocean was, however, in its turn cut off through the land upheaval, and the Baltic again became fresh. Thus the so-called Ancylus Lake of the early post-Glacial Period was formed (Fig. 12); its name is derived from the fresh-water gastropod, *Ancylus fluviatilis*, found in sediments of this time. The Ancylus Lake drained westward through a channel across Sweden, at the site of the former connection with the ocean, later through a southern outlet. The Ancylus stage seems to have had a short duration (perhaps 300–400 years) and ended in a sudden drainage down to the level of the sea through the Belts because of a crustal sinking in the outer, southwestern part of the updoming area (Sauramo, 1953).

A new transitional stage in the history of the Baltic set in: the Mastogloia Sea characterized by low salinity and named for the diatom *Mastogloia braunii*, followed by the Littorina Sea (Fig. 13). Thanks to the then comparatively broad and deep connections, through the Danish sounds, with the ocean, the salinity reached considerably higher values than in the Baltic of today, at the height of the post-Glacial warm period, about 4000–5000 B.C., by *ca.* 5 ‰; for instance, the isohaline for 8 ‰,

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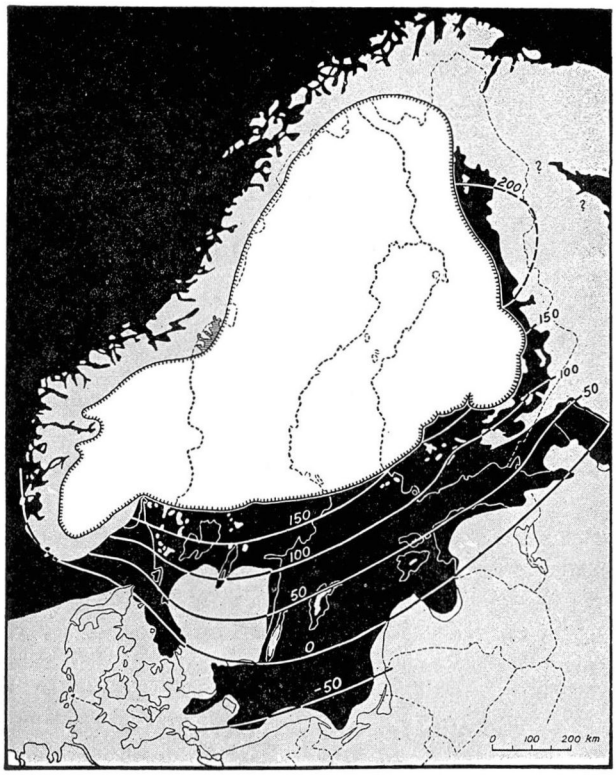

FIGURE 11.—*Yoldia Sea about 7500 B.C., with its isobases*
From Granlund, Erik, and Lundqvist: Sveriges geologi, 1949

now lying at Rügen, was extended into the inner part of the Gulf of Bothnia. On the ancient shores of the Littorina Sea hundreds of shell banks are found, even far up in the Gulfs; they are formed mainly by the mussel, *Mytilus edulis*, but also contain shells of other mollusks—*e.g.*, the gastropod, *Littorina litorea*, which has given the name to the epoch concerned and is today, in the Baltic, confined to the southern waters (innermost localities at Rügen and Bornholm) (Fig. 15).

As the outlets became shallower again, the Littorina Sea gradually changed to the less salty stage, characteristic of our days. This stage is called the Lymnaea Sea, for the fresh-water gastropod, *Lymnaea peregra* (*ovata*, *limosa*) which commenced to spread into the Baltic at the beginning of the Bronze Age. The latest phase in the development of the Baltic is the Mya Sea, named for the bivalve *Mya arenaria*, which invaded the area from the ocean, apparently very late—not until the sixteenth century and possibly even later; this stage differs only faunistically, not hydrographically, from the Lymnaea Sea.

Land is still rising in the inner Baltic area, isolating the inner basins of coastal aters and thus forming new fresh-water areas out of old brackish-water ones; another matter of hydrographical and biological interest is the rising of the submarine thresholds between the basins of the inner Baltic.

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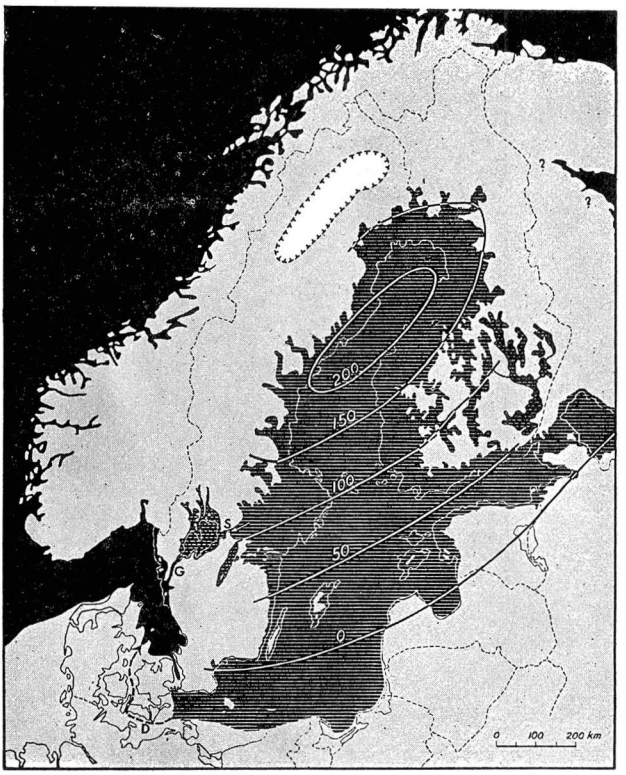

FIGURE 12.—*Late stage of the Ancylus Lake, with its isobases*
From the same source as Figure 11

Against the historical background outlined above, the immigration of the plants and animals living today in the Baltic may be concluded to have occurred as follows:

(1) The first immigrants were lacustrine continental forms which entered the Baltic from fresh waters which were dammed between the ice-cap and the northern slopes of the Continent; as these waters drained to the Baltic, as a consequence of the retreat of the ice-margin, they brought inhabiting organisms to the basin.

In the same way the Baltic was also invaded by the relicts *Limnocalanus macrurus* (from which the present Baltic form, *L. gramaldii*, developed), *Pontoporeia affinis*, *Pallasea quadrispinosa*, and *Mysis relicta*; these forms had reached the ice-dammed waters from the White Sea region, via an ice-lake, into which they had been "sluiced up" from the White Sea; *Pallasea*, a lacustrine form of Siberian origin, might have entered the lake from fresh waters of the area.

(2) As the margin of the ice-cap withdrew, new fresh-water organisms were brought into the Baltic basin from the Continental area. By that time, when the mouth of the Gulf of Finland was freed from ice, a second group of relicts reached the basin, viz. *Mesidotea entomon*, *Gammaracanthus lacustris*, *Cottus quadricornis*, and *Phoca hispida*; these forms had invaded the Gulf of Finland from the aforementioned ice-lake in the White Sea region.

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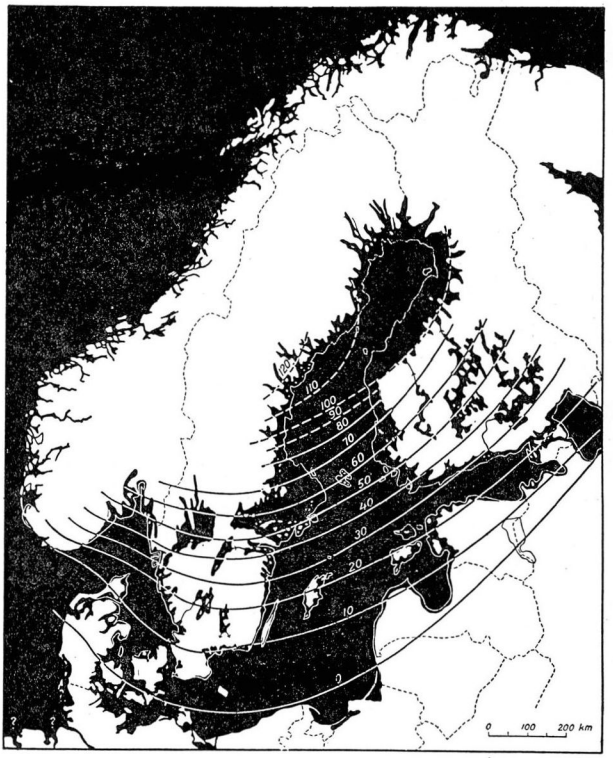

FIGURE 13.—*Littorina Sea at the time of its maximum, with isobases*
From the same source as Figure 11

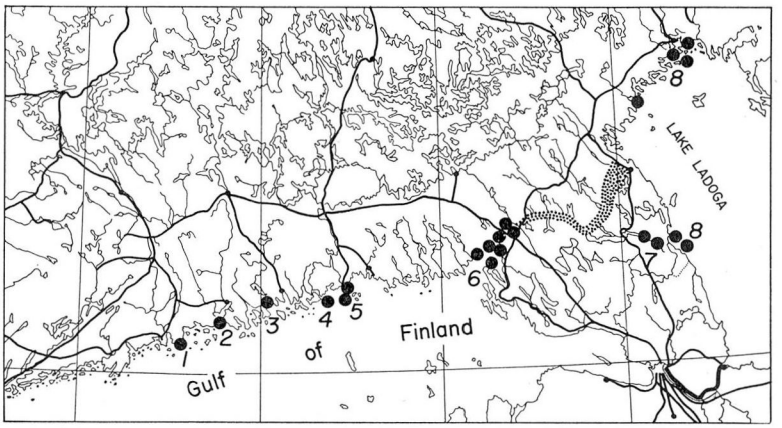

FIGURE 14.—*Distribution of the fresh-water fish,* Pelecus cultratus, *in the Gulf of Finland and in Lake Ladoga*

Showing the lower course of River Vucksi. 6: Bay of Viipuri (Viborg), 7: lower course of River Vuoksi, 8: Lake Ladoga. Nos. 1–5 indicate occasional finds, Nos. 6–8 permanent occurrence. The former outlet of Lake Ladoga stippled. R.N. = River Neva. The other lines are railroads. From Järvi (1936).

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FIGURE 15.—*Innermost Baltic finds of certain marine and genuine brackish-water animals*
Compiled from various sources

Immigration of lacustrine forms from the Continent was possible up until the Littorina Period, owing to the continually fresh or slightly brackish nature of the Baltic water.

(3) When the Littorina Period set in, it brought catastrophe to most of the lacustrine inhabitants of the Baltic, as well as to the relicts mentioned (excepting *Phoca*), which could not tolerate the higher salinity. From refuges in the most diluted parts of the Littorina Sea, many forms were, however, allowed to spread again, when the Littorina Period ended and the salinity decreased; among those who died out was one of the relicts, *Gammaracanthus*.

On the other hand, the salty Littorina water allowed members of the Atlantic fauna and flora to enter the Baltic. Some of them died out or withdrew to more southern areas, when the salinity dropped again; for instance, *Littorina littorea* once lived up to the middle of both Gulfs, but is today restricted to southern Baltic. In the last decades a new inward spread of marine forms on a modest scale has been observed; this feature is due to the increase in salinity of the Baltic water.

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The Baltic relicts of marine origin, *Pontoporeia femorata*, *Mysis mixta*, *Halicryptus spinulosus*, and some others, also immigrated with the salt water of the Littorina Sea, from nearby marine areas in the southwest, where they survived as remnants of the cold sea of the Glacial Age (Ekman, 1953).

The freshening of the Baltic water up to the Littorina period had special consequences on those peripheral parts of the basin which later, when the sea-level sank, were transformed into lakes. Owing to their former connection with the Baltic basin, these lakes harbor a much richer fauna and flora than would otherwise have been the case. This is especially evident in southern Sweden: in lakes which were once connected with the Baltic the number of fish species is as a rule considerably greater than in more westerly lakes beyond the reach of the Lake and draining into the Kattegat (Ekman, 1922).

An example of the opposite feature, that the present distribution of a lacustrine species in the Baltic depends on its range having formerly been continuous with that of a lake, seems to be offered by the fish, *Pelecus cultratus* (Järvi, 1936). This fresh-water species, which reached the Baltic basin from the southeast, probably during the Ancylus period, lives today, in the Gulf of Finland, permanently in its northeasternmost waters only, near Viborg (Viipuri) (Fig. 14). As *Pelecus cultratus* occurs also in the neighboring Lake Ladoga, it is assumed that the presence of the permanent stock of the Viborg waters is due to the connection which once existed between this district and Ladoga but which dried up when the land rose and the present outlet of the Ladoga, the Neva River, formed (Fig. 14).

GENERAL REMARKS ON THE FAUNA AND FLORA

As in other brackish waters, the number of species in the Baltic fauna is low. In the Belt Sea there is a clear decline caused by the reduction of the marine element and the near absence of specific brackish-water or lacustrine forms. In the Baltic proper the number of marine species is abruptly lowered much further, and, as the brackish- and fresh-water element of this area in no way constitutes an adequate compensation, owing mainly to the well-known but enigmatic inability of most of the forms to tolerate even a moderate salinity increase, the result is a very marked faunal and floral poverty (Remane, 1934; 1940).

The ensuing monotony of the fauna and flora of the Baltic proper is accentuated by the strikingly great horizontal range of many species and further by the widening of the vertical range: many species which outside the area are confined to shallow shore waters are found in greater depths in the Baltic proper. Examples are the bivalve, *Macoma baltica*, and the polychaete, *Scoloplos* armiger, which reach more than 100 m depth (the latter up to 140 m.) (Hessle, 1924) in the Baltic and, among the algae, *Fucus vesiculosus*, the lower limit of which lies at 11–12 m in the inner Baltic against *ca.* 5 m in the Kattegat (Wærn, 1952). This phenomenon seems mainly to be due to the weakening of competition (or persecution through predators) in the Baltic, owing to the absence or many marine forms (in the case of bivalves, especially of their main enemies the echinoderms (Petersen, 1918). The descent commonly involves a change in habitat—*i.e.*, forms confined off oceanic coasts to a sandy bottom occur in the Baltic also on mud, the main substratum at greater depths.

The faunal monotony of the Baltic is further augmented by the lack of true deep-water animals even in the greatest depths; all the species occurring there live also in shallow waters. One reason for this is obviously the shallowness of the inlets to the Baltic, which has excluded forms from the depths outside (Remane, 1940).

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The marine species penetrate generally into waters with a lower average salinity, and, reciprocally, the lacustrine ones into waters with a higher average salinity than in estuaries and other areas with strong salinity fluctuations. For instance, in the Gulf of Finland the inner limit of the marine isopod, *Idotea baltica*, lies at 3–4 ‰, (Fig. 15), but in Randers Fjord, on the east coast of Jutland, at 10–15 ‰ (Johansen 1918); in the case of the lacustrine gastropod, *Lymnaea* (*Radix*) *peregra* (*ovata*, *limosa*), again, the outer limits reach 10–11 and 5–7 ‰ respectively (Jaeckel, 1950; Johansen, 1918). This increased range of species of marine and lacustrine origin respectively involves increased regional overlapping of both elements and thus adds to the monotony of the Baltic fauna and flora. The phenomenon is important from a theoretical point of view also, as it underlines the impossibility, stressed in previous literature (Hedgpeth, 1951; H. Luther, 1951) of applying a given salinity system to every brackish area.

In investigations into the inner limits of marine species of the Baltic other factors besides the salinity must also be taken into account: (1) the decrease of the temperature toward the northern parts of the area; for instance, the absence of *Macoma baltica* in the Bothnian Bay (Fig. 15) and the very rare occurrence in the inner Baltic of the prawn, *Crangon crangon*, seem to be thermally conditioned. On the other hand, the increase of the temperature landward may be a limiting factor; for instance, the amphipod, *Gammarus zaddachi zaddachi*, which in coastal water penetrates farther inward—*i.e.*, into more diluted areas—than do *G. zaddachi salinus* and *G.* (*zaddachi*) *oceanicus*, tolerates a higher temperature than do the latter forms (observations and experiments by the author). (2) Unfavorable chemical factors other than the salinity drop, *e.g.*, the low oxygen supply in the Baltic deeps, which, because of their saltiness, otherwise offer good conditions for marine animals, and, in the case of plants, poor nutritional conditions; (3) The exposure. For instance, the isopod, *Idotea granulosa*, in the Tvärminne waters occurs only on shores exposed to the open sea and is thus confined to the outermost coastal zone even in cases of homogeneous salinity (observations by the author). (4) The occurrence of a species in a given area may be occasional and due to transport or immigration from its range proper.

As is to be expected in a brackish area, the low number of species in the Baltic proper is often in contrast to the high number of individuals. Examples of this phenomenon, which is in strict accordance with a well-known ecological rule, are seen in Plate 4. The production (weight) of the bottom fauna per sq m cannot, however, compete with that recorded from waters with high salinity, owing to the poor representation or lack of large forms (bivalves, echinoderms, etc.).

THE MARINE ORGANISMS

A number of marine animal groups do not penetrate at all into the Baltic area or at most are found sporadically in the Belt Sea and the Sound. Such groups are the Madreporaria, Octocorallina, Echiuroidea, Solenogastres, Pteropoda, Scaphopoda, Cephalopoda (some species may often appear in the area but do not reproduce there), and Selachii. Others are strongly reduced in the Belt Sea and practically or entirely lacking in the Baltic proper, for instance the Porifera (excluding the lacustrine Spongillidae), Actiniaria, and Echinodermata (Fig. 16). The Bryozoa are represented in

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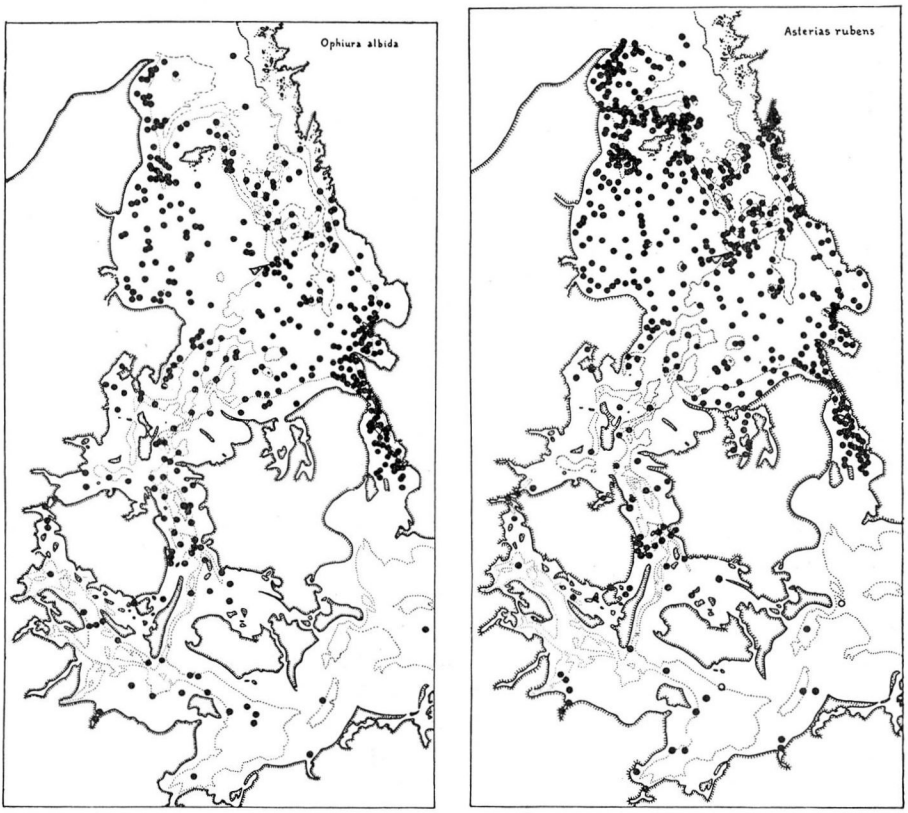

FIGURE 16.—*Examples of the influence on the fauna of the strong decrease in salinity at the entrances to the Baltic proper*

Distribution of *Ophiura albida* and *Asterias rubens*, the easternmost outposts among echinoderms in the Baltic. From Brattström (1941).

the Baltic proper by a few species. Table 2 gives the representation of other more euryhaline groups in different parts of the Baltic.

The strong decline of the marine element on passing into the Baltic proper is clearly seen from the table. If only the upper water layers are considered this feature is still more marked, as the more stenohaline marine species are confined to the saltier depths.

The innermost finds of some marine species are given in Figure 15. In addition, the innermost localities known for the following halophile insects may be mentioned: *Hemiptera: Sigara stagnalis:* Kalmar, Öland (mainly in brackish pools and lagoons); *Coleoptera; Berosus spinosus:* Åland-Tvärminne; *Enochrus bicolor:* Kristinestad (west coast of Finland) (Lindberg, 1948).

Schlieper (1935) suggests that the majority of the marine species occurring in the Baltic proper are, in an osmoregulatory respect, of the homoiosmotic type—*i.e.*, able to maintain the concentration of the body fluids on a level higher than that of the environment, when living in a diluted medium.

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TABLE 2.—*Number of marine species of certain animal groups in different parts of the Baltic and outside this area*

After Ekman (1935; 1953), modified

Group	Kattegat	Belt Sea	Arkona Sea	Gulf of Finland
Hydroidea	41–47	36	21	1[1]
Scyphozoa	4	4	2	1[2]
Polychaeta	193	143*	15**	3[3]
Decapoda	64	ca. 25	5	2[4]
Isopoda	36	20	7	4[5]
Amphipoda	132	ca. 52	17	5[6]
Lamellibranchiata	92	34	24	4[7]
Pisces	75	55	30	22[8]

* Includes the Sound

** "Southern Baltic"

[1] *Laomedea lovéni* [2] *Aurelia aurita* [3] *Nereis diversicolor, Harmothoë sarsi, Pygospio elegans* [4] *Leander adspersus fabricii, Crangon vulgaris* [5] *Idotea baltica, I. granulosa, Jaer amarina (albifrons)* [6] *Gammarus locusta, G. (zaddachi) oceanicus, Calliopius laeviusculus, Pontoporeia femorata, Corophium volutator* [7] *Cardium edule, Macoma baltica, Mya arenaria, Mytilus edulis* [8] No selachians

An odd feature in the vertical range of *Macoma baltica* in the inner Baltic is worth mentioning here (Hessle, 1924). North of Öland and Gotland this marine bivale avoids greater depths, in spite of their higher salinity; the lower limit of the vertical range lies at 40–50 m. It has been assumed that this phenomenon is due to a biotic factor. *Pontoporeia affinis,* which occurs in great abundance in deeper waters of the inner Baltic, may eat the young *Macoma* as they sink to the bottom, after the planktonic stage. This may also be the cause of a phenomenon observed in the Tvärminne waters; in depths over 20–30 m, where *Pontoporeia affinis* is as a rule very abundant, the renewal of the stock of *Macoma* has failed over periods of many years (Pl. 4) (Segerstråle, 1933b).

As in other brackish-water areas the dilution in the Baltic is often accompanied by reduction of the body size of animals. Well-known examples are offered by bivalves: *Mytilus edulis* attains a length of 110 mm near Kiel (Brandt, 1897) but only a little more than 20 mm at its eastern limit in the Gulf of Finland (Pl. 2); *Mya arenaria* also exhibits great reduction. On the other hand, in Finnish coastal waters with very good nutritional conditions *Macoma baltica* reaches at least 24 mm (Levander, 1899) —*i.e.*, more than is given for the North Sea; the shell is, however, thinner than in oceanic waters, owing to the comparatively low calcium content of the diluted Baltic proper. *Aurelia aurita, Asterias rubens,* and fishes such as the cod and the herring also marked reduction in size in this area. Other animal groups may be only little or not at all affected. For instance, the amphipods, *Gammarus zaddachi oceanicus* and *Corophium volutator,* as well as the prawn, *Leander adspersus fabricii,* grow to about the same size in the Gulf of Finland as in Danish waters; and in the microfauna no reduction in size is found except, as in the case of forms with a calcareous test shell (foraminifers), a reduction of the test (Remane, 1940).

Near the inner limit of their range many animals become unable to reproduce or develop. The specimens of *Asterias rubens* and *Ophiura albida* observed farthest into the Baltic (Fig. 17) have grown from larvae transported from saltier waters and do not attain sexual maturity (Brattström, 1941); the cod occurring in Finnish coastal

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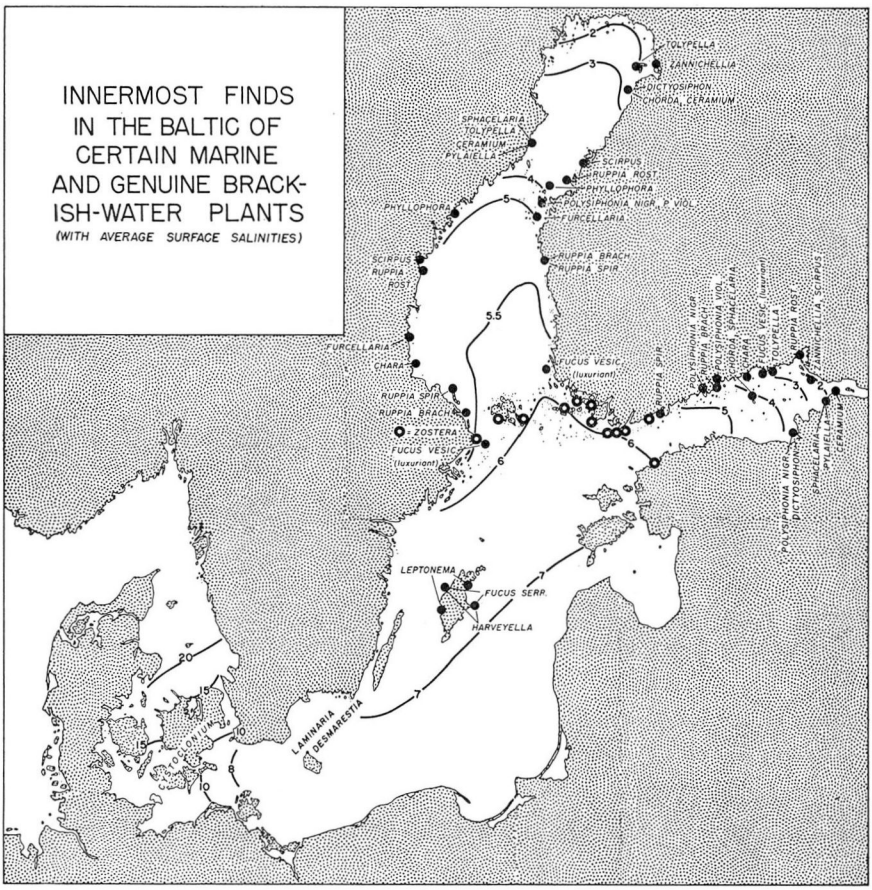

FIGURE 17.—*Innermost Baltic finds of certain marine and genuine brackish-water plants*
Compiled from various sources

areas is generally not able to reproduce there (Schnakenbeck, 1940); in a salinity of less than about 6 ‰, *Aurelia aurita* still produces normal germ cells, but the scyphistoma stage apparently does not develop (Segerstråle, 1951b).

The strong general decline of the marine faunal component of the Baltic fauna is in contrast to the flourishing of some euryhaline forms. As an example may be mentioned the amphipod, *Gammarus zaddachi oceanicus*, which is remarkably abundant, even in the inner Baltic proper.

In comparison with animals the marine plants are handicapped, from the point of view of their ability to enter the brackish Baltic, by being excluded from deeper waters where the higher salinity would favor them. On the whole, however, the marine flora exhibits the same features as the fauna. The number of algal species, already greatly reduced in the Belt Sea, shows a rapid drop when passing into the Baltic proper, especially the comparatively stenohaline Rhodophyceae; for instance, the Corallinaceae, with the exception of *Lithothamnion polymorphum*, remain outside

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the separating thresholds. On the coast of Bornholm the last *Laminaria* (*L. saccharina*) are found (Lund, 1941–1951), in the southern half of Gotland the last *Fucus serratus* (Svedelius, 1901). On the other hand, a number of marine algae are found even in the inner parts of the Gulfs (Fig. 17).

The decline of the red algae contrasts with the increase in the Chlorophyceae. Many representatives of this group even display unusually luxuriant growth. Brown algae may also be found thriving; for instance, *Pylaiella rupincola* is remarkably plentiful.

As a rule, however, the marine plants, like many marine animals, are reduced in size in the Baltic. For instance, the big species, *Laminaria saccharina*, is represented in the Arkona Sea by specimens only a few cm high. In many cases the reduction is combined with morphological modification, causing difficulties to the systematists. Great reduction in size probably always leads to sterility. For example, the reduced forms of the red algae, *Polysiphonia nigrescens* and *Rhodomela subfusca*, living in the inner Baltic, reproduce very rarely, if at all, by the sexual method.

THE LACUSTRINE ORGANISMS

This component of the Baltic fauna and flora clearly predominates in the innermost parts and near the coasts of both Gulfs, as well as in coastal waters with strong local fresh-water influence elsewhere in the area.

In shallow and sheltered waters insects contribute greatly to the fresh-water constituent of the fauna, as larvae only (Odonata, Ephemerida, Trichoptera, Diptera, etc.) or as larvae and imagines (mainly Coleoptera) (Pl. 4). Lacustrine gastropods, mainly pulmonates, are also important. Most of them tolerate at most about 3 ‰ salinity. In the neighborhood of Tvärminne (salinity ca. 6 ‰) the following species are still found: *Lymnaea stagnalis*, *L. peregra* (*ovata*), *L. palustris*, *Physa fontinalis*, *Anisus* (*Planorbis*) *vortex*, *Bithynia tentaculata*, and *Theodoxus fluviatilis*, which tolerate up to 10–11 (14) and 14 (18) ‰ respectively (Jaeckel, 1950) and thus occur even in the outer parts of the Baltic. Of fresh-water bivalves, *Anodonta cygnea piscinalis* and *Unio* species occur in coastal waters with a salinity of at most about 3 (–4) ‰. Many of the lacustrine gastropods of the Baltic are greatly reduced in size and have been described as special forms (*Lymnaea peregra* var. *baltica*, *Bithynia tentaculata* f. *bottnica*, *Theodoxus fluviatilis* f. *litoralis*) (Pl. 2). Besides, the kidney of Baltic fresh-water gastropods has proved to be subject to reduction in comparison with specimens of the same size from lakes; this reduction is regarded as due to the facilitation of the osmoregulatory function of the kidney in brackish water (osmotic dilut on of body fluids less strong) (Hubendick, 1948).

Some other lacustrine inhabitants of the Baltic, including the lacustrine isopod, *Asellus aquaticus*, and the larva of the lepidopter, *Acentropus niveus*, tolerate a remarkably high salinity (15–16 ‰) and consequently extend into the outer parts of the area (Remane, 1940).

In the macroscopic flora of the Baltic, fresh-water species, mainly aquatic phanerogams, predominate in about the same waters as the lacustrine animals. The water moss, *Fontinalis dolecorlica*, penetrates into the southernmost part of the Gulf of Bothnia (Öregrund Archipelago) (salinity ca. 5–5.5 ‰) (Wærn, 1952); in the Tvär-

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minne area (salinity ca. 6 ‰) many of these plants are still common, such as *Phragmites communis*, species of *Scirpus*, *Potamogeton*, *Myriophyllum*, *Ranunculus*; and, among algae, species of *Chara*, *Enteromorpha*, *Cladophora*. *Ulothrix zonata* extends to at least Kalmar Sound (Wærn, 1952), and *Potamogeton pectinatus* even to the Belts (found at a salinity of not less than 16–18 ‰) (H. Luther, 1951).

Oddly enough, quite a number of lacustrine animals and plants which occur in the inner Baltic are missing or very rare in the fresh water of neighboring land areas: the gastropod *Theodoxus fluviatilis* (Segerstråle, 1945), the sponge *Ephydatia fluviatilis* (Levander, 1901), and a number of aquatic Coleoptera and Hemiptera (*Haliplus immaculatus*, *H. obliquus*, *H. flavicollis*, *Enochrus melanocephalus; Gerris thoracicus*, *Noterus clavicornis* (Fig. 18) (Lindberg, 1948). Among plants may be mentioned *Najas marina*, *Zannichella repens*, *Z. pedunculata*, *Potamogeton panormitanus*, *Myriophyllum spicatum*, and *Utricularia neglecta* (Luther, 1951; Samuelsson, 1934). The causes of this peculiar feature are not well understood in detail but are obviously connected with the fact that the water comes largely from peat-bog districts and runs through Archaean rock regions (Luther, 1951). One important negative factor is, no doubt, the low pH value of the waters concerned; another, for instance in the case of *Theodoxus*, their poor calcium content.

Thermophile fresh-water forms, such as the beetle *Coelambus parallellogrammus*, may exhibit another interesting type of distribution in the Baltic; it is confined to the coastal waters in its southern part (Lindberg, 1948). Hydroclimatic conditions seem also mainly responsible for the fact that a number of aquatic insects and plants proceed farther to the north in the coastal waters of Finland than in the lakes of the neighboring Finnish mainland which are cooled earlier in the autumn. In this case, as in the case of the insects avoiding fresh water (*Haliplus*, etc.), the peculiar distribution may depend primarily on plants necessary for the animals concerned (species of *Chara*, *Cladophora*, etc.) (Lindberg, 1948).

GENUINE BRACKISH-WATER ORGANISMS

As usual in diluted areas, the number of species belonging to this ecologically interesting group is small in the Baltic, in comparison with the number of marine and fresh-water species. The following may be mentioned; the capital letters or localities after the names indicate how far up into the Baltic the species concerned is recorded: K Kalmar Sound (Forsman 1952a; 1952b), V Västervik (Forsman, 1948; 1951a), G Gdansk [Danzig] Bay (Demel 1933; 1935), F Gulf of Finland; cf. also Fig. 15.

CILIATA: *Tintinnopsis tubulosa* F, *T. brandti* F, *Leprotintinnus bottnicus* F.
CHIDARIA: *Protohydra leuckarti* F, *Pelmatohydra oligactis* (physiological race) F, *Cordylophora caspia* F.
TURBELLARIA: *Promesostoma baltica* F, *P. cochlearis* F, *P. lugubra* Kiel, *Koinocystis tvaerminnensis* F.
ROTATORIA: *Synchaeta fennica* F, *S. monopus* F, *Keratella* (*Anuraea*) *cruciformis eichwaldi* F, *K. quadrata platei* F, *K. cochlearis recurvispina* F.
NEMERTINI: *Prostoma obscurum* F.
POLYCHAETA: *Streblospio dekhuyzeni* (*shrubsoli*) K, *Alkmaria romijni* K, *Manayunkia aestuarina* (*Haplobranchus balticus*) F.

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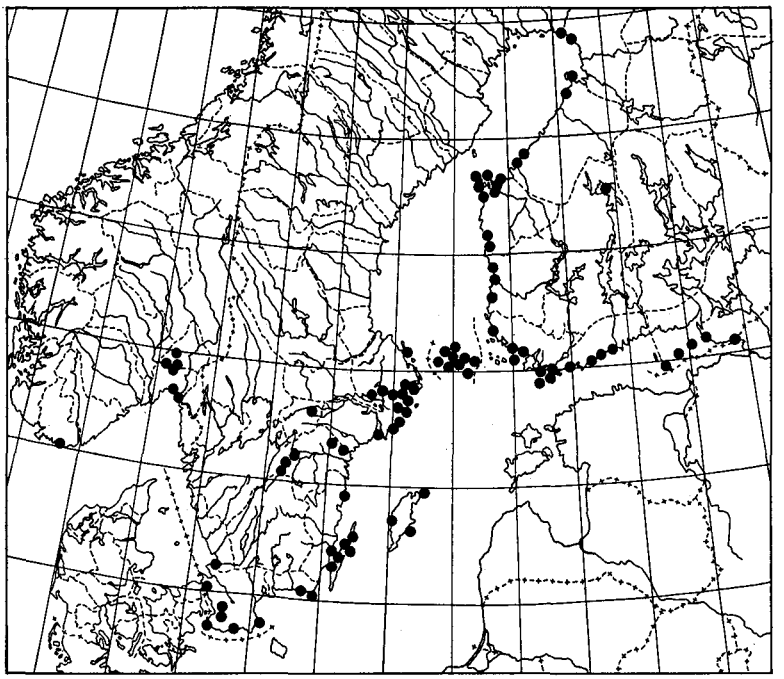

FIGURE 18.—*Example of the phenomenon that a number of fresh-water species among plants and animals are totally or practically confined in Northern Fennoscandia to the brackish Baltic*

Distribution of the aquatic beetle, *Haliplus immaculatus*, in the area concerned (main range: fresh water in southern Euro-Siberia; occurrence on the west coast of the Gulf of Bothnia unknown). From Lindberg (1948).

OSTRACODA: *Cytherura gibba* F, *Cytheromorpha fuscata* F. (*Cyprideis litoralis*, regarded hitherto as a genuine brackish-water species, has, as communicated by Prof. A. Remane, recently been found in Southern France in water of 60‰ salinity and cannot, in consequence, be included in the ecological group concerned).

COPEPODA: *Eurytemora affinis* F, *E. hirundoides* F, *Acartia bifilosa* F.

CLADOCERA: *Bosmina coregoni maritima* F.

DECAPODA: *Palaemonetes varians* (mainly in brackish pools) Greifswald.

ISOPODA: *Sphaeroma hookeri* K, G, *Cyathura carinata* G, *Idotea viridis* F.

TANAIDACEA: *Heterotanais oerstedi* G, V.

AMPHIPODA:? *Bathyporeia pilosa* F, ? *Melita palmata* K, G, *Gammarus zaddachi zaddachi* F, G, *G. zaddachi salinus* F, *G. duebeni* (mainly in brackish lagoons and pools) F, *Leptocheirus pilosus* F, *Corophium lacustre* F.

COLEOPTERA: *Ochtebius marinus* F, *Laccobius decorus* (known in the Baltic only from shores of its central and northern parts), *Haemonia mutica*, *H. pubipennis* (the former *Haemonia* species is known in the Baltic from the shores of its inner parts, the latter from the shores of its inner and central parts only).

GASTROPODA: *Hydrobia ventrosa* F, *Alderia modesta* F.

BRYOZOA: *Membranipora crustulenta* F, *Victorella pavida* F.

Among the comparatively few genuine brackish-water plants of the Baltic, the following may be mentioned:

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CYANOPHYCEAE: *Anabaena baltica.*
DIATOMACEAE: *Thalassiosira baltica, Chaetoceros subtilis, Ch. wighami, Synedra tabulata, S. pulchella.*
RHODOPHYCEAE: *Ceramium tenuicorne.*
PHAEOPHYCEAE: *Ectocarpus confervoides "fluviatilis", Porterinema fluviatile.*
CHARACEAE: *Tolypella nidifica, Chara baltica, Ch. canescenes (Ch. crinita).*
PHANEROGAMAE: *Scirpus parvulus, Zannichellia pedunculata, Najas marina.*

Brackish-water species are common to widely separated diluted areas. The following animals are recorded from such distant waters as diluted areas of the Mediterranean and/or the Black Sea: *Cordylophora caspia, Streblospio dekhuyzeni (shrubsoli), Palaemonetes varians, Cyathura carinata, Heterotanais oerstedi, Sphaeroma hookeri, Victorella pavida, Membranipora crustulenta* (varieties); etc. (Stammer, 1932).

As to the reasons why an organism should be mainly or wholly confined to waters with reduced salinity, biotic as well as physiological factors of course must be taken into consideration. In the Baltic fauna this is especially clear in the case of *Gammarus duebeni.* This species has proved able to reproduce even in water salinities as high as 23–25% (Forsman, 1951b) but is nevertheless almost exclusively confined to diluted areas, and even there it occurs principally in brackish lagoons, pools, and other more or less isolated habitats where competitors and enemies are rare or absent (Forsman, 1951b; Segerstråle, 1946) (cf. the flourishing in the Baltic of the euryhaline marine species *Gammarus (zaddachi) oceanicus* and *Pylaiella rupincola).* From a strictly physiological point of view such species cannot, of course, be regarded as genuine brackish-water forms.

GLACIAL RELICTS

The remnants from the glacial epoch constitute a most important and characteristic element of the Baltic fauna; in fact all glacial relicts within the marine boreal region are practically confined to this area. This is explained by its low water temperature,

PLATE 1.—AERIAL VIEW OF THE WATERS OF THE ARCHIPELAGOS OF THE INNER BALTIC

Near the Zoological Station of Tvärminne (southwest coast of Finland, surface salinity about 6‰). On the right the open sea. The two crosses indicate localities whose bottom fauna is seen in Plate 4. Depth in the little bay at center of the photo 3 m, in the other locality 35 m; the station is to the right of the bay. The vegetation is also typical of a strongly diluted marine area. In the bay and in similar sheltered localities the common reed, *Phragmites communis,* and other fresh-water plants, *Potamogeton, Myriophyllum, Batrachium,* etc., grow abundantly, whereas a luxuriant vegetation of the marine alga *Fucus vesiculosus* borders the shores of neighboring islands. From Segerstråle (1933a).

PLATE 2.—SIZE REDUCTION IN ANIMALS IN THE BALTIC SEA

FIGURE 1.—The common mussel, *Mytilus edulis,* from the Balt Sea (Kiel, left) and the Gulf of Finland (easternmost locality off the south coast; one of the largest specimens caught). 1.1 ×. From Segerstråle (1948).

FIGURE 2.—Pulmonate gastropod, *Lymnaea stagnalis,* a lacustrine form from a Finnish lake (Messukylä: Iidesjä; right) and the sea near Tvärminne (bay Krogarviken) on the south coast of Finland (both shells from the collections of the Zool. Museum of Helsingfors University, represent approximately maximum growth). Natural size.

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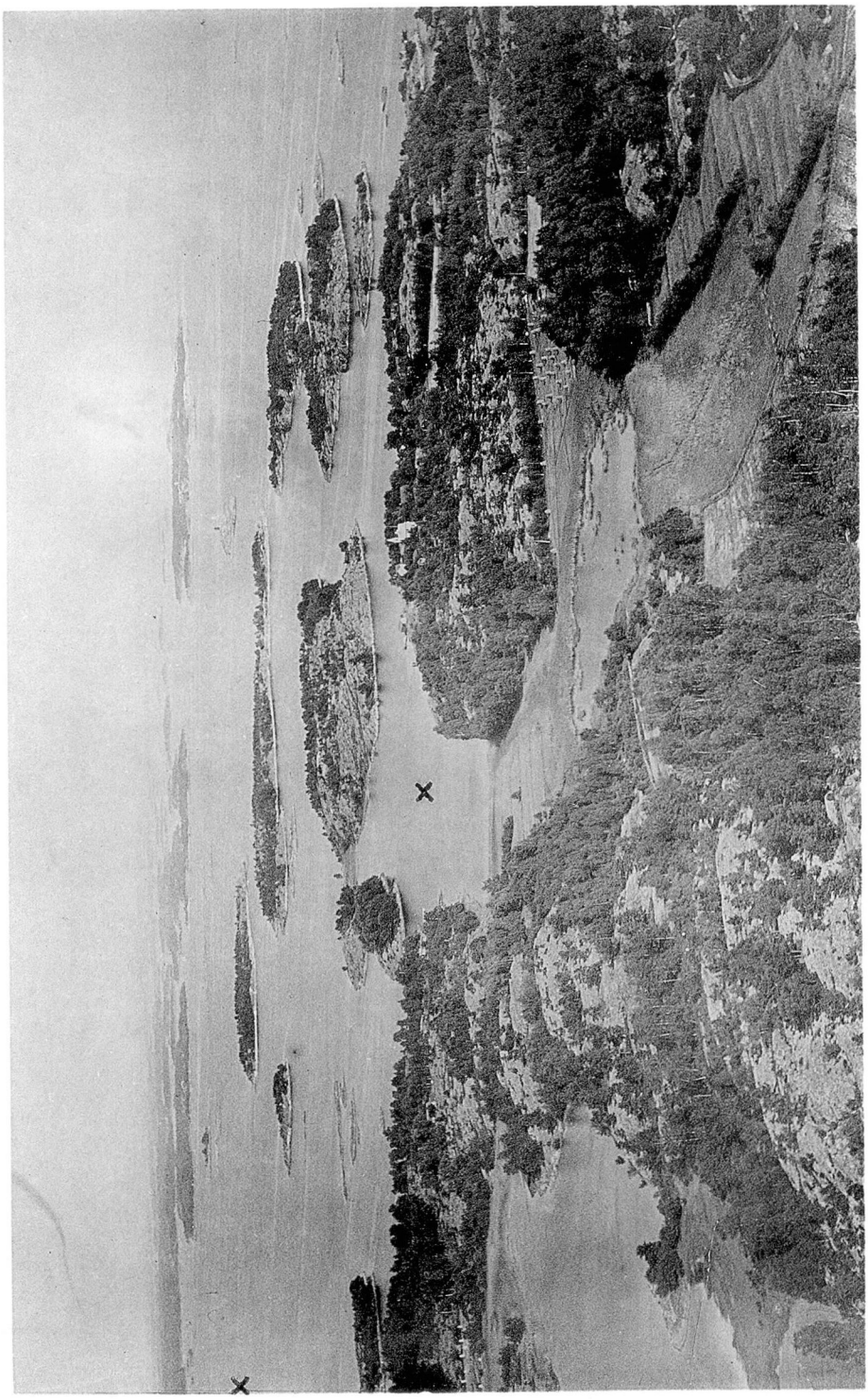

AERIAL VIEW OF THE WATERS OF THE ARCHIPELAGOS OF THE INNER BALTIC

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FIGURE 1

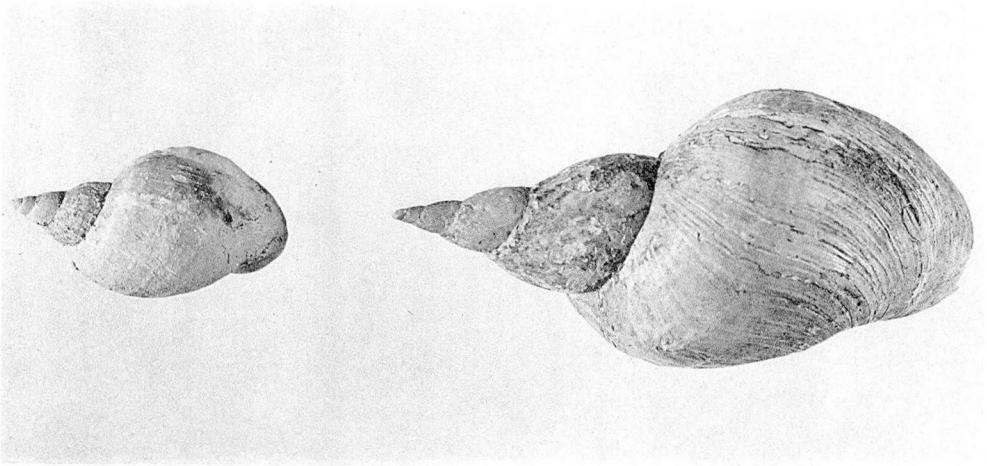

FIGURE 2

SIZE REDUCTION IN ANIMALS IN THE BALTIC SEA

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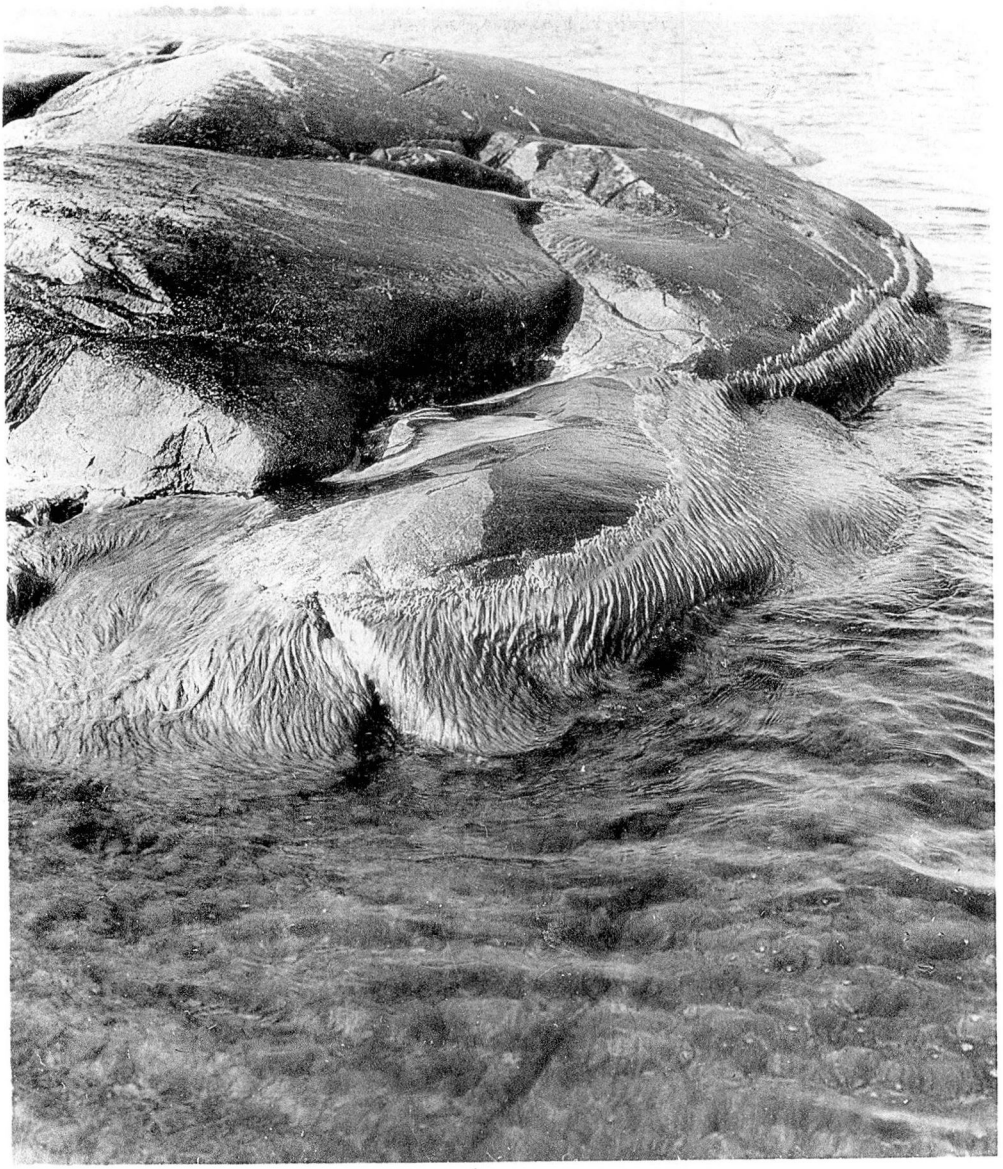

HYDROLITTORAL VEGETATION OF THE GREEN ALGA, *CLADOPHORA GLOMERATA*

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FIGURE 2

FIGURE 1

BOTTOM FAUNA OF THE INNER BALTIC

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especially in the winter and in the northern parts, and by the shape of the basin concerned. Its narrow connections with the ocean are confined to the south, and the comparatively cold northern parts are thus barred from the Polar Sea. As stressed by Ekman, it is, in fact, difficult to conceive a better combination of factors favorable for the development of a relict fauna than that offered by the Baltic.

The Baltic relict animals, most of which are crustaceans, are as follows (m: origin marine, br: indigenous in brackish waters):

HYDROZOA: *Halitholus cirratus* (syn. *Tiara pileata* partim, polyp generation *Perigonimus cirratus*) m.
OSTRACODA: *Paracyprideis fennica* cf. above.
COPEPODA: *Limnocalanus grimaldii*.
MYSIDACEA: *Mysis relicta* br., *M. mixta* m.
ISOPODA: *Mesidotea entomon* br. (Pl. 4)
AMPHIPODA: *Pontoporeia affinis* br., *P. femorata* m (Pl. 4), *Pallasea quadrispinosa*.
PRIAPULIDA: *Halicryptus spinulosus* (Pl. 4) m.
LAMELLIBRANCHIATA: *Astarte borealis* m.
PISCES: *Cottus* (*Myoxocephalus*) *quadricornis* br.
MAMMALIA: *Phoca hispida* (*Ph. foetida*) m. In addition, the parasitic worm, *Echinorchynchus salmonis*, may be mentioned, which is known from some lakes of Northern Europe and regarded as relict there; it seems possible that it also occurs in the Baltic, as the larva lives in *Pontoporeia affinis*.

In the Baltic flora very few species may be considered glacial relicts. To this category probably belong, among phanerogams, *Arctophila fulva* and *Potamogeton vaginatus*, occurring in the inner part of the Gulf of Bothnia (Fig. 20), and, among algae, possibly *Sphacelaria arctica*.

All the animals mentioned above, except *Pallasea*, are indigenous in the Polar Sea, and, as is seen, most of them are genuine brackish-water forms. *Pallesea*, which occurs sporadically in the inner Baltic only, is considered to originate from lacustrine

PLATE 3.—HYDROLITTORAL VEGETATION OF THE GREEN ALGA, *Cladophora Glomerata*

Low water. Southern part of the Gulf of Bothnia (Öregrund Archipelago). In large parts of the Baltic the lacustrine alga forms a well-developed belt above the belt of the marine *Fucus vesiculosus*. From Wærn (1952).

PLATE 4.—BOTTOM FAUNA OF THE INNER BALTIC

FIGURE 1.—Strong representation of lacustrine forms and glacial relicts. From the archipelago near the Zoological Station of Trärminne on the south coast of Finland. Caught in a little sheltered bay (depth 3 m, bottom mainly organic mud; for location, *see* Plate 1). Total number of animals per sq m is 4676. Marine forms: *Corophium volutator* (44 specimens seen in the figure), *Macoma baltica* (20), *Cardium edule* (lower row). Genuine brackish-water forms: *Pontoporeia affinis* (1; glacial relict), *Mesidotea entomon* (lower row, on left; glacial relict). Fresh-water forms: larvae of chironomids (17), *Tubifex tubifex* (1), lower row: *Theodoxus* (*Neritina*) *fluviatilis*, *Bythinia tentaculata*, *Asellus aquaticus*, larva of *Sialis*, larva of a trichopteran. From Segerstråle (1933b).

FIGURE 2.—Bottom fauna at Tvärminne (depth 35 m, bottom fine, almost black, mud, mainly organic; for location, *see* Plate 1). Explanations as for the preceding figure. Total number of specimens per sq m: 7604. Marine forms: *Macoma baltica* (6), *Harmothoe sarsi* (3, in three of the corners), *Pontoporeia femorata* (lower row; glacial relict). Genuine brackish-water forms: *Pontoporeia affinis* (127; glacial relict), *Halicryptus spinulosus* (1, inferior left corner; glacial relict), *Prostoma obscurum* (lower row, on the left), *Mesidotea entomon* (lower row, on the right; glacial relict). From Segerstråle (1933b).

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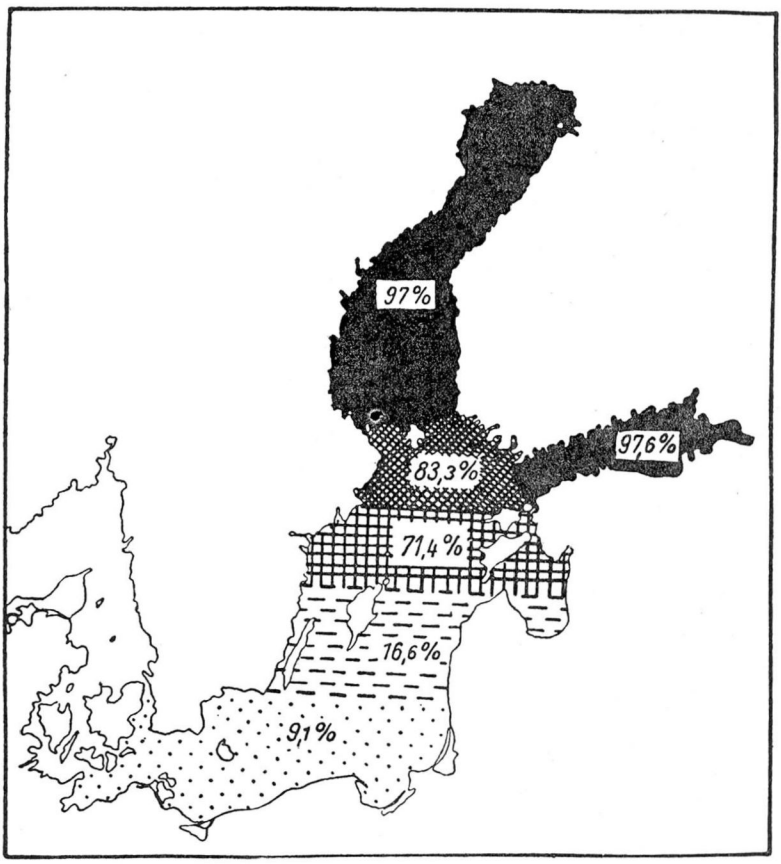

FIGURE 19.—*Occurrence of the glacial relict copepod,* Limnocalanus grimaldii, *in the Baltic*

The figures represent the percentage of hauls containing *Limnocalanus*. Like the relict *Mesidotea entomon* and *Pontoporeia affinis*, which are also indigenous in brackish water, this species is especially abundant in the more diluted (and colder) inner parts of the area. From Ekman (1914).

ancestors in northern Asia (Ekman, 1918). The immigration history of the relicts has been treated in an earlier section.

A number of the relicts in the present Baltic are also found in neighboring lakes which were isolated from the late- and post-Glacial Baltic by the land elevation: *Limnocalanus* (represented in lakes by *L. macrurus*, which is derived from *L. grimaldii*), *Mysis relicta, Mesidotea, Pallasea, Pontoporeia affinis, Cottus,* and *Phoca. Mysis relicta, P. affinis, Limnocalanus macrurus,* and *Cottus* also occur as relicts in lakes of the glaciated northern parts of North America. As a consequence of the glaciation, several of the Baltic relicts, in identical or only slightly modified form, are also met within the Caspian Sea: *Limnocalanus, Mesidotea, Pontoporeia affinis, Phoca.* As shown by Ekman, some of the relicts of the North European lakes, especially *Limnocalanus,* exhibit morphological deviations from the original arctic form, and in two lakes of North America (Nipigon and Cayuga; records from the latter not published, material sent to the author in 1953 by Dr. E. Bennette Henson) a form of the *Pontoporeia affinis* male (*P. affinis brevicornis*) was found, which seems to have developed

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FIGURE 20.—*Distribution in the Baltic of the aquatic phanerogam,* Arctophila fulva, *one of the glacia relicts in the Baltic flora*

Outside the area figured the species occurs in arctic Russia and on Bear Island. From Hultén (1950).

from the normal form since the Glacial Age through partial inhibition of metamorphosis (*e.g.*, the elongation of the male antennae is much less strong (Segerstråle, 1937).

The relicts play their greatest role in the comparatively cold and highly diluted inner parts of the Baltic, which obviously offer very favorable conditions to the brackish-water forms among them. *Halicryptus* and *Pontoporeia femorata* do not penetrate into the Bothnian Bay nor into the inner parts of the Gulf of Finland, and *Astarte* is confined to the southernmost Baltic.

ENDEMICS: RECENT IMMIGRANTS

As is understandable from the very young age (geologically speaking) of the Baltic, only a few endemic forms are known from this area. To this category belong three planktonic animal species—*viz.*, the rotifers, *Keratella quadrata platei* and *K.*

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cochlearis recurvispina, and the crustacean, *Bosmina coregoni maritima*, and two algae, the planktonic *Anabaena baltica* and the benthic *Monostroma balticum* (Hoffman, 1950).

A number of the animals at present living in the Baltic have only recently invaded the area—some only in the last few decades or years.

The fresh-water bivalve, *Dreissensia polymorpha* (fam. Mytilidae), widespread in eastern, central, and western Europe, was found in 1824 in great abundance in the highly diluted bays Frisches Haff and Kurisches Haff on the southern coast of the Baltic; later it was reported also from Stettiner Haff and Schlei (mean salinity in the Schlei locality 4.73 ‰) (Thienemann, 1950; Jaeckel, 1950). In Sweden the species was observed in Lake Mälaren in the 1920's and in brackish water outside Stockholm—*i.e.*, in the Baltic—about 1940. The young bivalve is said to tolerate the salinity of the Baltic. Since, moreover, the species can attach itself to various substrates with its byssus threads, it is easily transported; it is, for instance, assumed that it was introduced into England with timber from the Baltic area (Hessland, 1946).

Congeria cochleata may also be mentioned here, although its occurrence in the Baltic is not established with certainty (Thienemann, 1950). Since 1835, when it was first observed in Europe (in the harbor of Antwerp), this species, indigenous in the fresh waters of western Africa, has spread into fresh and brackish areas in western Europe. In 1928 it was found in the brackish Kiel Canal and in 1933 near Pillau in what was formerly East Prussia; the nature of the locality—fresh, or Baltic, water—is, however, unknown. The occurrence of *Congeria* in brackish waters also on the European continent indicates the possibility that it may become a member of the Baltic fauna.

In the last century the little prosobranch gastropod, *Potamopyrgus jenkinsi* (*Potamopyrgus crystallinus*, *Hydrobia jenkinsi*), invaded brackish and, later, fresh waters in western Europe (Thienemann, 1950). It came, according to recent new investigations (Boettger, 1951), from New Zealand, where the species is recorded from fresh water only (previously it was assumed to be a native of the West Indies). In 1887 this gastropod had reached Wismar Bay on the north coast of Germany and thus the Baltic, where in 1926 it was observed in the Åland Isles, in 1927 near Riga, and in 1945 in the innermost part of the Gulf of Bothnia. Doubtless also the whole of the Gulf of Finland is already occupied by the species (found there in 1936 at about 27°E. (Suomalainen, 1939). In the Tvärminne waters off the southwest Finnish coast it was first observed in 1933 and is now quite common there. The rapid spread of the species in Europe is assumed to be mainly due to its being parthenogenetic, to the absence of parasites in Europe, and to transport by birds (Boettger, 1951).

Since 1912, when it was first found in Europe (in the river Aller, a tributary of the Weser, in western Germany), the Chinese Mitten Crab, *Eriocheir sinensis*, has spread with exceptional rapidity in western and central Europe and has become, especially in Germany, a real scourge (Thienemann, 1950). For reproduction the crab migrates down the river it inhabits to its estuary. From the first half of the 1930's occasional specimens have been caught in the Baltic also, in the coastal waters of all the countries concerned (innermost localities: in the Gulf of Bothnia, the archipelago off Luleä (Enequist, 1946); in the Gulf of Finland, Koivisto (Kairasuo,

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1953), and Viipuri (Viborg) (Thienemann, 1950). In all probability the Baltic finds are due to transport of the specimens in the ballast water tanks of ships (in this way, too, the first specimens are assumed to have been brought to Europe from China). This may be concluded from the fact that the crabs caught in the Baltic were full grown; furthermore, the salinity of the Baltic is, to judge from experimental studies, much too low as to allow oviposition and development of the eggs. It is, consequently, obvious that *Eriocheir* will not become a real new member of the Baltic fauna.

The plankton copepod, *Acartia tonsa* (Vorstman, 1946), an inhabitant of coastal waters of the continents, from the tropics to the temperate zone, has since about 1910 invaded the North Sea coast of western Europe and, later, also the Baltic; it probably came from North America. In 1925 the species was observed in the Bay of Gdansk, in 1934 in the Luga Bay on the south coast of the Gulf of Finland; in 1939 it had reached the waters near Helsingfors and the Bay of Esbo west of that town. In the last-mentioned waters off the Finnish south coast *Acartia tonsa* obviously was not present before 1935. Although the salinity of the open Baltic does not exceed the optimum range of the crustacean, as established in the North Sea, it seems, in the former area, to be confined to isolated waters quite near the coast. On the other hand, the species may occur in striking abundance in such localities and may constitute up to 90 per cent of the whole zooplankton. The explanation is that *Acartia tonsa* requires a comparatively high temperature for reproduction and is much favored by eutrophication of the water (Dr. H. Buchholz, Kiel, in letter).

The small crab *Rhithropanopeus harrisi* subsp. *tridentatus* (*Pilumnopeus tridentatus*, *Heteropanope tridentatus*) (Thienemann, 1950; Buitendijk and Holthuis 1949; Kinne and Rotthauwe, 1952), known in Europe since 1782 from the coastal, mainly brackish waters of Holland and seemingly introduced there from the east coast of America by ships, was in 1936 also observed in the North Sea-Baltic Canal (Kiel Canal) into which it is assumed to have been transported in 1910–1914 by Dutch ships engaged in dredging work. Later the species was also found in a Baltic water—*viz.*, the long and narrow bay of Schlei, northwest of Kiel (locality of find Lindaunis, with a mean salinity of 8.5 ‰) (Kinne and Rotthauwe, 1952). The salinity factor would not prevent further spread within the Baltic area, as the crab can tolerate even fresh water, but, on the other hand, observations on its reaction upon low temperature (Kinne and Rotthauwe, 1952) suggest that the water of the inner Baltic may in winter be too cold for its thriving.

The latest invaders of the Baltic are marine forms which have managed to get a foothold in the area owing to the recent rise in salinity (as mentioned before, marine forms are continually carried into the Baltic with the incoming salt-water current). Forsman, who in recent years has found a number of animals new to the Baltic in Kalmar Sound, thinks that at least the bryozoan, *Alcyonidium polyonum*, belongs in this category (Forsman, 1952b).

According to Hessland's (1946), *Mya arenaria* was abundant off the European coast during the later part of the Pliocene but became extinct during the Ice Age. It is assumed that the new invasion came from the Atlantic coast of America and was brought about by the unconscious assistance of man since transoceanic sea voyages began in the sixteenth century. Not until the seventeenth century does the

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species seem to have gained its prominent position in the European littoral fauna. According to these new results the clam has thus belonged to the Baltic fauna for a much shorter period than was assumed previously, when it was thought to have invaded the area during the Iron Age.

VEGETATION

Like the fauna, the vegetation of the Belt Sea is practically marine with a reduced number of species. Down to about 10 m depth (in the Sound 15 m) wide areas are covered with submarine meadows of *Zostera marina*, which is a most important producer of bottom detritus and thus of food for the benthic animals of the area. Owing to the absence of rocky shores, the large brown seaweed vegetation is confined to stones and moraine boulders occurring along the coast. It consists mainly of *Fucus vesiculosus* which is found down to *ca.* 10 m depth; *F. serratus* is also common (vertical range 4–15 m). *Laminaria* occurs, but below *ca.* 6 m only, and *Ascophyllum nodosum* is present only as loose-lying, greatly reduced and sterile specimens (*F. scorpioides*), which have developed from fragments carried into the area from outside. Deeper down, to *ca.* 30 m, the vegetation consists mainly of red algae.

In the Baltic proper, up to the entrance of the Gulf of Bothnia and to the eastern part of the Gulf of Finland, the vegetation of rocky shores, from the upper limit of the permanently submerged zone (the sublittoral), or, in exposed localities, from 2–3 m, down to about 10–11 m. (Wærn, 1952), is as a rule dominated by *Fucus vesiculosus* and thus very monotonous; *F. serratus* is known up to the southern shores of Gotland only. Above this belt there is normally a zone (the hydrolittoral) about half a meter deep, of filiform annual algae, mainly the lacustrine green alga *Cladophora glomerata* (Pl. 3) (*Dictyosiphon*, *Phylaiella*, *Ceramium*, *Eudesme*, and *Enteromorpha* are also locally of great importance), which develop in summer when the belt concerned is again submerged after the low water in spring. *Cladophora*, like most of the other algae mentioned, also occurs among the *Fucus*; of other species growing there the marine brown algae *Pylaiella rupincola* and *Chorda filum* may be noted. *Pylaiella*, *Elachistea fucicola*, *Dictyosiphon foeniculaceus*, and *Stictyosiphon tortilis* are found epiphytic on *Fucus*. Below the *Fucus* belt (the upper sublittoral) follows a zone (the lower sublittoral) characterized mainly by the red algae *Furcellaria fastigiata*, *Phyllophora brodiaei* (loose-lying form), *Rhodomela subfusca*, *Polysiphonia nigrescens*, the brown alga *Sphacelaria*, etc. The lower limit of this zone—*i.e.* of the vegetation—lies at about 20 m.

In the major part of the southern Gulf of Bothnia, the Bothnian Sea, no *Fucus* is visible in the shore waters; the alga is restricted to greater depths and shows reduction even there (Fig. 17) (Häyrén, 1952; Waern, 1952). North of Kvarken almost exclusively loose-lying *Fucus* has been found (Häyrén, 1952). The marine brown alga in question is largely replaced by lacustrine green algae, mainly *Cladophora glomerata* and *C. aegagropila*. On soft bottoms in the inner Gulf of Bothnia *Chara tomentosa* (up to the south of the Bothnian Bay) and *C. aspera* occupy large areas even in waters near the open sea. At the inner end of the Bothnian Bay the vegetation is purely lacustrine.

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A corresponding transition is observed in the Gulf of Finland, but *Fucus* and other marine algae penetrate into much more diluted water in this area (Fig. 17).

In the archipelagoes and other sheltered waters of the Baltic proper soft-bottom areas are largely covered with a vegetation of a pronouncedly lacustrine type (Pl. 1). *Chara tomentosa*, *Chara aspera*, and phanerogams are especially abundant: species of *Ruppia*, *Zannichellia*, and *Potamogeton*, *Myriophyllum spicatum*, *Ranunculus obtusiflorus*, and up to the entrances to the Gulfs also *Zostera marina* (Fig. 17). *Phragmites communis* and species of *Scirpus* are also of great importance. In the Bothnian Bay water mosses (*Drepanocladus* and *Fontinalis*) may cover extensive areas in inner, sheltered waters.

In bays which penetrate far into the mainland and receive river outflow, the features typical of the Baltic proper may be studied within a short distance. This has been done with special accuracy near Tvärminne, in the bay of Pojoviken, and in the waters outside, which offer a good opportunity to follow the changes in the vegetation from the outermost skerries (salinity about 6‰) with their luxuriant *Fucus* belt up to the zone with *Nymphaea alba* and other plants typical of lakes in the innermost part of the bay (Luther, 1951).

BOTTOM AND PHYTAL FAUNA

According to Petersen (1918) who divided the benthic fauna of Danish and neighboring waters into communities named after their characteristic forms, the deeper parts of the Belt Sea are inhabited by the *Abra* (*Syndosmya*) *alba* community, of impoverished marine and, interestingly enough, clearly arctic, type. In the eastern part of the Belt Sea another bivalve of the community, *Macoma calcarea*, begins to predominate. The *Macoma calcarea* community, which also contains several arctic animals (species of the bivalve *Astarte*, the polychaetes *Terebellides stroemi*, *Harmothoë imbricata*, etc.), is found not only in the eastern Belt Sea but even in the deeper parts of the southern Baltic proper.

The shallower parts of the Belt Sea harbor the *Macoma baltica* community, characterized by such organisms as the bivalves *Macoma baltica*, *Cardium edule*, and *Mya arenaria*. These species are widely distributed in the Baltic proper; *Macoma* descends to unusual depths there. For this reason Petersen referred the whole of the area concerned to the *Macoma baltica* community. *Cardium* and *Mya* are, however, missing in deeper waters, and in the innermost part of the Gulf of Bothnia, as well as at depths below the 40–50 m line in the whole of the inner Baltic, even *Macoma baltica* is absent. As stressed by Remane, the bottom fauna of the open Baltic proper is, in reality, characterized by forms other than those of the *Macoma baltica* community. The most important of them are glacial relicts or other forms at home in arctic waters: *Pontoporeia affinis*, *P. femorata*, *Mesidotea entomon*, *Halicryptus spinulosus*, *Terebellides stroemi*, etc.; in the south, in addition, *Macoma calcarea*, *Astarte borealis*, *Priapulus caudatus*, and others. Toward the north the role of *Pontoporeia affinis* and *Mesidotea entomon* greatly increases, and in the inner part of the Central Baltic and in the Gulfs these relict crustaceans, together with *Macoma baltica*, are the predominant bottom animals in open waters. As *Macoma* is missing in the depth,

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the bottom fauna of the inner Baltic area is best characterized as a continuous *Pontoporeia-Mesidotea* community (Pl. 4) (Hessle, 1924). The deeps around Gotland, with their unfavorable oxygen conditions, are inhabited by extremely few species; on a muddy bottom the polychaete *Scoloplos armiger*, and in clayey localities *Pontoporeia femorata* and *Terebellides stroemi* are the only animals caught. In the Baltic proper, the *Macoma baltica* community is confined to shore waters; there, besides *Macoma*, *Cardium*, and *Mya*, it includes as important marine elements the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor*; in sheltered muddy localities in addition lacustrine forms, especially larvae of chironomids, may be important constituents of the bottom fauna (Pl. 4). In waters of this type with luxuriant vegetation of aquatic phanerogams larvae and/or imagines of other insects (Odonata, Trichoptera, Coleoptera) as well as fresh-water gastropods are also regularly found. In the inner parts of the Gulfs and in other highly diluted coastal waters, such as the Haffs and the bay of Pojoviken, the fresh-water component is, as a matter of course, overwhelmingly predominant.

The bottom fauna of the Baltic proper may, in contrast to its low number of species, exhibit a strikingly high number of individuals (Pl. 4). Quantitative investigations off the coast of Finland, covering a longer period, have, however, proved that almost all common species may fluctuate markedly from one year to another (Segerstråle, 1933b).

As to the inhabitants of the phytal, the fauna of the often luxuriant vegetation of the *Fucus vesiculosus* of the Baltic proper is of special interest on account of its great extent, abundance, and mixed composition. In comparison with the littoral fauna of oceanic coasts it is, of course, poor in species. On the other hand, the number of individuals may be remarkably high (Segerstråle, 1944).

Most of the *Fucus* animals belong to marine and brackish-water crustacean species: *Gammarus* (*zaddachi*) *oceanicus* (range mainly arctic), *G. zaddachi salinus*, *G. zaddachi zaddachi*, *Idotea granulosa*, *I. baltica*, *I. viridis*, *Jaera albifrons* (*marina*), *Praunus flexuosus*, *P. inermis*, *Leander adspersus fabricii* (in sheltered waters only). Other forms: attached to the weed, the marine *Mytilus edulis*, young *Cardium edule*, *Balanus improvisus*, and *Laomedea loveni*, and the brackish-water *Membranipora crustulenta* and *Pelmatohydra oligactis*. The lacustrine element is represented by *Theodoxus fluviatilis* which is numerically one of the most important inhabitants of the *Fucus* of the Baltic, *Lymnaea peregra* (*ovata*), and larvae of chironomids. In more sheltered waters, in addition, larvae and pupae of Trichoptera are common (they use the marine weed as material for their cases!). Fresh-water worms, such as *Planaria* spp., *Polycelis nigra*, *Stylaria lacustris*, *Nais elinguis* are also common; more sporadically the lacustrine sponge, *Ephydatia fluviatilis*, is found.

The great zoogeographic role played in the Baltic proper by the *Fucus* vegetation is readily observed when comparing its fauna with that of the shores of the inner parts of the gulfs where *Fucus* is missing; the decline, especially in the number of individuals, is very remarkable.

Studies of the microfauna of the Baltic benthal and phytal have been carried out mainly in the waters near Kiel and off the south coast of Finland.

From the extensive sand regions near Kiel, since the 1920's, Remane and his

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collaborators have obtained their most interesting results (Remane, 1933; 1952; Remane and Schulz, 1934). Remane was one of the first in the world to reveal the existence of a new faunal realm—*viz.*, the complex and amazingly dense population of protozoans and micrometazoans inhabiting the interstitial water between the sand grains. In the waters concerned hundreds of species have been recorded from this peculiar habitat, and every year new forms are described by the Kiel zoologists. Species characteristic of this interstitial fauna (mesopsammon) are turbellarians, gastrotrichs, archiannelids, tardigrades, harpacticoid copepods, and nematodes; the last-mentioned two groups are especially abundantly represented. The members of this fauna show interesting adaptations to life in the minute interstices between the sand grains: even the metazoans are very small, the body is often pronouncedly linear and very flexible, organs for sticking to the grains are commonly present, etc. Modifications are also observed with respect to the locomotion, nutrition, reproduction, etc. Remane distinguishes, in the Kiel waters, between two sand communities, characterized by their microfauna: the *Halammohydra* community in comparatively rough sand, and the *Turbanella hyalina* community in pure and fine sand. The interstitial fauna of the area comprises almost exclusively marine forms.

In this connection also the mesopsammon of the subterranean zone immediately inward from the water edge deserves mentioning, as far as it is influenced by the Baltic water. In the Kiel district the part of this zone which lies within the normal reach of the waves is characterized by the abundance of turbellarians of the group Otoplanidae (*Otoplana* zone). Many of the species inhabiting this brackish ground water are assumed to belong to the group of genuine brackish-water forms. Inward the sea water gradually changes into fresh ground water. It is assumed that such strongly diluted subterranean waters on the shore have been utilized by marine animals as an immigration route into fresh water and vice versa.

Near Tvärminne and in the adjacent waters off the Finnish coast the turbellarian fauna is fairly well known, thanks mainly to the work carried out by A. Luther (1920) and Karling (1931). More than 100 turbellarians are recorded from the area; three quarters of them are marine, the rest lacustrine (communication by Professor Luther). More than 40 species are new to science, and hitherto undescribed forms are continually being found. Other more thorough faunistic investigations have concerned the ostracods (Hirschmann, 1909; 1912) and nematodes (Schneider, 1906; 1926; 1927). A quantitative study on the microbenthos of the Tvärminne waters (Purasjoki, 1945) showed a maximum of 103,400 animals per sq m (7 stations, depth 9–55 m, bottom mostly sand and mud or mud and clay); most of them were nematodes and ostracods.

Many microscopic forms—protozoans, rotifers, cladocerans, copepods, etc.—from the benthal and phytal of the archipelago west of Helsingfors have been known since the pioneer work there by Levander at the end of the last century. In these waters the hydrachnids have also been studied (Nordenskiöld, 1894).

The hydrachnids have recently been subject to investigations on the Swedish coast of the inner part of the Bothnian Bay (archipelago off Luleä and Kalix); salinity 2–3 ‰; 25 species, almost all lacustrine, recorded (Svenonius, 1949).

Apart from the regions mentioned above, the Baltic microbenthos has been studied

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in the Sound only, off Copenhagen (Krogh and Spärck, 1936). Nematodes, foraminifers, prosobranchs, and copepods proved to be the most abundant forms; the total numbers of specimens amounted maximally to 236,000 per sq m; (4 stations, depth 5.5–54 m, bottom mud or clay).

PLANKTON

As a consequence of the intensive mixing in the Belt Sea of oceanic and Baltic water this area may harbor both stenohaline marine forms of the North Sea or even the Atlantic (*Calanus finmarchicus, Noctiluca miliaris, Beroë cucumis, Nyctiphanes couchi*, etc.) and forms typical of the inner Baltic (*Limnocalanus grimaldii, Synchata monopus*, etc.) (Remane, 1940; Jensen et al. 1937; Kändler and Wattenberg, 1940). Normally, the following marine species predominate: in the zooplankton, *Tintinnopsis fusus, Oitbona nana, Paracalanus parvus, Eurytemora hirundo, Centropages hamatus, Acartia longiremis*, and species of *Sagitta*; in the phytoplankton, species of *Chaetoceros* and *Rhizosolenia, Ceratium tripos balticum, C. fusus,* and species of *Dinophysis* and *Peridinium.*

As in the case of the benthic fauna and flora, a sudden change toward pronounced brackish-water conditions is also observed in the composition of the plankton when passing from the Belt Sea (and the Sound) into the Baltic proper. The comparatively high salinity in the depths, however, allows stenohaline marine animals, such as *Halitholus cirratus, Sagitta elegans, Oithona similis*, and *Hyperia galba*, to penetrate as far to the north as the Gotland Deep; this category is restricted by the bad oxygen conditions prevailing in the depths. With the deep-water current *Halitholus cirratus, Pleurobrachia pileus*, and *Fritillaria borealis* may even be brought into the Gulf of Finland.

The phytoplankton of the Baltic proper is dominated by species of Cyanophyceae: the lacustrine *Aphanizomenon flos aquae* (brackish-water race?), the ubiquitous *Nodularia spumigena*, and the brackish-water *Anabaena baltica*, and by diatoms: the euryhaline marine *Chaetoceros danicum*, the brackish-water *Thalassiosira baltica, Chaetoceros wighami*, etc. *Aphanizomenon, Nodularia, and Anabaena* often cause a pronounced "water-bloom" during summer and autumn.

The zooplankton of the Baltic proper is mainly composed of copepods, cladocerans, rotifers, and protozoans (tintinnids). The cladocerans and rotifers, typical freshwater groups, are especially common in the Gulfs. Another characteristic of the zooplankton of the Baltic proper is the poor representation of larval stages: only those of *Macoma, Hydrobia, Harmothoë*, and *Membranipora*, as well as the nauplii of the copepods and *Balanus*, occur regularly. The following species are typical of the open Baltic proper outside the Gulfs: marine and brackish-water tintinnids; rotifers: marine and brackish-water species of *Synchaeta* and *Keratella* (*Anuraea*); copepods: the brackish-water *Acartia bifilosa* and *Eurytemora hirundoides*, the marine *Pseudocalanus elongatus* and *Temora longicornis*; cladocerans: the marine *Evadne nordmanni* and species of *Podon*. In the Gulfs, as well as in the archipelagos of the outer Baltic proper, the following brackish-water copepods are especially important: *Eurytemora hirundoides, Acartia bifilosa*, and *Limnocalanus grimaldii.* The last-mentioned relict species occurs in great abundance, together with the

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likewise relict mysid, *Mysis relicta*, in the depths. The brackish-water cladoceran, *Bosmina maritima*, is the most common crustacean of the plankton in late summer, when it constitutes the main food of the Baltic herring. The rotifers are represented mainly by brackish-water and lacustrine species of the genera *Synchaeta* and *Keratella*, the tintinnids by *Tintinnopsis* species. In the inner parts of the Gulfs and the archipelago zone near their entrances, species of fresh-water copepod and cladoceran genera

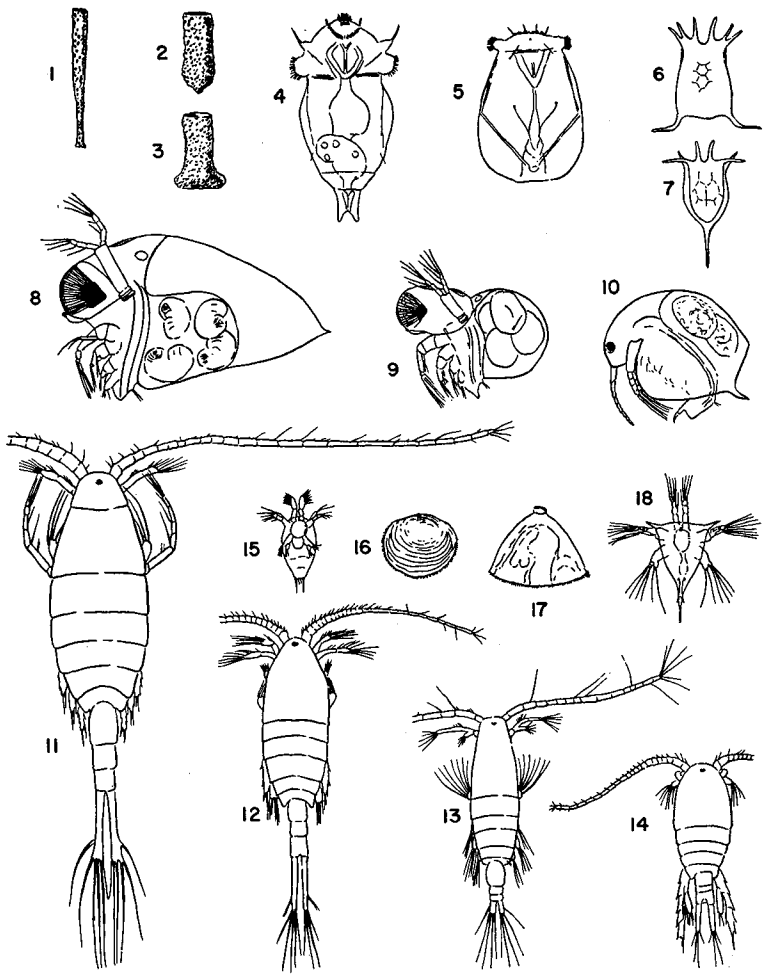

FIGURE 21.—*Zooplankton forms typical of the inner Baltic proper (m marine, br genuine brackish-water form)*

Ciliata: 1 *Leprotintinnus bottnicus* (br), 2 *Tintinnopsis tubulosa*, 3 *T. brandti* (br). *Rotatoria:* 4 *Synchaeta baltica* (br), 5 *S. monopus* (br), 6 *Keratella quadrata platei* (br), 7 *K. cochlearis recurvispina* (br). *Cladocera:* 8 *Evadne nordmanni* (m), 9 *Podon polyphemoides* (m), 10 *Bosmina maritima* (br). *Copepoda:* 11 *Limnocalanus grimaldii* (br; glacial relict), 12 *Eurytemora hirundoides* (br), 13 *Acartia bifilosa* (br), 14 *Temora longicornis* (m). *Larvae:* 15 copepod *nauplius* (*Eurytemora hirundoides*), 16 *Macoma baltica* (m), 17 *Cyphonautes* (larva of *Membranipora crustulenta* (br), 18 nauplius of cirripede (*Balanus improvisus*, m). Magnified. From Purasjoki (1948).

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(*Cyclops*, *Daphnia*, *Leptodora*) become common; on the other hand, the very euryhaline marine cladoceran, *Evadne nordmanni*, is found even at the ends of the Gulfs. An interesting lacustrine component of the Baltic zooplankton consists of larvae of the dipteran *Corethra* (*Chaoborus*) which have been found in abundance in the bay of Bråviken on the east coast of Sweden (northeast of Gotland) and also in the archipelago of the Åland Sea (depth of the localities 21–40 m, salinity recorded 5.5–6.35 ‰ (Hessle and Vallin, 1934).

In the Baltic proper the macroplankton is practically represented by *Aurelia aurita* only, the reproduction area of which extends to the outermost parts of the Gulfs, whereas drifting specimens are found considerably farther inward (Fig. 9).

As may be expected, the composition of the Baltic plankton exhibits great fluctuations in the course of the year, especially in the northern parts of the area. Characteristics of the seasons are: in spring rapid development of immense quantities of diatoms, in summer abundance of cladocerans, in winter predominance of copepods.

Investigations into the plankton production in the Baltic proper have shown that its southernmost part (the Arkona Sea) is very sterile at least in the summer (Gessner, 1933b); another area with remarkably low production is the Gulf of Bothnia (Buch, 1932). On the other hand, high values are found in the Gulf of Finland (Buch, 1932) and in locally fertilized coastal waters; the production is, on the whole, higher near the coasts of the Baltic (Rothe, 1941). These differences are due to corresponding regional differences in the supply of nutrient salts. An exception is to be noted for the zooplankton of the Bothnia Sea. There comparatively high production values are found in the depths, owing to the abundance of the big deep-water relict crustaceans, *Limnocalanus grimaldii* and *Mysis relicta*, which seem to be able to utilize food (humus) derived from neighboring land districts (Hessle and Vallin, 1934).

In July-August 1950, a striking mortality in *Eurytemora hirundoides*, the commonest and most widespread plankton copepod of the inner Baltic during the warm months of the year, was observed in a part of the Bothnian Bay (mainly off Sundsvall) (Vallin, 1951). The large quantities of dead *Eurytemora* clogged the herring nets and caused difficulties to the fishery. The phenomenon was caused by a parasitic water mould (Saprolegniaceae) which is obviously specifically related to *Eurytemora hirundoides* as host. The disease reappeared in the following summer and is expected to be a regular feature in the northern Baltic and especially intense and widespread in warm summers. As the copepod concerned is an important source of food for the Baltic herring the disease may cause a seasonal severe deterioration in the nutritional conditions for this economically important fish.

FISH

As is seen from Table 2, the fish fauna of the Baltic includes no selachians. The table also shows that the number of marine species in the Kattegat, 75, drops to 22 in the Gulf of Finland. Most of these fish are indigenous in boreal-arctic waters; one, the sculpin *Cottus quadricornis*, is a glacial relict. The Baltic race of herring (*Clupea harengus membras*), caught all over the region, is of outstanding economic importance, as are the sprat (*Clupea sprattus*) and the cod (*Gadus morrhua*), whose northernmost breeding area is in the depth of the Bothnian Sea; as mentioned previously, the Baltic stock of cod has increased greatly since the recent rise in salinity was observed in the area. Other economically significant species are the flat fishes, *Pleuronectes*

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platessa and *P. limanda*, which are, however, confined to the southern Baltic. *Pleuronectes flesus*, regarded as a brackish-water species, is also caught in considerable numbers as far as the entrances to the Gulfs.

As may be expected in a pronouncedly brackish-water area, lacustrine fish also play a great role in the Baltic. About 20 such species are regularly present off the southern coast of Finland. Those of especially great economic importance are: in the Gulf of Bothnia, the whitefish species, *Coregonus lavaretus* and *C. albula*; in both Gulfs, as well as in more diluted coastal areas elsewhere, down to southern Sweden, the common pike (*Esox lucius*), the perch (*Perca fluviatilis*), and the brame (*Abramis brama*).

Anadromous fishes, particularly the Atlantic salmon (*Salmo salar*) and the European eel (*Anguilla vulgaris*), also add much to the catch of the Baltic fishermen.

The peculiar composition of the fauna of the inner Baltic proper is, of course, reflected also in the food of the fishes. Among nonpelagic animals utilized there are especially to be mentioned: in the bottom fauna *Macoma*, *Mytilus* (epifauna), *Pontoporeia*, *Corophium*, *Mesidotea*, and larvae of chronomids; in the *Fucus* fauna, *Gammarus*, *Idotea*, *Mysis*, *Lymnaea*, and larvae of trichopterans.

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Chapter 25

Black Sea and Sea of Azov

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INTRODUCTION

A biological study of the Black Sea and of the Sea of Azov presents considerable difficulties to western scientists, because a large number of the newer Soviet journals are not available, either in Western Europe or in America, and reprints of papers are not obtainable. An attempt has nevertheless been made to prepare as detailed a report as possible for inclusion in the present work. Purely faunistic lists have had to be subordinated to a general ecological account and to a historical review, and the biological peculiarities associated with the hydrographic cycles require special emphasis.

For several years the writer had the opportunity to make faunistic and ecological studies on the Black Sea, especially on the Bulgarian coast, which had previously been studied very little. He also visited the Rumanian coast, including the Danube delta, the Russian area at Odessa, the Crimean coast, the Caucasian coast, and a part of the Sea of Azov. There are scarcely any observations available for the Anatolian coast, so that a general biological account of the Black Sea must depend on inference for this section.

A valuable base for the present review has been Zenkevich's *Fauna and Biological Productivity of the Seas, Vol. II, The Seas of the USSR* (1947). Some of the references, unavailable to the author in the original, are taken from this work.

I. PHYSICAL GEOGRAPHY OF THE BLACK SEA

The Black Sea and the Sea of Azov form an almost isolated body of water, extending far into the greatest continental area of the world between Europe and Asia. There is only a narrow connection with the Mediterranean Sea via the Bosporus (and the Dardanelles), and this is about 3000 km from Gibraltar, the nearest point on the Atlantic.

The Black Sea extends between Latitudes 46°32′ and 40°55′ North, and Longitudes 27°27′ to 41°42′ East. Its greatest length is 1149 km, the breadth 610 km. The surface area is 413,488 sq km, and the volume is 529,954 cubic km. The greatest depth is 2243 m, the average depth 1197 m.

The Black Sea is a relatively uniform deep marine basin, with long coasts. There are almost no islands. In the north, the Crimean peninsula extends far into the basin, and the peninsulas of Kerch and Taman, extending westward and eastward, separate the Sea of Azov, which is connected with the Black Sea only by the narrow Strait of Kerch.

The Black Sea lies north of the belt of mountain chains that extends across Southern Europe and in the north overlaps the flat plains of Eastern Europe. The Balkan mountain range that extends as far as Cape Kaliakra, where it is truncated by the Black Sea, may be followed through the Crimea as the Jaila chain and then farther

† Karl P. Schmidt, one of the great American Naturalists, died on September 26, 1957, of complications following the bite of an African snake, the boomslang (*Dispholidus typus* Smith).

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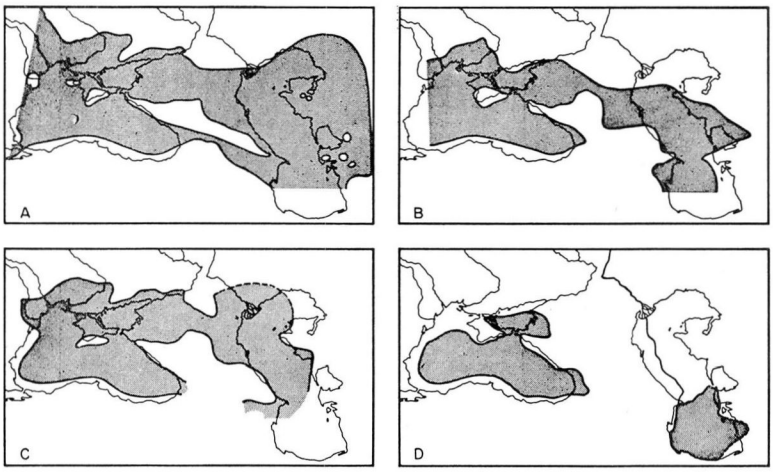

FIGURE 1.—*Stages in the geological history of the Black Sea region*

A, the Sarmatic Basin; *B*, the Meotic Basin; *C*, the Pontic Basin; *D*, the basin of the Cimmerian epoch. From Zenkevich (1947, after various sources)

along the northern part of the Caucasus. High mountains normally form the coast line of Bulgaria south of Varna, of Turkey, and the Caucasus in general, and along the south of Crimea. The slopes are 4°–6°, in places 12°–14°. These abrupt slopes in many places continue beneath the sea to depths beyond 1000 m. North of these mountain belts the coasts are low, mostly with low clay cliffs, and in some stretches there is a flat sandy coast with sand dunes. The sea bottom along the Rumanian and Ukrainian coasts is correspondingly shallow, as shown by the 200-m isobath in Figure 15. Flooded older river mouths ("Limans"), which have narrow extensions far inland (Sokolov, 1895), are characteristic of this part of the coast

In the areas of the sea north of the mountain belts, there is considerable freezing over in severe winters, especially in the shallower parts. The south coast of the Crimea, the Caucasian zone, and the Anatolian coast, are always ice free.

GEOLOGICAL AND FAUNISTIC HISTORY[1]

In the whole Black Sea-Caspian Sea region, as Andrusov (1918) has emphasized, one may discern an increasing degree of isolation from the open ocean since late Tertiary time. This is correlated with a general freshening of the surface zone, though this is subject to oscillations.

During the Early and Middle Miocene the basin was filled by a great salt sea, a part of the vanishing Tethys, and the fauna was typically Mediterranean. Connection with the ocean probably was lost at the end of the Middle Miocene, and a progressive freshening began. This process affected different parts of the area variably, since the Mid-Miocene sea was separated into distinct basins, whose faunas changed greatly according to the degree of freshening of their waters By the Late Miocene

[1] This account is based on Andrusov and Arkhangel'sky for the older periods. The most comprehensive account is that of Arkhangel'sky and Strakhov (1938). Pfannenstiel (1944; 1949; 1950) gives excellent accounts of the Quaternary development.

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the Sarmatian Basin had been formed (Fig. 1A), and the halobiotic element of the Mediterranean disappeared from it. This included the echinoderms and such mollusks as *Arca*, *Pectunculus*, *Leda*, *Pecten*, *Venus*, *Corbula*, *Conus*, *Natica*, and *Turritella*. A few forms persisted for some time, including *Pleurotoma*, *Murex*, *Lucina*, and *Loripes* (Zenkevich, 1947). The only mollusks that survived were the bivalves *Modiola*, *Tapes*, *Mactra*, *Syndosmya*, *Donax*, *Ervilia*, and small species of *Cardium*, and the gastropods *Cerithium*, *Trochus*, *Buccinum*, and *Nassa*. Bogachev (1933) has described the changes in the vertebrate fauna. There was a typical Sarmatian fish fauna; it included mullets, cods, and herrings, together with dolphins, whales (*Cetotherium*), and seals. The surface water of the Sarmatian Basin finally became extensively freshened. Denser salt water stagnated at greater depths, in which hydrogen sulfide accumulated. The result was the near disappearance of the whole Sarmatian fauna.

The progressive restriction of the connection between the western and eastern parts of the sea continued until the formation of the so-called Meotic Basin in the Miocene (Fig. 1B). At this period connection with the ocean was re-established, and the salinity of the water increased, at least in the western area. A whole series of Mediterranean species re-entered the area, including *Ostrea*, *Venerupis*, *Lucina*, *Dosinia*, *Cerithium*, and *Arca*. At the end of this period the oceanic connection narrowed; Mediterranean species declined, and brackish-water mollusks like *Congeria*, *Neritina*, *Hydrobia*, and *Micromelania* appeared (Andrusov, 1929). In the eastern basin, which at this stage had only a narrow connection with the western, the deep water continued to stagnate and to accumulate hydrogen sulfide (Arkhangel'sky, 1927).

At the beginning of the Pliocene, the next phase of development was the appearance of the Pontic Sea (Fig. 1C), which was completely isolated from the ocean. The result was a complete faunal change, although there were certain features that recall the Meotic stage. It was characterized by *Dreissena*, forms related to *Cardium* (*Limnocardium*, with *Didacnia*, *Monodacna*, and *Posodacna*); with these there were a few gastropods of the families Melanopsidae, Paludinidae, and Limnaeidae (Gerasimov and Markov, 1939a). Andrusov (1929) believes that this fauna originated in the western part of the basin and spread eastward. At the end of the Pontic Stage—*i.e.*, the Cimmerian Epoch—an elevation of the land broke the connection between the western and eastern basins (Arkhangel'sky and Strakhov, 1938; Baturin, 1931), and the independent Caspian Basin began its own faunal evolution (Fig. 1D). Later there was a renewed short-term connection of the two basins during which the Caspian area received a new influx of Black Sea elements; but this occurrence had no appreciable counter influence on the fauna of the Black Sea.

The basin of the Black Sea was brought essentially to its modern extent by the end of the Tertiary. During the Quaternary the salinity of the waters was determined by the alternate opening and closing of the connection with the Mediterranean. The low salinity at the beginning of the period was reduced still further, and at one stage the water was fresh. A new connection then led to a weak influx of salt water, then, as the seas were separated again, freshening was resumed. This did not go so far as in the earlier stage, and at the end of the glacial period the salt water again entered the brackish-water sea via a new Mediterranean connection. In general, the periods

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TABLE 1.—*Correlation of the stages of development of the Black Sea with the glacial epochs*
From Arkhangel'sky and Strakhov (1932); North American equivalents in parentheses

Modern Black Sea	Brackish, av. 18‰	Recent
Older Black Sea Basin	Weak increase of salinity	Post-glacial ("Climatic Optimum")
Newer Euxenian Sea	Brackish	Würm (Wisconsin) glaciation
	(Mediterranean closed at end of the stage)	
Karangat Sea	Increased salinity	Riss-Würm (Sangamon) interglacial stage
Post-Uzunlar Basin	Brackish to fresh	Riss (Illinoian) glaciation
	(Mediterranean connection)	
Uzunlar Basin	Brackish to saline	Mindel-Riss (Yarmouth) interglacial stage
Older Euxinian Sea	Brackish to fresh	Mindel (Kansan) glaciation
Chaudinian Sea	Brackish to fresh	Gunz (Nebraskan) glaciation

of glacial advance corresponded to periods of freshening, and the interglacial periods with incursions of salt water. These are related to eustatic changes of sea level, transmitted via the Mediterranean (Arkhangel'sky and Strakhov, 1938; Pfannenstiel, 1944; 1949; 1950). Table 1 shows the correlation with the glacial and interglacial stages.[2]

At the turn of the Tertiary-Quaternary came the Chauda stage. The Chauda beds (Andrusov, 1890) contain the remains of a fauna with a typical Caspian aspect. Index forms are *Didacna baeri crassa* and *D. tschaudae*. Andrussov and others regard these beds as uppermost Upper Pliocene. It is not yet determined what, if any, stages of the older Quaternary were involved. No sediments are preserved from the immediately post-Chauda epoch. According to Arkhangel'sky they were removed by erosion during the periods of emergence of the borders of the basins.

The sediments of the succeeding Old Euxinian phase are characterized by Paludinidae and a large number of bivalves. The index fossils are especially *Didacna pseudocaspia*, *D. pontocaspia* (= *D. crassa*), *Didacna crassa*, *Adacna plicata*, and *Monodacna pseudocardium*. All these deposits represent a brackish sea, which connected across the Manych plain with the Caspian, and via the Uzboy Valley with the broad basin of the Aral-Sarykamic depression (Fig. 2). In the west it reached beyond the present delta of the Danube.

Following the Old Euxinian stage of the Pontic basin there was a considerable influx of salt water in the Uzunlar stage. A terrace about 35 m above the present level, which may be followed for great distances, was formed by the climatically controlled eustatic rise of sea level. This is the Tyrrhenian terrace of the Mediterranean and Surry or Wicomico terrace of North America. The species adapted only to weakly brackish water or to fresh water died, while the true brackish-water forms like *Dreissena* and *Didacna* were mixed with the incoming Mediterranean species. Characteristic of this "Uzunlar stage" of the Black Sea are the Mediterranean forms *Cardium edule*, *Syndosmya ovata*, and *Mytilogaster monterosatoi*.

The high level of the Black Sea in the Uzunlar stage was followed by a considerable regression. The post-Uzunlar sea again became an inland basin with a brackish and fresh-water fauna. The surface was 15 m below present sea level, and the shore line lay well out on the continental shelf. This fall of water level was essentially a eustatic regression conditioned by the Riss glaciation period, though there were also epeirogenic movements on some stretches of coast.

[2] Compare also the time scale for the developmental stages of the Black Sea and Mediterranean given by Pfannenstiel (1944, p. 423), in which the ideas of Andrusov (1929), Arkhangel'sky and Strakhov (1932; 1938), Grahmann (1937), and Blanc (1937a; 1937b) are combined with those of Pfannenstiel.

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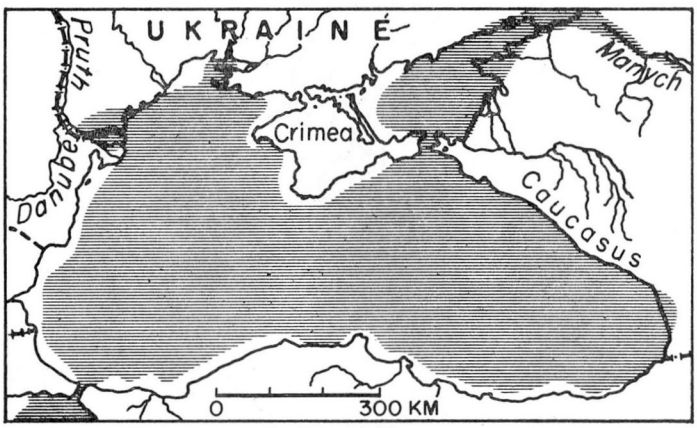

FIGURE 2.—*Extent of the Black Sea during older Euxenian times (Mindel glaciation to Riss glaciation)* After Arkhangel'sky and Strakhov, from Pfannenstiel (1950)

The following interglacial period, between the Riss and the Würm glacial advances, was marked by a considerable increase in the amount of water by the melting of the glacial mass. The sea level rose to 12 to 15 above the present, as demonstrated by numerous terraces today along Mediterranean and Black Sea coasts. The Russians termed this period the Karangat stage. For the Mediteranean it corresponds to the "Tyrrhenian II" or Main Monasterian *s. s.* (Blanc, 1942), and in North America to the Talbot (Sangamon) terrace. Reflecting the warmer climate, southern animals were represented. The *Strombus bubonius* fauna ranged into the Black Sea, where its remains may be found in the terraces that extend from the Dardanelles via the Sea of Marmara to the west coast of the Black Sea and the Crimea. Examples of localities on the Black Sea coast are Varna and the Serpent Islands off the mouth of the Danube.

Pfannenstiel cites the following as Karangat mollusks: *Gibbula albida, Calyptraea chinensis, Cerithium reticulatum, Natica* sp., *Retusa truncatula, Aporrhais pes pelicani, Ostrea taurica, Pecten varius, P. glaber, Nucula nucleus, Tellina nitida, Scrobicularia plana, Thracia papyracea, Mactra corallina, Venus verrucosa, Ensis ensis, Strombus bubonius, Tapes calverti, Cardium tuberculatum*, and *C. edule. Echinocyamus pusillus* also lived in the Black Sea at that period. *Strombus bubonius* is a form of the subtropical Atlantic, now extinct in the Mediterranean as well as in the Black Sea. It is found living today on the coasts of the Canary Islands and Senegal.

As was shown by Salomon-Calvi (1940) the Sea of Marmara flowed through a narrow water gap in the coastal mountain chain into the Manyas-Apolyont depression, extending from Iznik and probably from Bursa in Asia Minor. There was at that time no Bosporus at Istanbul. Pfannenstiel has shown convincingly that the connection between the Sea of Marmara and the Black Sea extended in a prolongation of the graben-faulted gulf from Izmid to Adapazar via the Sapanca Sea and the narrows of the Sakaria River to Incioli, before reaching the Black Sea. This connection is named the "Sakaria-Bosporus" by Pfannenstiel. This explains the modern relict fish fauna of Mediterranean and Black Sea forms in the Lakes Manyas, Apolyont, Iznik, and Sapanta (see Section VIII).

During the high-water level of this period the Black Sea spread out via the lowlands of Rostov on the Don and the Manych depression to the Caspian basin. As a result, bivalves from the Black Sea could enter the less saline parts of the Caspian (*e.g., Cardium edule*), where they persist to the present time as interglacial immigrants. The whole volume of the Danube poured through the now broad and dry valley of the Karasu during this interglacial period (Pfannenstiel, 1950). The modern Danube-delta had not yet been formed; that area was merely an estuary for streams entering from the Carpathian Mountains and Bessarabia.

The succeeding Würm (Wisconsin) glaciation lowered the water level to 80–100 m below the present level, and a broad coastal plain was laid bare. This was the post-Tyrrhenian regression (Würm

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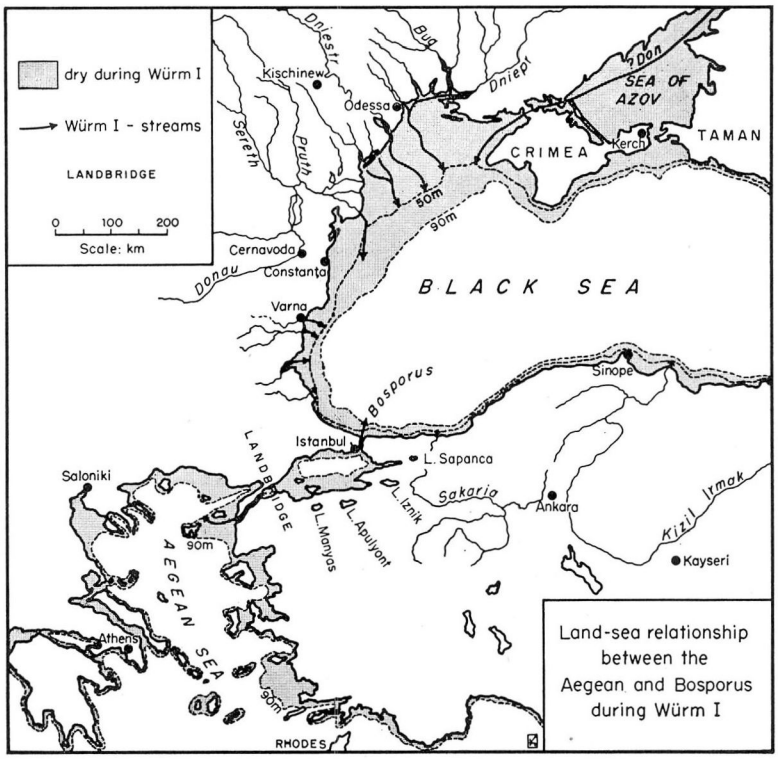

FIGURE 3.—*Black and Aegean seas during the Newer Euxinian phase*
From Pfannenstiel (1951)

I; *i.e.*, the Newer Euxinian Phase of Russian authors); it can be traced everywhere in the Mediterranean region. This eustatic lowering of sea level cut off the Sea of Marmara, from both Black Sea and Mediterranean. The European continent had a broad connection with Asia Minor.

Arkhangel'sky did not consider the influence of eustatic changes of sea level of the Mediterranean upon the Black Sea. He explained the changing history of high and low levels and of increasing and decreasing salinities as the result of a tectonic rise or lowering of the borders of the Black Sea, and especially of the Dardanelles and Bosporus area. Pfannenstiel (1944) agrees with him as to the Tertiary history, but does not think that orogenic movements of the Pontic coasts are sufficient to explain the Quaternary phenomena. (*See* also Grahmann, 1937.)

During the Newer Euxenian phase the Bosporus represented a meandering valley. The water came from the valley of the Golden Horn and discharged into the Black Sea, which gradually freshened. A land bridge connected the Rumanian region with the Crimea (Fig. 3). The Sea of Azov was not yet in existence. The mouth of the Danube became a deep erosional valley. Likewise, because of the eustatic lowering of sea level, all the river valleys that enter the Black Sea became extended across the continental shelf (Nastase, 1935). The estuaries ("Limans") of the present day occupy the deeply eroded valleys of that period.

Arkhangel'sky and Strakhov (1938) describe the shallow borders of the New Euxinic fresh-water basin as being occupied by swampy and lacustrine formations. There are *Monodacna* clays and sands, with *Dreissena polymorpha*, *D. rostriformis* var. *distincta*, *D. pontocaspica*, *Monodacna pontica*, *Adacna plicata*, *Monodacna colorata*, *Hydrobia* sp., *Caspia* sp., and *Neritina sp.* (Fig. 4). According to Arkhangel'sky these were dredged from the shallow northwest area of the Black Sea. Andrusov (1893) found great masses of subfossil shells at depths of 400–800 m. They consisted of *Dreissena poly-*

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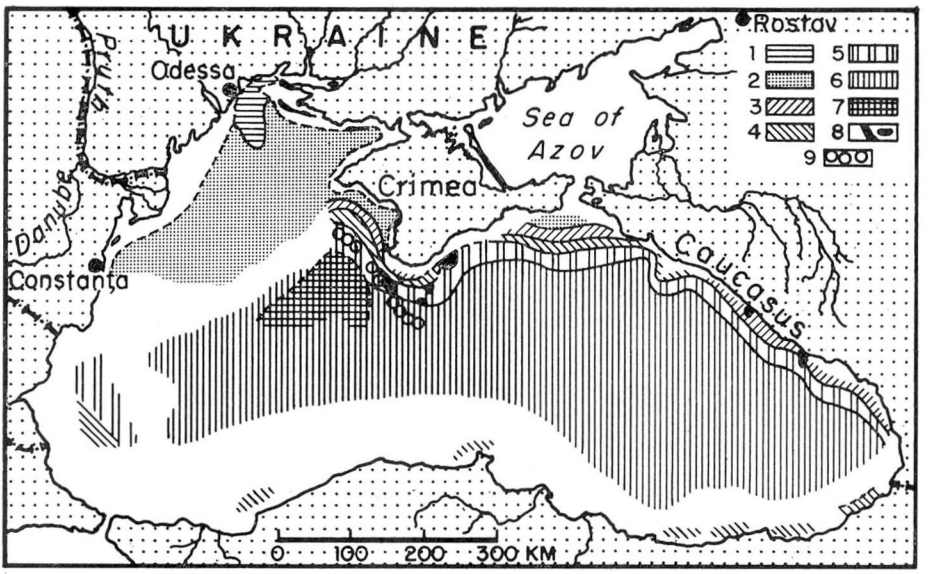

FIGURE 4.—*Distribution of sediments in the Black Sea during Newer Euxinian times*

1, *Monodacna* clay; 2, sand of the *Dreissena polymorpha* biocoenosis; 3, clay of *D. pontocaspia* biocoenosis; 4, *D. rostriformis* v. *distincta* clay; 5, gastropod clay; 6, fauna-free deep-water clay; 7, thin-layered diatom-calcareous ooze; 8, boulder zone; 9, southern border of boulder zone. From Pfannenstiel (1950)

morpha, *D. rostriformis*, and *Micromelania*. Thus there must have been either considerable tectonic downwarping or submarine landslides since the deposition of the New Euxinic sediments (Arkhangel'sky, 1930).

In contrast with modern conditions, the supply of water to the Black Sea must have been less than its loss:

> The Bosporus became a river valley debouching into the Black Sea. The amount of water evaporated was not replaced during Würm I. The sea level inevitably became lowered. It is probable, even certain, that the tributary streams brought less water, for the greater part of the precipitation remained as snow and ice. The Ukrainian streams brought a reduced amount, since the precipitation was reduced in the vicinity of the inland ice mass, as is to be seen in recent lakes in Greenland and Antarctica. Evaporation must have exceeded the lowered precipitation and reduced supply, so that in New Euxinian times the unstable water economy of the Black Sea became negative and the shelf was laid dry. (Pfannenstiel, 1951, p. 45)

As stated above, the submarine river beds of the Würm period can be traced out onto the continental shelf of the Black Sea.

After the Würm I ("Iowan" in North America) glaciation, there was again a rise of water level, interrupted by temporary regressions in Würm II ("Peorian") and Würm III ("Mankato"). There were warm interstadial periods between each of these readvances. The situation shown on the modern map was gradually reached with the Flandrian (or ?Post-Glacial Transgression).

By the beginning of Würm II the waters had transgressed the Constantinople-Skutari submarine ridge. The first salt-water forms entered the Black Sea via the Bosporus as a marine strait—*e.g.*, *Cardium edule*, *Mytilaster monterosatoi*, and *Syndosmya ovata*. In the shallow coastal waters of the Black Sea a narrow transition zone was formed with a mixed fauna composed of the Mediterranean immigrants and the benthic brackish-water mollusks of the New Euxinic stage. The latter gradually died out, or in some small degree found refuge in the estuaries of rivers (Pfannenstiel, 1944). The level of the Bosporus at the end of Würm II/III interstadial was still 11 m lower than today.

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With increasing salinity the fauna of the basin underwent a progressive transformation, corresponding to the increased inflow of Mediterranean water following the eustatic rise of the waters from −19 to −5 m below present level. At this stage, *Modiola phasiolina* entered the basin. The change affected only the upper levels of the Black Sea; the great depths with their poisonous H_2S concentrations were not affected.

At the time of the postglacial "Climatic Optimum", the sea rose in the Black Sea, as in the oceans in general, to a stage above that of the present day, forming the +5-m terrace (the *Tapes* terrace of Nansen), which extends to the Caucasus.

The submarine bank which still exists today between Constantinople and Scutari likewise determines the boundary between pure ocean water and the brackish-fluviatile waters of the Black Sea, although the inflow from the Sea of Marmara has been continually eroding the barrier from the beginning, lowering and widening it. Makarov (1885) pointed out that a rise of the floor of the Black Sea of only a few centimeters would interrupt the inflow of salt water at the bottom (Merz, 1918; 1921; Merz and Möller, 1928; compare, however, the divergent view of Ullyott and Ilgaz, below). Raising of the bank a few centimeters would produce the same result, and slight variations of level of the Mediterranean would have a similar effect. It is therefore to be expected that further considerable changes in the hydrography and thus in the biology of the Black Sea will take place within a geologically short time.

II. HYDROGRAPHY OF THE BLACK SEA

The first general insight into the oceanographic structure of the Black Sea resulted from the expeditions of Spindler and Wrangel in 1890–1891. They discovered that considerable amounts of free hydrogen sulfide occur from about 180 m downward; thus all the deeper parts of the sea are uninhabitable for higher forms of life, and in fact are without any life except anaerobic bacteria. The life of the Black Sea is accordingly limited to a shallow zone at the surface. The benthos occupies a correspondingly narrow upper zone on the steep coasts, while a broader development in shallower waters occurs only in the northwestern area and in the Sea of Azov.

It is only since 1923 that additional Russian investigations, especially by the Black Sea and Sea of Azov Fisheries Expedition, have further clarified these interesting relations. A series of reports by Knipovich (1932; 1933), presents this material. The uppermost water layers, above 250–300 m, were investigated (the greatest depth to which observations were made was 600 m). Knipovich drew a schematic picture of the surface circulation, and this has been confirmed as to its general features by a study of the dynamics involved on the basis of the available data (Neumann, 1942). The main cyclonal stream along the coasts encloses the two separate eddies of the eastern and western basins. A few depth measurements from the transects made by the Russian Hydrographic Office and the Biological Station at Sevastopol have been recorded by Skvortsov (1929), Shokal'sky (1934), and Shokal'sky and Nikitin (1927); *see* also Neumann (1943a). In general the available data are still quite inadequate, so that many hydrographic relations, especially those of the circulation at greater depths, remain unknown or unsolved.

VERTICAL STRUCTURE OF THE WATER MASS[3]

By way of introduction, an illustration of three profiles in the eastern Black Sea showing the vertical distribution of temperature, salinity, density, oxygen, and hydrogen sulfide is given (Fig. 5). These are July stations: Station PM 298 lies in the

[3] This account follows that of Neumann (1943a), supplemented by a series of more recent Soviet investigations.

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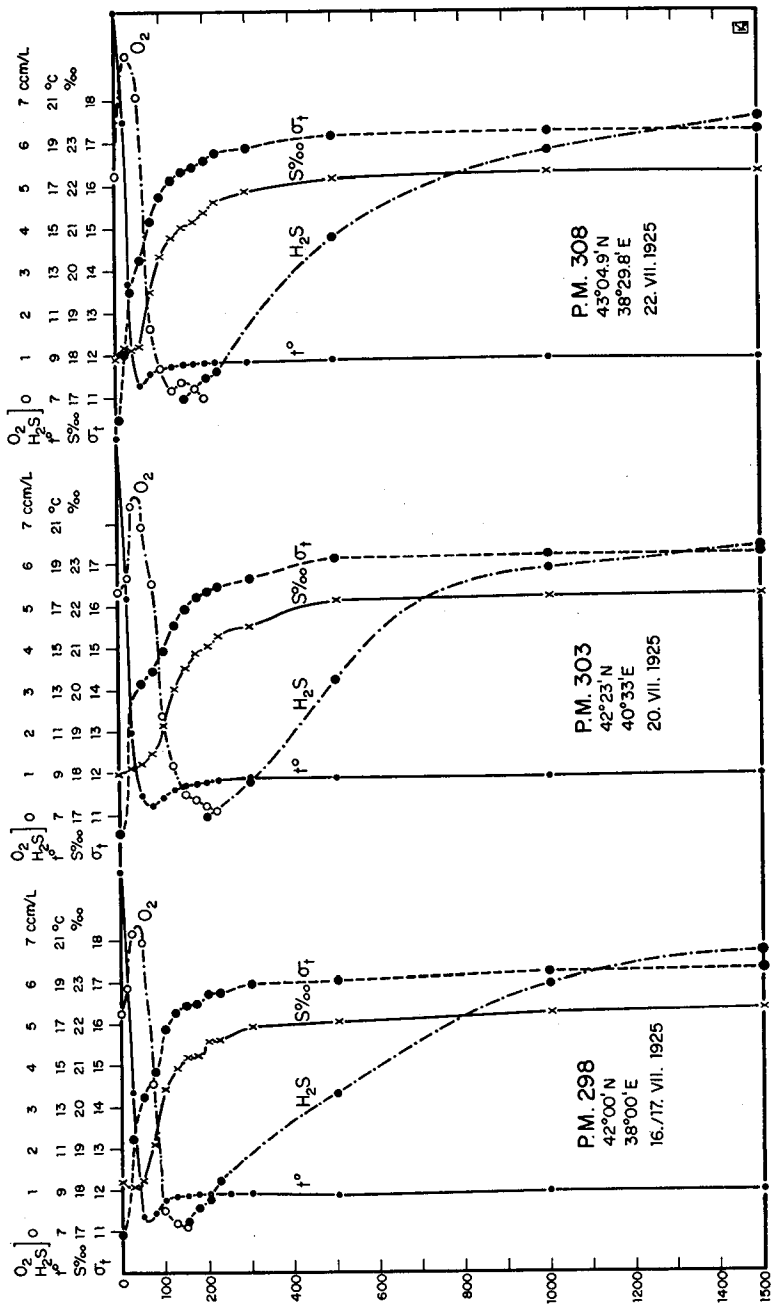

FIGURE 5.—*Vertical distribution of temperature, salinity, density, oxygen, and hydrogen sulfide at three July stations in the eastern part of the Black Sea*
From Neumann (1943a)

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southern part, and 308 in the northern part of the central eastern deep basin; Station 303 lies southwest of Suchum in the region of strong current on the Caucasian coast.

In vertical section the water mass is divided into layers, the "Troposphere" and the "Stratosphere" of Defant. The troposphere extends downward from the surface to about 200 m and is characterized by rapid increase in density from top to bottom; the stratosphere, below the troposphere, is about 10 times the mass of the troposphere and varies only slightly in density. The transition between the two great zones coincides fairly well with the upper limit of hydrogen sulfide. This boundary layer is not constant but is strongly dependent on dynamic relations.

The troposphere is more strongly stratified. At depths of 50 to 70 m the summer temperature minimum is 6.5°–7.5°C., which varies regionally as to depth. The surface zone above this temperature minimum has a quite constant salinity, which increases slowly, but only locally with depth. In correlation with the good mixing of the waters (which produces the uniformity in salinity) the oxygen supply is good. At 20–30 m there is an especially strong oxygen concentration, which results from the metabolism of phytoplankton.

Knipovich (1930) has given special consideration to the distribution of oxygen in the upper zone and its relation to the vertical circulation. Neumann (1943a) points out that the lower limit of the vertical circulation, which coincides with the temperature minimum and with an oxygen content of about 5 cm^3/liter, is more correctly only the lower limit of the thermal vertical circulation.

The stratification of the troposphere depends mainly on the existence of a separation between the upper zone, subject to vertical circulation, and a lower zone with less circulation. The latter zone passes gradually into the stratosphere. The oxygen supply for the lower troposphere is also provided by vertical exchange of currents whose importance and extent is not yet understood. In addition to the dynamic processes, physical, chemical, and biotic factors come into play.

In the stratosphere the boundary between the oxygenated upper layer and the the lower one containing hydrogen sulfide separates wholly dissimilar water masses. The lower limit of the troposphere reaches a temperature of about 8.7° and is thus essentially identical with the rather constant 8.8° of the stratosphere (Table 2). In general, the stratosphere is homothermal, with only a very slight increase of temperature between 300 m and the bottom. Neumann (1943b) assembles the average data for the depths of 100 to 2000 m for a square degree (Table 3).

As Neumann emphasizes, there is no adiabatic temperature increase down to the bottom as was supposed by Skokalsky. The temperature *in situ* increases regularly only to 1500 m and is then constant to 2000 m. Potentially, the water becomes some-

TABLE 2.—*Average distribution of temperature in the Black Sea*

(After Chigirin, 1927)

Depth, m	0	100	200	300	500	1000	2000
Ave. T, *in situ*	13.80	7.95	8.69	8.80	8.83	8.93	9.00°C
Ave. Potential T.		7.94	8.67	8.76	8.77	8.81	8.75°C

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TABLE 3.—*Average temperature from 100 to 2000 m depth for the square degree 43°N.–33°E.* After Neumann (1943b)

	July–August	All months						
Depth, m.	100	150	200	300	500	1000	1500	2000
Temperature *in situ*	8.42	8.64	8.73	8.83	8.86	8.92	8.98	8.98
Potential temperature	8.42	8.63	8.71	8.80	8.81	8.82	8.83	8.77
Number of observations	15	31	33	29	17	14	13	13

what colder again at about 1000 m, as has been confirmed by observation in various parts of the sea. Thus there is an approximation to an adiabatic temperature distribution only in an intermediate layer at about 1000-m depth. Chemobiological processes may have a role in this distribution of temperatures.

The hydrogen-sulfide content increases toward the bottom to about 6.2 cm^3/l.

The position of the interface between troposphere and stratosphere requires somewhat more detailed discussion. It is dependent on the dynamics of the upper water layers. The interface lies at about the upper limit of the hydrogen sulfide region, the 0.5 cm^3/l layer of H_2S lying about 50 m. below. In general it may be defined as the layer with the greatest density gradient (Fig. 5).[4]

As Knipovich had supposed, this interface is not horizontal. It is domed upward in the central parts of the eastern and western basins. The topography of the upper limit of the H_2S layer (with 0.5 cm^3/l) is shown in Figure 6. In the central parts of the sea the H_2S zone rises to 175 or 150 m, and even higher at certain places, whereas along the coast it is depressed to 250 m and more. In the whole area, to be sure, there are some irregularities. The separation of the eastern and western doming is distinctly developed south-southwest of the Crimea (between 33° and 34°E.) Opposite the shelf of the shallow northwestern bay (southeast of Constanza) it is notably high. In general the vertical position of this boundary layer is closely correlated with the system of surface currents. As Neumann (1942; 1943a) determined by evaluation of the Russian measurements, the maximum density gradient at the boundary between the troposphere and stratosphere is usually more sharply defined in the central parts of the sea, which are the areas of weakest currents, than in vicinity of the coast, where the transition is more gradual. The depth of the layer of maximum density gradient (Fig. 7) also shows the close relation between the dynamic structure of the troposphere and the stratification of the water. It lies closer to the surface in the central parts of the cyclonic circular currents than at the coasts, the effect being correlated with the strength and breadth of these circular currents.

Within the troposphere another important interface is formed between the upper surface layer, in which there are strong vertical movements of water, and a lower "subtroposphere." This lower limit of thermal vertical convection is formed in the fall and winter when the surface water becomes heavier and sinks to the depth at which it reaches water of its own density. This upper layer is almost homothermal from February to March, and its temperature is lower than that of the subtroposphere. During the summer the warming up of the surface is transmitted gradually to the lower layers by turbulence. Heat transport to the depths by turbulence is slowed down by the increasing density of the water, so that a strong thermocline develops above the boundary of thermal vertical convection. In the thermocline the temperature drops rapidly to the winter temperature of the surface, which is preserved through the summer in the subtroposphere at 6.0°–7.5°C. In the central parts of the sea the upper limit of this layer lies at a level of about 50 m, and along the coasts at 70 to 80 m (only rarely deeper). In general the doming of the limiting layers is also evident in this respect, although at a lower angle.

This analysis of the interfaces concerns the upper zone. In the stratosphere there are no such

[4] Neumann (1943a; 1943b) introduces the term tropopause for this interface, continuing the analogy of the marine zones with those of the atmosphere.

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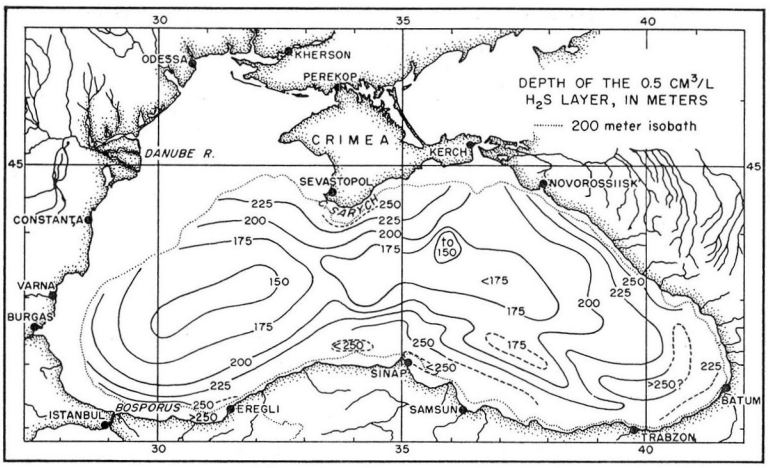

FIGURE 6.—*Depth of the 0.5 cm³/l H_2S layer*
From Neumann, (1943a)

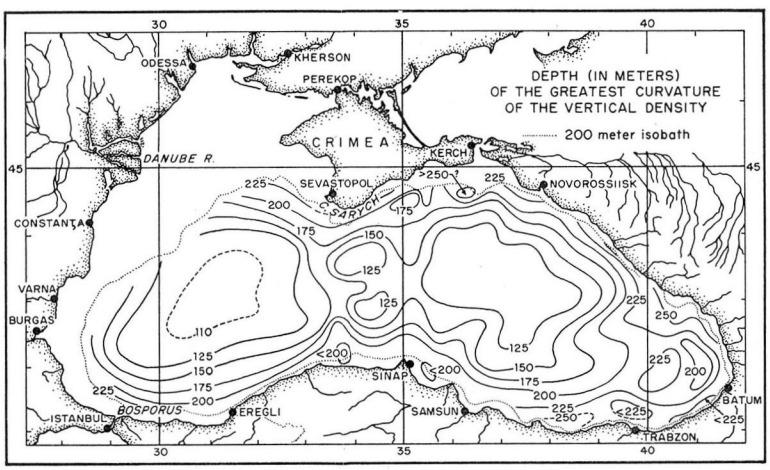

FIGURE 7.—*Depth of the maximum density gradient*
From Neumann (1943a)

limiting surfaces. The stratification of the lower zone may be understood by evaluating the salinity determinations, using Neumann's (1943a) analysis for this purpose. In the lower layers of the stratosphere there is a slight increase in salinity (Table 4).

As may be seen, the salinity at first increases rapidly with depth, then more slowly.

Figure 8A shows the distribution of salinity at the surface for July, August, and September. The freshening by the rivers at the northwest is evident, and this is also observed at certain places on the Anatolian coast. In correlation with the doming of the interfaces in the central parts of the sea, there is an accumulation of water rich in salt in the central parts of the eddies, but this picture is modified by local effects, such as river mouths, evaporation, and precipitation. A relation between the distribution of the isohalines and the surface currents is also only partly discernible.

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TABLE 4.—*Vertical salinity distribution from 100 m to 2000 m for the square degree 43°N.–33°E.*
Average values; after Neumann (1943a)

Depth, m	100	150	200	300	500	1000	1500	2000
Salinity, ‰	20.36	20.98	21.35	21.73	22.09	22.31	22.31	22.34
Number of observations	30	27	31	24	15	11	13	10

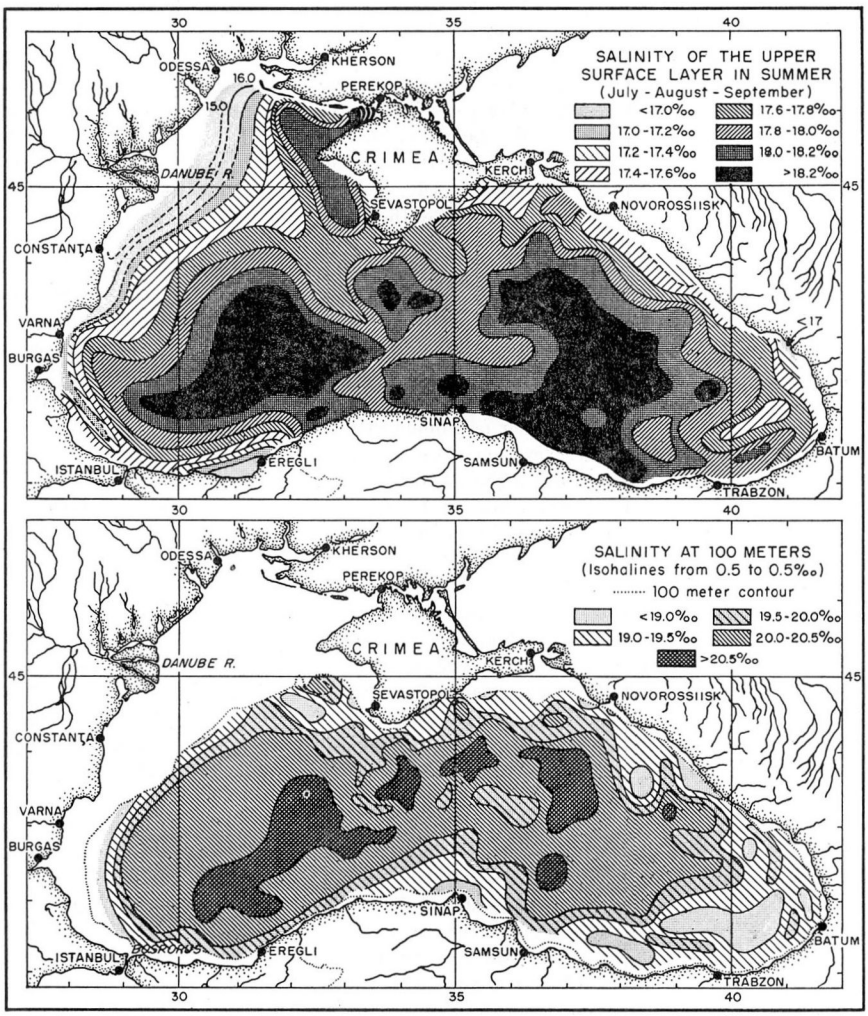

FIGURE 8.—*Salinity distribution in the Black Sea*
A, at the surface; *B*, at 100 meters. From Neumann (1943a)

The relation between isohalines and currents is clearer at 100 m, (Fig. 8B), where external influences have almost lost their effect. The accumulation of saltier water at the centers of the cyclonal eddies is distinct, and the salinity rises to more than 20.5‰, whereas at the coasts it is less than 20‰. At 500 m this distribution is still

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evident, and the difference between the salinity of the water and that of the coastal areas amounts to 0.2–0.3‰. At 1000 m the picture is no longer the same, and at 1500 m the gradient seems even to be reversed; the water at the coasts is in general saltier than in the central parts of the sea. (*See* map and tables in Neumann, 1943a.)

Neumann (1943a) has calculated, according to Defant's method, the dynamic reference surface, which is the water layer in which the horizontal pressure gradients disappear, hence the layer of no motion. This layer lies at a depth of 125–150 m in the central parts of the sea and at 300 m and more along the coasts. Thus; the topography of this reference surface resembles the interface between troposphere and stratosphere. The conspicuously reduced lowering off the shelf in the northwestern embayment is discernible, as is the separation between the western and eastern doming. (*See* maps in Neumann.) There is agreement also in other details, but the gradients are more pronounced.

The 0.5 cm^3/l H_2S layer lies about 50 m below the lower limit of plankton and the layer of maximum density gradient. If we take into account the layer in which there are still traces of H_2S all three boundaries become nearly congruent—namely, the lower limit of plankton, the layer of maximum density gradient, and the approaching limit of the H_2S region. In the eastern part of the section the lower limit of plankton is nearer the surface in the vicinity of the coast.

Neumann accordingly comes to the conclusion that in the Black Sea, as elsewhere, the layers of constant dynamic depth difference of adjacent pairs of stations unite into a closed system. From this is derived the further conclusion that since the interfaces of these water masses agree to a great extent in form and depth with this layer D = const., a nearly or completely motionless deep zone must exist.

Neumann has set up dynamic calculations for the cyclonic eddy system, which cannot be reproduced here in detail. He shows that their rate diminishes rapidly with depth and becomes zero at the lower limit of the troposphere. Next comes a great motionless intermediate zone whose characteristics are interfaces in the structure of the sea. Beneath this zone movements of the water appear that are anticyclonal in direction, whose rate reaches a maximum at a depth of about 1000 m. With increasing depth the rate is reduced, and in the layers near the bottom we may assume that there is very probably no motion.

Neumann (1943b) has presented a special work on the stability of water stratification in the Black Sea, in order to clarify the relations of the interfaces with the water masses.[5]

The stability relations are shown in Figure 9 in a vertical section from the southern tip of the Crimea to the southeast. An intermediate maximum stability can be discerned at 50–70 m, in which the lower limit of the thermal vertical convection finds expression; this is the "sealing layer" (Sperrschicht), which is of such importance in the oceanography of the Black Sea. This maximum is determined by the salinity gradients in this layer. It is recognizable in the vertical section as a continuous layer of higher stability values (in part $10^8 E > 4000$). In the zone from 0 to 25 m negative values of E appear, representing lability.

In the zone from 125 m to 250 m there is a constant second intermediate maximum of stability, which is caused also by a disturbance of the vertical stratification of salinity. This zone of disturbance in the decrease of stability extends almost without interruption through the Black Sea at about 200 m. Above this maximum layer $10^8 E$ = 250 to 500, below it E is always <250. Figure 9 shows the depth of the layer with H_2S content of 0.5 cm^3/l and also the depth of the dynamic reference surface (the vertical arrows). Both are widely congruent with the layer of maximum stability. Figure 10 is a corresponding section from Cape Sarich southwest to Kefken, passing directly through the western eddy of the Black Sea. The agreement in the vertical position of the three interfaces is also conspicuous in this section. All show a doming at the center of the eddy.

Neumann's analysis leads to the conclusion that the lower intermediate maximum of stability is not only the boundary between two different water masses, but also a further indication that this layer contains the boundary between two circulation systems of the Black Sea.

[5] For the stability of a water mass Hesselberg and Sverdrup have defined the expression E, which is proportional to the acceleration with which a water particle is driven back to its position of equilibrium when there is vertical displacement. When $E > O$ the layers are stable, when $E < O$ they are unstable, and $E = O$ represents the condition of indifferent equilibrium.

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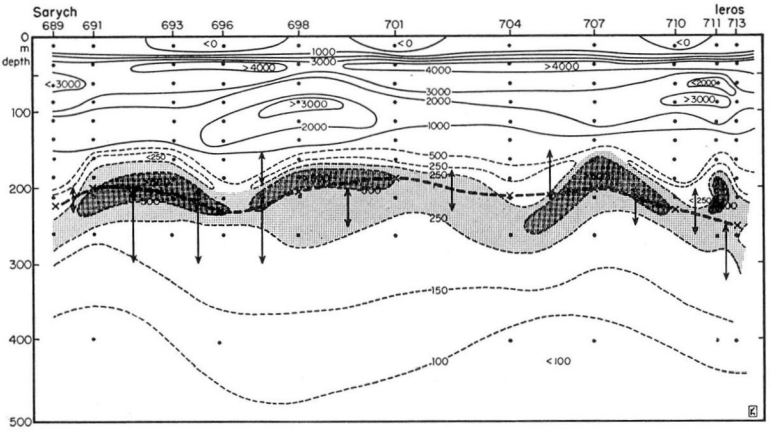

FIGURE 9.—*Vertical section showing the stability relations from Cape Sarych southeast to Ieros, November 22–25, 1926*

The perpendicular arrows indicate the vertical extent of the layer of constant dynamic reference surface; the heavy dashed line shows the depth of the 0.5 cm^3/l H_2S layer as determined from the indicated stations. Stippled area: Intermediate maximum of stability. From Neumann (1943b).

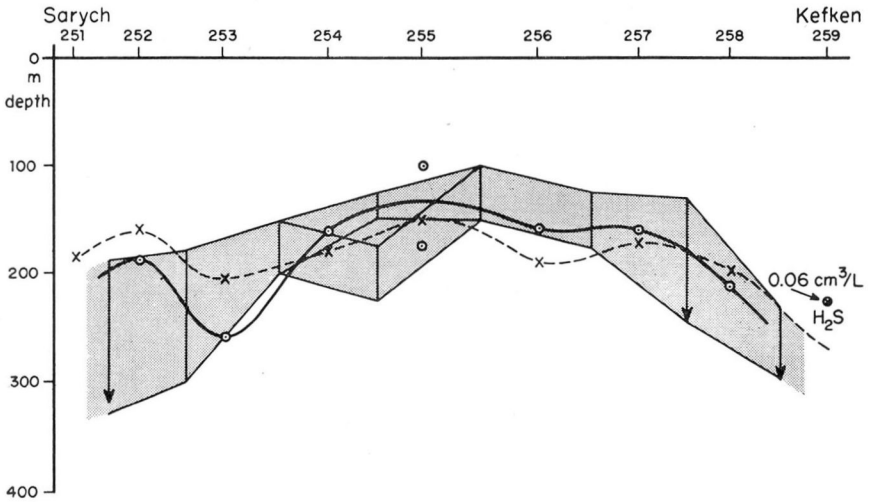

FIGURE 10.—*Depth of the intermediate layer of maximum stability* (—○—); *of the 0.5* cm^3/l H_2S *layer* (—×—), *and the layer of constant dynamic reference surface (stippled) between stations of a section from Cape Sarych to Kefken, June 26–July 2, 1935*
From Neumann (1943b)

THE SURFACE CURRENTS[6]

The scheme of currents in the Black Sea given by Knipovich shows a system of circular currents, as shown on the map of the currents by Neumann (1942) (Fig. 11).

[6] Wissemann (1906) attempted the first calculation of the surface currents resulting from density and winds on the basis of data from the first Black Sea Expedition of 1890–1891 (Spindler and Wrangel, 1899–1900). His results were based on an erroneous premise. Shokal'sky (1917) recognized the western and eastern cyclonic eddies. Knipovich then presented an especially detailed study (1926; 1933). His scheme of the currents, based mainly on the distribution of the hydrologic and hydrobiologic factors (temperature, salinity, oxygen, hydrogen sulfide, and plankton) was questioned as to important sections by Skvortsov (1929); *see* also Nikitin, (1931), and Nikitin and Skvortsov (1925).

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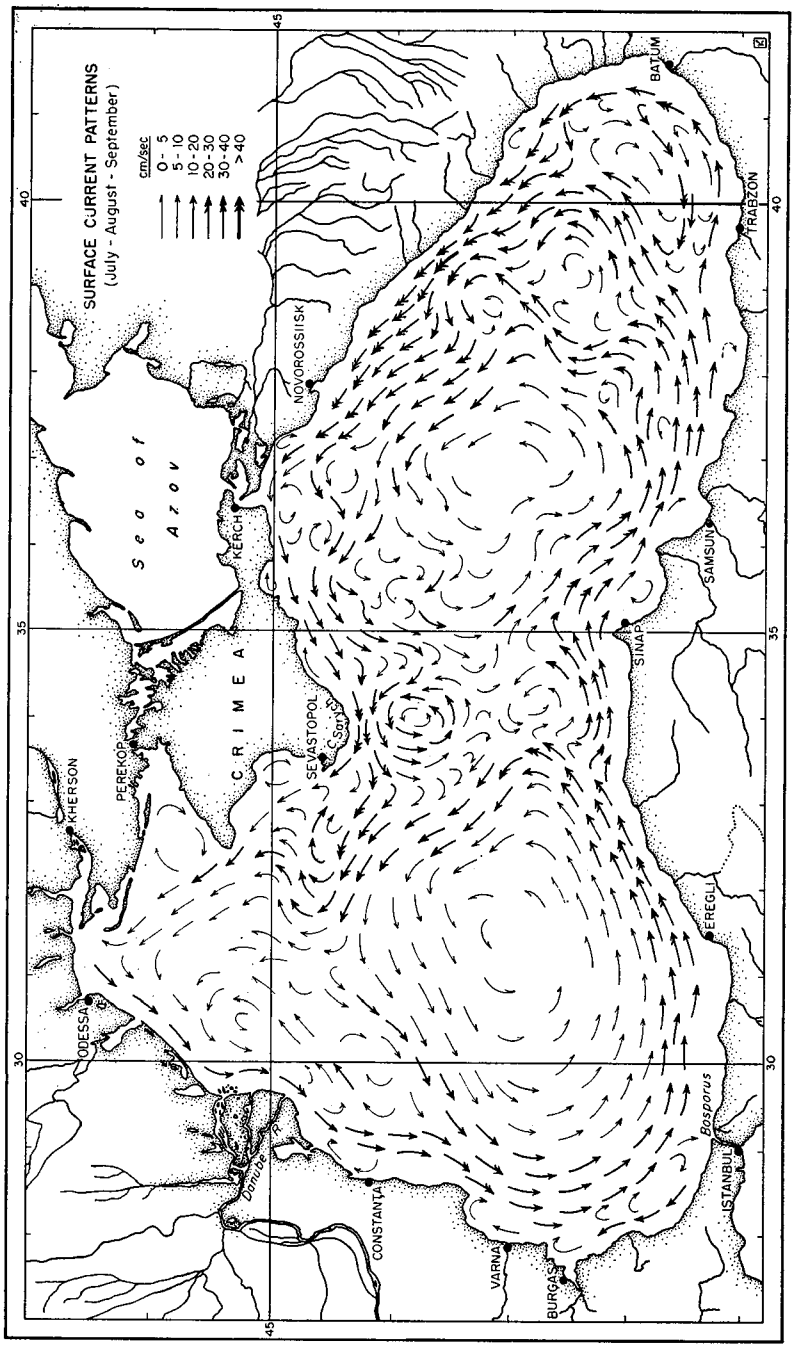

FIGURE 11.—*Current chart of the Black Sea*
Showing midsummer surface-current patterns. From Neumann (1942)

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The deep central parts of the sea are enclosed by a cyclonically directed main current, which follows the coast closely, to the 200-m isobath. From this unified main current, a branch separates off on the western part of the Anatolian coast, about at Eregli, and flows northward to re-enter the westward-flowing main current southwest of the tip of Crimea. This produces a subsidiary eddy in the western half of the sea. Southeast of the Crimea a current branches off to the south. The branch turns southeast and enters the southeast-flowing main current again off the Anatolian coast. This results in an eastern subsidiary eddy. In the middle of the Black Sea there is accordingly both a northwardly directed and a southwardly directed current. The great cyclonal main eddy is thus supplemented by two cyclonal subeddies (*see* in this connection the critique of Skvortsov).

The causes of the currents in the Black Sea are to be sought in the main in the relatively great differences of pressure produced and continued by the inflow of salt water in the bottom zone of the Bosporus and on the other hand by the continuing inflow of less saline water, especially in the northwestern area. These pressure differences were taken by Neumann (1942) as the base for his calculations.[7]

The pattern of the currents in the sea as a whole is excellently shown in the presentation of the gradients involved (Fig. 11).

With the premise of stationary and frictionless movement, the current was calculated from the dynamic isobaths; the rate could be taken from the differential.

A moderately strong current (10–20 cm/sec) sets eastward from the Bosporus. Flowing close to the coast, it takes a northeasterly direction at about Eregli, where the rate increases to 40 cm/sec. This current divides north of Kerempe into two branches, of which the stronger continues northeasterly, and with gradually diminished rate turns north and then northwest. The second and narrower branch flows around the entire eastern basin, following the Anatolian coast closely, and turning, accordingly, to the southeast beyond Sinope. At Sinope, from the northwest, the current of the eastern cyclonal subcurrent joins it, with a rate of up to 20 cm/sec. At about 37°E the current divides. One branch flows northeast and later to the north, whereas the second continues about parallel to the coast and turns northeast and north later. Between these branches small eddies form in an area generally weak in water movement. The two branches then reunite off the Caucasian coast and form a strong current whose rate may reach 40 cm/sec and more. It flows northwestward parallel to the coast until it breaks up, south of the Strait of Kerch, into individual smaller branches, interrupted by partial eddies. These, however, reunite and then flow southwest in a broad stream around the Crimean peninsula. A few narrow branches of the current turn off to the south and later enter the current along the Anatolian coast. The main current continues around the south tip of the Crimean peninsula. A rather strong and constant eddy develops south of the Crimea.[8]

Ciocârdel (1937) came, however, to conclusions similar to those of Knipovich, (the Russian Atlas of 1939 figures the currents in the sense of Skvortsov). The Knipovich account, especially for the western region, has been confirmed by Neumann. Neumann examined the data from the Russian expeditions in the light of the dynamics and calculated the topography of the computed sea surface for the demonstration of the gradient-current system. We follow the treatment of Knipovich, elaborated by Neumann (1942) and also by Vodyanitsky (1948).

[7] It remains to be decided as to whether the new hypothesis of Ullyott and Ilgaz concerning the currents in the Bosporus make necessary a correction of these calculations; the basic scheme will certainly not be affected.

[8] This eddy is characterized by a notable depression in the physical sea level (Neumann, 1942).

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The current flowing westward south of the Crimea gives off a small branch to the northwest, which follows the west coast of the peninsula. The main stream maintains a rate of 30–40 cm/sec and unites with the branch current, coming from the southeast, of the western cyclonic current. By their meeting on the shelf, the combined current is turned off to the right in the direction of the projecting Tarchankutsky peninsula of the Crimea; there it makes a sharp left turn and flows northwestward, encircling the shallow shelf region of the great northwestern embayment of the Black Sea. A weaker stream from the western cyclonic eddy follows the isobaths due west and unites off the Rumanian coast with the south-flowing waters. It then passes some distance off the Bulgarian coast, where it is called "Devil's Stream". Close in along this coast there is a weaker counter current with local eddies (Ciocârdel, 1937). The current flowing to the south along the west coast of the Black Sea takes up the considerable water masses of the large rivers that enter in this region, the Dnieper, Bug, Dniester, and the Danube.[9]

In the Bay of Varna the salinity ranges from 11.0 to 18.4 ‰ and usually is 16 to 17 ‰ (Paspalev, 1933; 1939b; Rozhdestvensky, 1949; 1952). With continuing westerly winds the surface water is driven out of the bay into the open sea, so that saltier water from the depths is brought to the surface (Caspers, 1951a). The temperature of the water ranges from +14°C. to +29°C (Paspalev, 1942). The salinity of the "Devil's Stream" varies considerably (Nechaev and Chernev, 1937a; 1940–1941a)

The system of currents described above was calculated by Neumann from the distribution of mass of the sea. The currents may be overlain in the uppermost layers by currents of varying strength.

The current pattern calculated from the gradient pattern agrees most closely with the actual one in the less windy summer months. When there are continuing strong winds, the direction of the currents may be completely reversed, as has been observed by Nechaev and Chernev (1937a; 1940–1941a) for the "Devil's Stream." But these are only temporary disturbances of the great current system produced by the differences of pressure.

The surface water of the Black Sea flows through the Bosporus into the Sea of Marmara, and thence into the Mediterranean. The Bosporus channel connecting the two seas has a width of about 4 km and a depth of 40–90 m. The salinity of the outflowing water rises from about 18 ‰ to 30 ‰ in the Dardanelles area. The classical investigations of the currents in this narrow channel are those of Merz (1918; 1921) and Merz and Möller (1928), following the early observations of Spratt (1870–1871), Makarov (1885), Wharton (1886), Gueydon (1886), and Magnaghi (1894). Merz and Möller concluded that the surface of the Black Sea is at a higher level than that of the Sea of Marmara, so that the movement of the surface water of the Black Sea southward through the Bosporus is a simple flow down a surface slope. At the same

[9] For the hydrography of the western and northwestern region of the Black Sea, *see* also Belchenko and Tarkhov, 1930; Morzhov, 1930; Popovici, 1936; Andreitcheva-Vankova, 1926, and Gavrilescu and Popovici, 1937.

With continuing offshore winds, a strong upwelling of deep water takes place along the south coast of the Crimea, at capes Chersones and Aitador, and also at Chauda, Yalta, Tarchankut, and at the Vorontsov Lighthouse. On such occasions the fall of temperature in the surface water may amount to 7° or 8°C. in a single day; the temperature dropped 11° in 11 hours on one occasion at Cape Sarych.

The large rivers also have an effect on the temperature of the water off their estuaries. In the summer the water streaming out of the Sea of Azov is warmer, and in the winter much colder than that of the adjoining waters of the Black Sea.

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time, denser water from the deeper layers of the Sea of Marmara flows northward along the floor of the Bosporus, which slopes toward the Black Sea basin. It is this deeper counter current, flowing northward, that cuts the canal steadily deeper.

Objections concerning the nature and extent of this deeper current through the Bosporus into the Black Sea have been raised by Ullyott and Ilgaz (1943a; 1943b; 1946a; 1946b), by Ilgaz (1944), and by Ullyott (1953). They admit that there is a deep current of water of high salt content from the Sea of Marmara into the Bosporus with a salinity of 38‰; but on the basis of their own hydrographic measurements they believe that they can demonstrate that the inflow into the Black Sea from this source is only of "negligible quantity". By this they mean that only about 25 per cent of the water that flows from the Sea of Marmara into the Bosporus remains in the Black Sea.[10] Merz and Möller left out of account a most important geographical structure, namely a threshold extending in semicircular fashion from the European to the Anatolian shore, so that the most northerly apex of the formation lies some 4 km outside the actual northern mouth of the Bosporus (Ullyott, 1953). This barrier rises to about 40 m below the surface.

Under normal weather conditions, the greater part of the dense, salty water which leaves the deep layers of the Sea of Marmara becomes mixed with the superficial southward flowing surface current, so that, as the deep current progresses successively further northward, it becomes increasingly depleted. The deep water which has been thus mixed with the superficial current on account of the great turbulence to be found in the Bosporus channel, is, of course, retransferred to the Sea of Marmara along with the waters which originally came from the Black Sea (Ullyott, 1953).

The deep water of the Sea of Marmara must consequently be replenished by the inflow of water at depth from the Aegean Sea. A prerequisite of our hypothesis is, therefore, that the threshold at the Dardanelles between the Aegean and the Sea of Marmara be deep enough to admit deep water from the Aegean. The shallowest part of the connection between the two seas, northeast of the strait, has a depth of about 65 m., which is ample to permit the flow of deep water. This conclusion is not new; it has been enunciated by earlier writers on the Bosporus, including Merz, whose hypothesis, like ours, requires such a flow. A second prerequisite of our hypothesis is that the supply of water by drainage into the Black Sea be so related to the loss by evaporation and outflow through the Bosporus that no inflow of deep water through the Bosporus is required to effect a balance. Merz and Möller computed a water economy for the Black Sea that requires such an inflow from the Bosporus to balance it (Ullyott and Ilgaz, 1946).

Merz and Möller attempted a calculation of the relations of the inflowing and outflowing current at 12,600 m^3/sec., and the inflowing one at 6,100 m^3/sec. The difference, 6,500 m^3/sec., they regarded as the excess of rainfall and river inflow over evaporation. If the rainfall is estimated at 7600 and the river inflow at 10,400 m^3/sec.,[11] the evaporation amounts to about 11,500 m^3/sec. (or 354 km^3/year). The resulting lowering of level by evaporation for the whole region of the Black Sea given by Merz and Möller is 84 cm/year. It is almost certainly too high. When, however, Ullyott and Ilgaz reject the idea of a deep current passing through the Bosporus into the Black Sea, the question is naturally raised as to how the salt-water economy of the Black Sea is held constant. The salt constantly being withdrawn from the Sea must be compensated for. Ullyott, in his work of 1953, points out the circumstance, previously established, that the strong south winds of summer may produce a reversal of the upper current.

. . .the whole of the waters in the Bosporus including the most superficial layers move up as a single mass in the direction of the Black Sea. While the waters are in this state there is no question whatever that the main mass of water which leaves the Sea of Marmara enters the Black Sea. On the other hand there is a reverse condition which occurs during northern storms of great violence. Then the water mass entering the Bosporus channel from the Black Sea sweeps out all the water tending to enter from the Sea of Marmara, so that the whole of the water in the Bosporus channel is now of Black Sea origin and composition.

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[10] Wachner (1943) thought that the amount of inflow into the Black Sea from the Bosporus exceeded the outflow. Markarov (1885), however, showed that the Black Sea receives considerably more water from rains and from its rivers than is lost by evaporation. The outflow must accordingly exceed the inflow, as was established by Merz.

[11] The amount of flow of the great rivers flowing into the Black Sea, the Danube, the Dnieper, the Don, and others is not accurately known, especially since it is subject to such great fluctuations that exact median values cannot be calculated. According to Antipa (1941) the annual amount of water poured in by the Danube is on the average 223 km^3.

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As Ullyott emphasizes, he is not yet in a position to calculate the balance between "normal" and "abnormal" inflow and outflow. Since the reversal of direction of the surface currents by "southerly storms of exceptional violence" is definitely exceptional, the fresh-water equilibrium of the great Black Sea basin can scarcely be explained by this phenomenon. The question is whether the admitted 25 per cent of bottom-current inflow is sufficient to effect the balance. The annual inflow of 200 km^3 calculated by Merz and Möller is also a relatively small amount; according to their further calculations this amount would mean a complete change of the water below the 30-m surface zone in a period of 2500 years. If the inflow is in fact considerably smaller, one would have to assume an actual and continuing recent freshening, which is yet to be demonstrated.

According to a verbal communication from Professor Kosswig, the measurements of current carried out by Demir (1954a) in connection with investigations of the plankton seem to provide quite new ideas as to the deep current in the Bosporus. It appears that the north-flowing current does not flow uniformly in the whole breadth of the deep channel but is directed toward one side and then the other. A cross section established from closely set stations shows that there are strong-flowing portions and likewise portions with less current. This seems to indicate that the inflow into the Black Sea is after all considerably greater than is supposed by Ullyott. The arrangement of the currents and the water economy of the Black Sea would thereby be more clearly explained. Light would be thrown on the relatively large differences of pressure between the northern and southern areas of the sea, which Neumann has called into consideration for the calculation of the gradients in the total current picture. The relatively high temperature of the deep water of the Black Sea would also be accounted for. The Ullyott hypothesis has been discussed in this detail because of the great importance of the Bosporus currents in the hydrography of this sea as a whole. It appears that his hypothesis is not in accord with the facts and will require considerable revision.

III. HYDROCHEMICAL CONDITIONS IN THE BLACK SEA; OXYGEN AND HYDROGEN SULFIDE

As a result of the considerable isolation of a water mass in the depths and the failure to develop vertical equalizing currents, oxygen loss takes place in the Black Sea with increasing depth, accompanied by a correlated increase in the amount of hydrogen sulfide (Table 5).

This is the most characteristic feature of the hydrochemistry and the controlling factor for biological conditions in this marine basin.

These conditions were first determined by Lebedintsev (1892). Isachenko (1925; 1929) and Isachenko and Egorova (1939) discovered the relation with bacteria. These relations were studied in detail by Danil'chenko and Chigirin (1926; 1929a; 1929b).

The chemical transformations are accomplished by the aid of bacteria (Isachenko, 1914; 1925; 1945; 1949). The genus involved is *Microspira* (*i.e., Desulfovibrio*) and especially *D. aestuarii*. Its life process is one of extreme reduction. The sulfates are reduced to hydrogen sulfide, and carbon dioxide is released. According to Danil'chenko and Chigirin (1926) 99.4 to 99.6 per cent of all the hydrogen sulfide in the Black Sea has its origin in this capacity of *Desulfovibrio*.

The process of H_2S formation has two phases. In the first sulfate is reduced to sulfide

$$R''SO_4 + 2C = R''S + 2CO_2$$

and in the second H_2S is formed.

$$R''S + CO_2 + H_2O \rightarrow R''CO_3 + H_2S$$

wherein $R''S_2O_3$ and $R''SO_3$ develop as intermediate products. The total process proceeds accordingly as

$$SO''_4 \rightarrow SO''_3 \rightarrow S_2O_3'' \rightarrow S''$$

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TABLE 5.—*Oxygen (O_2 cm³/l) and hydrogen sulfide (H_2S cm³/l) in the deep zones of the Black Sea*
After Zenkevich (1947)

Depth m	O_2	H_2S
0	4.57–7.62	—
25	2.51–8.64	—
50	1.05–7.76	—
100	0.12–7.16	—
125	0.00–3.16	—
150	0.00–2.71	0.088
200	0.00–1.88	0.470
300	0.00–1.93	1.480
500	0.00	3.779
1000	0.00	5.637
2000	0.00	5.796

TABLE 6.—*Carbonates and sulfates in the deep zones of the Black Sea*
After Danil'chenko and Chigirin (1929a)

Depth m	Carbonates g/l	Sulfates g/l	$S_2O_3 + SO_3$	Relative amount of sulfates
200	0.1040	1.477	1.15	1.502
300	0.1052	1.486	1.44	1.498
500	0.1155	1.518	1.58	1.497
1000	0.1259	1.515	1.77	1.485
2000	0.1304	1.506	2.83	1.474

There is a progressive increase in carbonates and decrease of sulfates with depth, with an increase in the intermediate products of the reduction process, S_2O_3 and SO_3 (Table 6).

The precipitation of carbonates is also caused by the action of denitrifying bacteria. Among other things, they produce NH_3, which combines with the carbonic acid of the bicarbonate, so that $CaCO_3$ cannot be kept in solution:

$$NH_3 + H_2O = NH_4OH$$

$$2\ NH_4OH + Ca(HCO_3)_2 \rightarrow (NH_4)CO_3 + CaCO_3 \downarrow + H_2O$$

NH_3 may also react with calcium sulfate in the presence of carbonic acid whereby $CaCO_3$ is again precipitated, according to the reaction:

$$2\ NH_3 + H_2CO_2 \rightarrow (NH_4)_2\ CO_3$$

$$(NH_4)_2CO_3 + CaSO_4 \rightleftharpoons CaCO_3 \downarrow + (NH_4)_2SO_4$$

Strakhov (1947) does not believe that the major part of the calcite content of the Black Sea sediments depends on this bacterial activity. This matter is discussed further in Section IV.

Because of the continuing supply of $CaCO_3$ from its rivers, the water of the Black Sea has two to three times the alkalinity of the open sea. It amounts to about a 3.1-mg equivalent at the surface. The pH value fluctuates accordingly from 7.7 to 8.45.

A part of the H_2S formed must be derived from the decomposition of the albumen

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of the autochtonous organisms of the sea. Data are lacking as to the amount of this portion of the total H_2S, relative to the amount derived from the $CaSO_4$ supply from the rivers. Strakhov (1947) believes it to be minimal. (*See* Section IV.)

The antagonistic roles of O_2 and H_2S appear in Table 5. In the intermediate zone between 150 and 300 m small amounts of both gases may be present.

The production of hydrogen sulfide in the Black Sea is not an exclusively Recent process but began in significant degree when the Pontic Sea fauna died off with the invasion of salt water from the Mediterranean. Since then H_2S continues to be formed anew with the sinking of organic remains to the depths.

NITROGEN AND PHOSPHORUS

In contrast with the conditions in the ocean, nitrates and nitrites are found only in the upper 300 m (Table 7).

Thus the ammonia content, which corresponds about to that of the ocean surface, increases with depth; it amounts to 1.10–1.26 mg/1 in the 1500–2000-m zone. According to Danil'chenko and Chigirin, production of ammonia is dependent primarily on the supply of organic substance, and only a small proportion is formed by the combination of nitrates with hydrogen sulfide. The reaction is

$$R\,NO_3 + 5H_2S \rightarrow NH_3 + RSH + 4S + 3H_2O$$

There is a sharp difference between surface and the depths in phosphorus content (Table 8).

According to Chigirin (1930a) the phosphorus contained in organisms in the lighted zone is carried to the depths to a considerable extent by the plankton, enriching the deep waters. The phosphorus content of the oxygen zone is correspondingly considerably higher in spring and summer.

CYCLE OF ORGANIC SUBSTANCES

It is evident from the oxygen cycle and the increase of hydrogen sulfide toward the depths that higher organic life is possible only in the uppermost 150–200 m of the Black Sea—that is, in a layer only 10–15 per cent of the whole volume of the sea. The whole of the deep zone is inhabited only by micro-organisms. Whereas the or-

TABLE 7.—*Average content of NO_3 and NH_3 in the Black Sea*
Danil'chenko and Chigirin (1929a)

Depth m	NO_3 mg/l	NH_3 mg/l
0	0.071	0.069
50	0.099	0.053
100	0.084	0.078
150	0.105	—
200	0.086	0.225
300	0.008	0.366
500	0.003	0.722
1000	0.000	1.079
2000	—	1.262

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TABLE 8.—*Average content of P_2O_5 in the Black Sea*
From Danil'chenko and Chigirin (1929b)

Depth m	P_2O_5 mg/l
0	62
25	78
50	88
100	143
200	360
500	483
1000	560
2000	632

ganic substance produced along the coasts returns in large part directly into circulation, a large part of the organic material produced in the vast region of the open sea sinks down into the anaerobic zone. Most of the detritus from the central production zone reaches the bottom, which may contain 2.5—3 per cent organic substance. The high content of nitrogen, ammonia, and phosphorus results from the breaking down of this material.

Nikitin held that a large part of the sunken organic substance was completely withdrawn from circulation. Kriss and Rukina (1949a; 1949b; 1949c) and Kriss, Rukina, and Biryuzova (1951) have now shown that complete reduction—*i.e.*, mineralization—takes place in the depths by microbiological processes. These authors maintain that the high values of organic carbon content of the deep-sea ooze (up to 20 per cent) apply to the deposits of the *old* Black Sea basin. In the Recent upper ooze deposits of the central basin the content of organic carbon is 1.74 to 2.51 per cent, and 4.54 per cent in the calcareous sediments (Arkhangel'sky and Strakhov, 1938). Ravich (1926) determined the carbon content at about 2000 m at 1.05 to 3.12 per cent. These are values that are known also from the depths of other seas. Higher values, in the Black Sea, are to be found only where a small deposit of mineral sediments has resulted in an increased enrichment of the organic detritus (Strakhov, 1941). Strakhov emphasizes the fact that neither the highest values nor the average content of organic carbon may be used for any calculation of the normal gas cycle of the Black Sea.

A strong decrease in organic remains, to about $\frac{1}{10}$ to $\frac{1}{15}$ of the highest values, sets in at about 100 m (Table 9). Nannoplankton form the greatest part of the organ-

TABLE 9.—*Number of plankton organisms and their remains per liter in the Black Sea 1 to 1750 m*
From Kriss and Rukina (1949a; 149b; 1949c) and Kriss, Rukina, and Biryuzova (1951)

Depth m	Number of organisms and their remains	Depth m	Number of organisms and their remains
1	10280	200	280
5	14040	225	400
10	8480	250	640
25	15200	300	1880
37	6160	500	240
50	6800	750	440
75	3440		
100	960	1250	680
125	360	1500	320
150	280	1750	400
175	480		

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isms (*see* also Morozova-Vodyanitskaya, 1948). Skopintsev (1948) has calculated that the forms of the size range of 50 μ sink at the rate of 1.2 m in 24 hours, at 12°C. Thus, from the lowermost layer in which they can live, the organic cells would require 250 days to sink to 500 m, 460 days to reach 750 m, and 670 days to reach 1000 m. It is therefore more astonishing that even at great depths quite undamaged cells containing protoplasm are to be found, as well as indestructible skeletal materials.

The peculiarity of the Black Sea in this matter consists in the fact that, in contrast with other seas, the remains of plants and animals that sink to the bottom are not devoured by a bottom fauna. Their reduction depends entirely on the microorganisms, which are unable to decompose all of the organic materials before they reach the bottom (transl. from Kriss, Rukina, and Biryuzova, 1951).

Thus organic remains in various stages of decomposition, from completely preserved animals and plants to unrecognizable submicroscopic particles, are to be found even in the zones poisoned with hydrogen sulfide. It is a mistake, however, to conclude that there is any "preserving action" by the hydrogen sulfide waters of the depths. The numbers of heterotropic and anaerobic micro-organisms in these zones contradict any preservative action (Kriss and Rukina, 1949a; 1949b; 1949c).

As early as 1894 Andrusov found remains of higher organisms in the deep-sea ooze of the Black Sea; Isachenko (1933) found such remains at 2188 m; Arkhangel'sky and Strakhov (1938) showed that frustules of diatoms and other sketal material were to be found in almost all zones. These findings are confirmed by Kriss, Rukina, and Biryuzova (1951) (Fig. 12; Table 10).

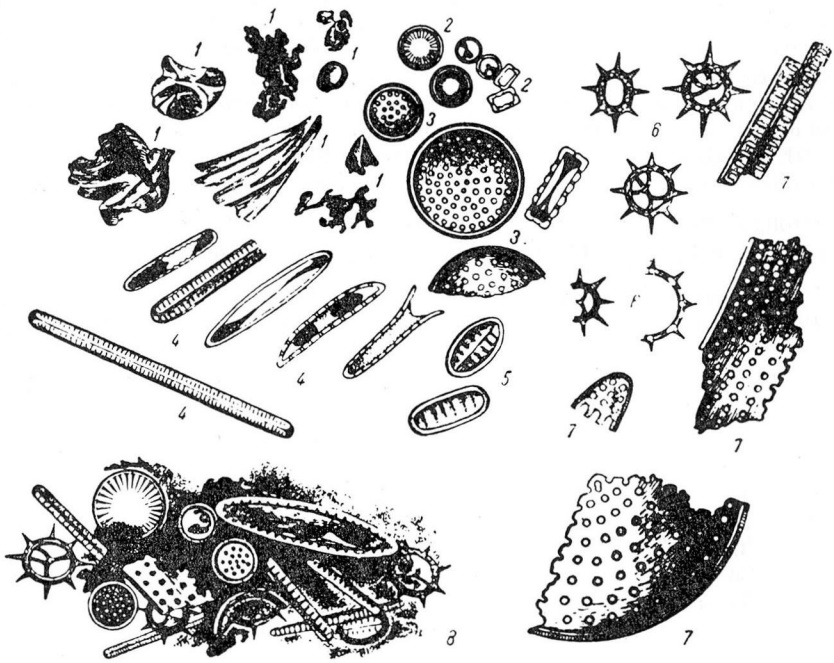

FIGURE 12.—*Organic remains from the upper surface layers of the deep ooze in the central basin of the Black Sea*
From Kriss, Rukina, and Biryuzova (1951)

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TABLE 10.—*Number of organic fragments in 1 g of the surface of bottom ooze from the central Black Sea, at three stations*

From Kriss, Rukina, and Biryuzova (1951)

Irregular particles that take erythrocin	1,850,000	338,000	3,072,500
Colorless skeletons of small, round diatoms	120,000	60,000	367,500
Colorless skeletons of porous, larger diatoms	60,000	120,000	142,500
Colorless narrow long diatom skeletons	200,000	140,000	210,000
Colorless skeletons of oval diatoms	2,500	20,000	—
Colorless skeletal remains of siliceous sponges	482,500	620,000	375,000
Colorless fragments of large diatoms	40,000	30,000	45,000
Clumps of skeletons, loosely assembled, of various organisms, yellowish	—	100,000	67,500

TABLE 11.—*Number of microorganisms in 1 g (dry weight) of surface ooze from the bottom of the greatest depths of the Black Sea*

From Kriss, Rukina, and Biryuzova (1951)

Year	Station no.	Total number of microbes in millions	Number of colonies, in Thousands	Titer of the micro-organisms			
				Albumen-splitters		Desulfurizers	Denitrifiers
				Aerobic	Anaerobic		
1946	2		159	10^6	10^2	10^4	10^7
	3		513	10^6	10^5	10^5	10^7
	4		310	10^6	10^5	10^6	10^7
	5		224	10^6	10^6	10^6	10^5
1948	4		10	10^6	10^3	10^3	10^5
	7		50	10^6	10^4	10^1	10^7
	8		320	10^7	10^3	10^1	10^7
	10		60	10^4	10^2	10^4	10^5
1949	1	2962	10.8				
	2	2499	30				
	3	1522	50				

The "rain of bodies" to the bottom beneath the hydrogen-sulfide zone provides nourishment for numerous micro-organisms, through whose action complete mineralization is accomplished. The available information is reported by Kriss, Rukina, and Tichonenko (1950) (Table 11).

Kriss (1953) gives a graphic representation of the density of bacteria, comparing summer and winter, for a vertical section from 0 to 200 m at a station 30 miles from the coast (Fig. 13). In June the maximum bacterial concentration is between 25 to 75 m, and thus in the thermocline and a little below it. This reflects the maximum for the summer. In February, at the same place, the bacteria are distributed with essential uniformity through the whole section, with increases between surface and about 75 m and between 125 to 175 m. In correspondence with the sinking of the detritus to the bottom, there is a high bacteria content in the lowermost water layer.

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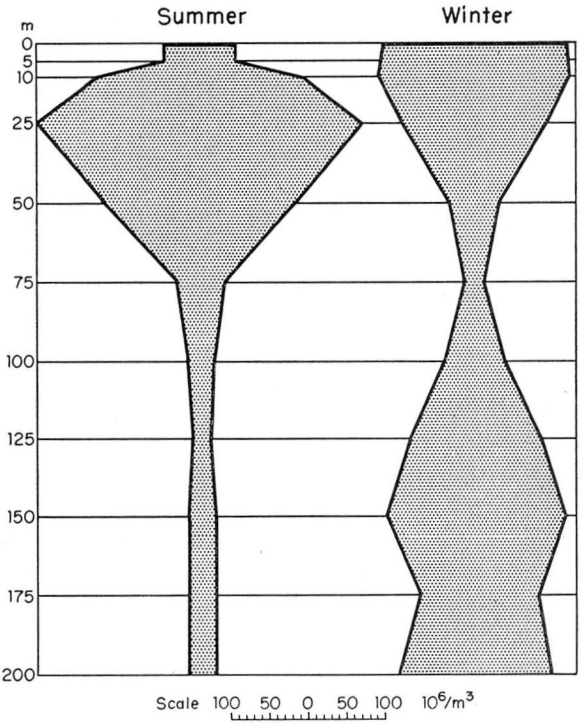

FIGURE 13.—*Vertical distribution of bacterial concentrations in the oxygenated zone of the Black Sea*
From Kriss (1953)

In the central part of the sea, according to the investigations of M. N. Lebedev (cited from Kriss), the biomass of the micro-organisms is strongly reduced at the upper H_2S limit, at about 150 m. It is then considerable from this level to the bottom (Fig. 14). One cubic meter of water in the H_2S zone contains 48 mg of bacteria, whereas in the O_2 zone it contains 17 mg. The average biomass of phytoplankton amounts to 59 mg per cubic meter in the O_2 zone (Morozova-Vodyanitskaya, 1950). The biomass of micro-organisms in the H_2S zone accordingly exceeds that of the O_2 zone and is only a little less than that of the phytoplankton (Datsko, 1951) (Fig. 14). Vodyanitsky (1948) demonstrated an exchange of water between the O_2 and H_2S zones and its effects on the production of phytoplankton and secondarily of zooplankton by supplying the nutrients produced by the action of the micro-organisms. Kriss concludes that the micro-organisms are of distinctly greater importance than are the phytoplankton in the primary productivity of the Black Sea.

The figures given for the quantity of micro-organisms in the deep-sea zones of the Black Sea lie within the range of variation of such figures for seas in which oxygen reaches the deep waters. Thus a significant utilization of the sinking organic substances takes place in the Black Sea, though in this case only the micro-organisms have a role. The Russian literature refers to the deep waters of the Black Sea as a "gigantic biochemical laboratory." The accumulations of nitrogen and phosphorus

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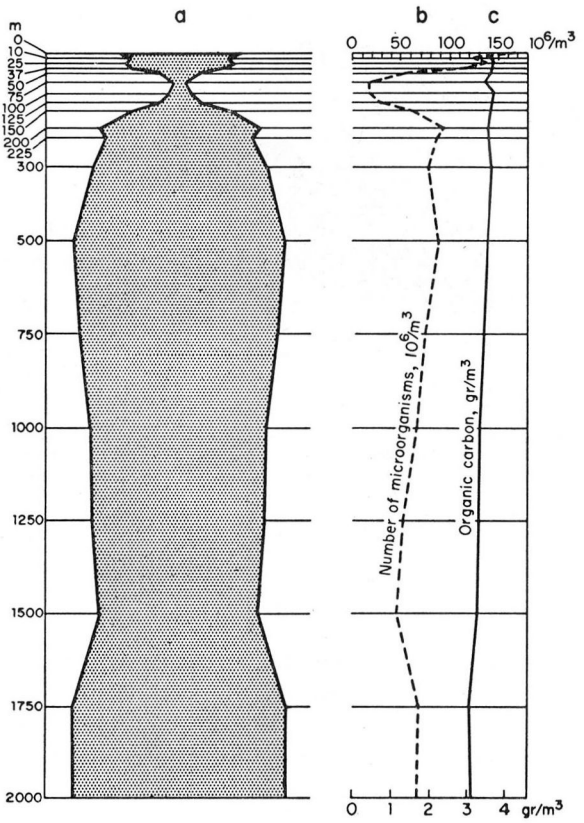

FIGURE 14.—*Vertical distribution of micro-organisms in the Black Sea from surface to 2,000 meters* *a*, biomass; *b*, counts of micro-organisms and *c*, organic carbon content. From Kriss (1953).

in the deep zones, again brought out by Nikitin (1950), depends on the mineralization process at the bottom, which, in contrast with the ideas of older authors, is accordingly not a withdrawal of biological materials from the cycle.

IV. BOTTOM DEPOSITS

For an account of the sediment types in the Black Sea, their composition, their origin, and their correlation with the hydrographic circulation system of the Sea, *see* Arkhangel'sky (1927; 1928; 1930), Arkhangel'sky and Strakhov (1938), and Strakhov (1937; 1941; 1946; 1947); Von Raupach (1952) gives a summary in German.

The steep dropoff of the bottom from 180 to 3000 m and the H_2S poisoning of the water in the deeper zones produce a sharp separation of the sediments of the coastal shelf from those of the deeper regions. On the shelf, especially fine-grained sediments are accumulated in local basins. There is an extraordinarily high rate of deposition of silt and clays in the limans. The steeper slopes downward from the shelf form a zone of reduced accumulation of sediments. In the deep basin the bottom topography is

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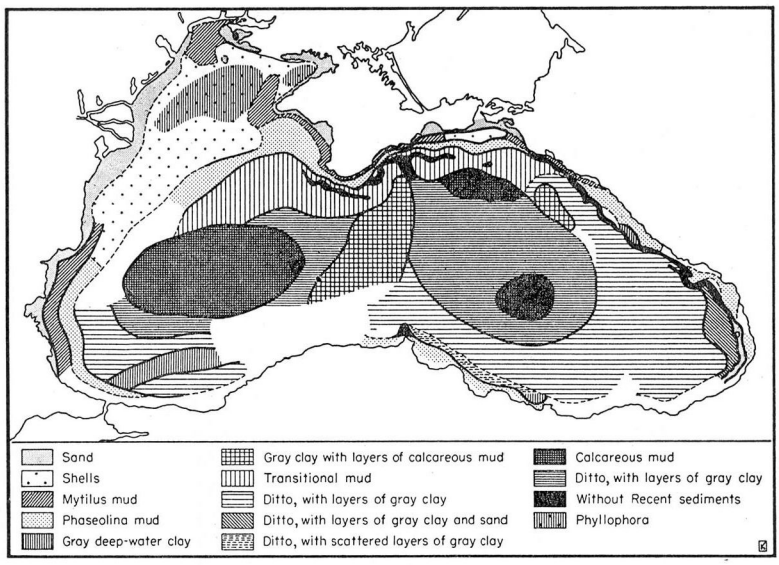

FIGURE 15.—*Distribution of Recent sediments in the Black Sea*
Schematic, from Arkhangel'sky and Strakhov (1938)

of slight importance in the distribution of the sediments as sedimentation is governed by the current system and the development of hydrodynamic zones (Fig. 15).

It is difficult to estimate the amount of sediments brought annually into the sea by the rivers. For the Danube this amount is calculated at 48,000,000 metric tons per annum, on the basis of 211 mg of solid matter per liter (Wachner estimates 75,000,000 tons). Because of the arid climate and the absence of tides, coastal erosion plays only a subordinate role. The principal part of the deposits consists of terrigenous material; Strakhov (1947) has determined its distribution in the sediments for the last 2500 years.[12] It is surprising to find that the accumulation of sediments in the eastern half of the sea is significantly greater than in the western. This is because large amounts of clastic materials are carried into the sea by the mountain streams of the Caucasus and the Anatolian region; these materials are soon deposited. On the other hand, the western lowland streams bring in smaller amounts of materials, mainly in solution, which are distributed over the whole surface of the sea by the currents; the deltas and limans catch a considerable amount of the material from the rivers of this region. The distribution scheme as a whole is complex and is only in part clearly correlated with the surface currents, though many relations can be demonstrated (Fig. 15).

Shelf deposits: To a depth of about 15 m (30 m at most) sandy coastal sediments predominate, with a rich fauna of bivalves. In some areas there are reefs of *Mytilus* and *Ostrea*. This zone has a considerable development in breadth only on the west coast. The distribution of these sediments in the Bay of Varna has been dealt with by Caspers (1951a). At depths of 15 to 65 m the *Mytilus* mud of fine sand and clay predominates, with *M. galloprovincialis*. It occupies a broad zone on the western and northern coasts. At Odessa these deposits rise almost to the surface. North of parallel 45°N. the

[12] By terrigenous material is meant that part of the sediments remaining after removal of the $CaCO_3$ and the organic constituents.

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alga *Phyllophora rubens* forms an extensive *Phyllophora* meadow, to the extent of some 10,000 km². At depths of 65 to 150 m the Phaseolina mud appears, named from the abundant bivalves of this zone, *Modiola phaseolina*. The sediment in this zone is almost pure clay, with little sand. The Phaseolina mud presumably forms a continuous ring around the entire deep-sea basin.

Deep sea deposits: In the region of the steep dropoff on the Caucasian and Anatolian coasts a gray deep-sea clay is deposited to depths of 1500 m. This occasionally exhibits distinct fine stratification. Terrigenous material composes 75 per cent of it, and 14 per cent is calcium carbonate. In the vicinity of the Bosporus this clay is still found at a depth of 2000 m, 100 km from the coast. This Von Raupach attributes to the effect of the strong deep current.

In the central parts of the eastern and western basins calcareous ooze is deposited. It is a dirty white marl that exhibits a fine stratification with white calcareous layers alternating with dark clayey sapropelitic layers. The calcareous ooze contains 28 per cent terrigenous material and 59 per cent calcium carbonate. In the remaining deep portions of the basins the bottom is characterized by transitional types of sediments. Gray clay, calcareous mud, and extremely fine sand are present in alternating layers of 1–5 cm thickness. Calcium-carbonate content ranges from 12 to 43 per cent (average 25 per cent), and terrigenous components from 41–85 per cent, (average 64 per cent). There may be in addition a calcareous-diatomaceous ooze. Gray, micaceous sands with grains .05 to .01 mm in diameter appear usually only as more or less pure deposits. The distribution of the deep-sea deposits seems also to be dependent on the deep currents, but these are not yet sufficiently known to make any clear correlations discernible.

In a series of cases the recent sediments have been distinguished from those of the Old Pontic period. The older beds in the shelf area lack *Modiola phaseolina*, so that the deposits characterized by this form must be regarded as Recent. Beneath the Phaseolina beds lies Old Pontic *Mytilus* mud, whereas recent *Mytilus* muds overlie Old Pontic bivalve sands. Beneath the Recent deep-sea deposits, which Strakhov regards as laid down during the last 2500 years, lie sapropelitic clays. The reasons for this change in type of sediment are discussed by Von Raupach (1952). According to Arkhangel'sky and Strakhov (1932; 1938), the south boreal Black Sea had a much shallower shelf than is the case today. The oxygen-rich surface zone over the deep basins was accordingly less extensive. From this it may be concluded that the dead plankton components were exposed to decay for a shorter period, while sinking, and thus that they provided a larger amount of material to the bottom. It has also been thought that there could have been a greater productivity of organic substance in those earlier times (Rauzer-Chernousova, 1930). Furthermore, the greater numbers of mollusks might have bound a larger proportion of carbonate in the shallow seas, resulting in a proportionately greater amount of organic substances for deposition in the deep basins. Tectonic processes would then have produced the change in the composition of the sediments. A study of the literature suggests that such hypotheses lack adequate foundation and that renewed geological investigations as well as further analysis of sediments are needed.

The rate of sedimentation is given by Arkhangel'sky and Strakhov as 0.5 mm/year for the whole Black Sea basin, the considerable regional differences being averaged in their calculation. The rate of deposition of the deep-sea gray clay is placed at 0.2 mm/year. For the calcareous clay it is distinctly less—0.04 to 0.08 mm/year (Strakhov, 1947). According to Arkhangel'sky (1928) a similarly slow rate of sedimentation is to be assumed for the Old Pontic black clay. In the limans, where, in some places, the thickness of the sediments may exceed 10 m, more than 4 cm of sediment may be deposited in a year.

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About two-thirds of the carbonates enter the Black Sea primarily as bicarbonate $Ca(HCO_3)_2$, and the remaining third as finely divided calcium carbonate, $CaCO_3$. The solid carbonate from the rivers is distributed like other terrigenous material. The dissolved bicarbonate is more widely distributed and is thus more uniformly deposited. According to Strakhov (1947) the calcite, in powder form, represents the chemically precipitated carbonate. It is found in the Phaseolina mud; in the deep-sea deposits it is the only form of carbonate (with the exception of washed-in mollusk shells).

Strakhov (1947) has raised objections to the generally accepted theory that the carbonates in the sediments of the Black Sea are produced by the activities of the desulfurifying and denitrifying bacteria (Section III). According to his views, the assumption that the calcite results from the action of desulfurifying bacteria would require that the amount of calcite precipitated since the beginning of the accumulation of H_2S in the sea (thus since the beginning of the Old Pontic era) would have to be proportional to the amount of H_2S contained in the water. He regards the amount of H_2S produced by the decomposition of albumens as so trifling that it need not be considered. Calculating the amount of carbonate to be expected in the deposits from the amount of H_2S in the deep water, the figure for biochemical production of carbonate would be 1.86g of $CaCO_3$ per cm^3 of sediment. The fact is that the amount is 7–10 g/cm^3. Strakhov calculates that only 18–25 per cent of the calcite in the deep sediments could be produced by the desulfurifying bacteria. Since the NH_3 produced by bacteria is neutralized by the excess of carbonic acid, he also regards the role of the denitrifying bacteria in calcite production as subordinate. Strakhov calculates further that since at all depths the amount of NH_3 is only one-fifth of the amount of H_2S, the amount of calcite produced by denitrifying bacteria would be only one-fifth of that from the desulfurifying bacteria; this would mean that only 22–30 per cent of the calcite in the deep deposits could be of bacterial origin. He concludes that much the greater proportion of $CaCO_3$ is precipitated chemically. The already precipitated calcite particles from waters near the coasts, stirred up by currents, serve as centers of crystallization.

Strakhov's calculations as to a disproportion between the amount of H_2S in the open water and the amount of carbonates in the sediments, and the conclusions drawn by him, need to be reviewed. The H_2S content of the open water cannot be regarded as an unchanging constant, as is more or less the case with the carbonate content of the sediments. There is no doubt that oxidation of the hydrogen sulfide takes place at the interface of the H_2S zone with the oxygenated upper zone, and this effect, reinforced by the convection currents in the sea, must involve a continual loss of H_2S from the deep waters.

V. THE PLANKTON

The more important works on plankton distribution in the Black Sea are by Nikitin (1926; 1927; 1929a; 1929b; 1929c; 1931; 1939; 1945), Nikitin and Mal'm (1934), Nikitin and Skvortsov (1925; 1927). The phytoplankton is dealt with by Morozova-Vodyanitskaya (1948) in a systematic work.

PHYTOPLANKTON

The phytoplankton lists of Morozova-Vodyanitskaya and those by Usachev (from a manuscript report of 1946, which may have subsequently been published) for the northwestern part of the Black Sea are compared by Zenkevich (Table 12). Usachev has fewer species, for he excludes all the benthic forms.

The common genera of diatoms are *Chaetoceras* (37 species), *Coscinodiscus* (13 species), *Rhizosolenia* (9 species), and *Melosira* (6 species). Other common species are *Skeletonema costatum*, *Cerataulina bergonii*, *Leptocylindrus donicus*, and *Thalassionema nitzschioides*. The dinoflagellates include the genera *Peridinium* (23 species),

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TABLE 12.—*Phytoplankton species in the Black Sea*
From Zenkevich (1947)

	According to	
	Morozova-Vodyanitskaya	Usachev
Diatomaceae	136 (56.7%)	52 (36%)
Dinoflagellata	73 (30.4%)	36 (15%)
Schizophyceae	20 (8.4%)	28 (20%)
Chlorophyceae	8 (3.4%)	22 (16%)
Silicoflagellata	3 (1.1%)	3 (2%)
	240	141

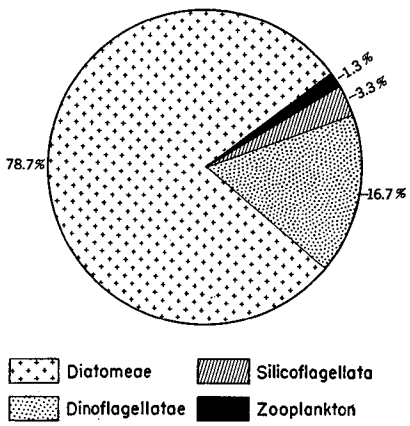

FIGURE 16.—*Percentage representation of the most important plankton organisms in the vicinity of Batum*
From Zenkevich (1947)

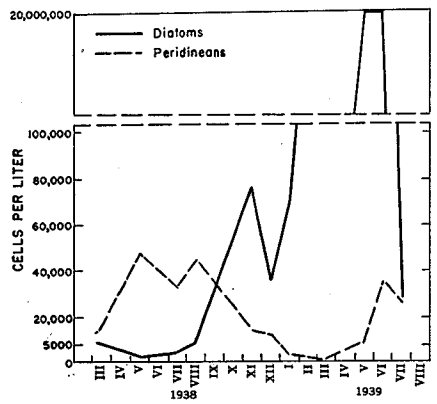

FIGURE 17.—*Annual cycle of diatoms and peridinians in the Bay of Sevastopol*
From Zenkevich (1947)

Dinophysis (9 species), *Gonyaulax* (7 species), and *Ceratium* (4 species), together with *Prorocentrum micans*, *Glenodinium*, and *Exuviella cordata*.

Data on the quantitative horizontal distribution of the phytoplankton are primarily from Morozova-Vodyanitskaya (1941; 1950) and Malyatsky (1940), and also Nikitin (1939), for the Batum region. Diatoms make up 78.7 per cent, with dinoflagellates next at 16.7 per cent, of the total plankton in this region (Fig. 16). Toward spring there is an enormous increase in the diatoms (up to 20,000,000 per liter); the increase begins in October and reaches its maximum in May–June. The mass development of dinoflagellates in summer (up to 48,000/l) is much less (Fig. 17). By July the diatoms have dropped off very rapidly. The principal forms at the peak of abundance are *Skeletonema costatum*, *Chaetoceras radians*, *Thalassionema nitzschioides*, and *Cerataulina bergonii*. The summer plankton is characterized by the dinoflagellates (*Exuviella cordata*, *Prorocentrum micans*, *Gonyaulax polyedra*, and several species of *Glenodinium* and *Peridinium*). With these there are large numbers of the diatom

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TABLE 13.—*Phytoplankton averages in the Black Sea, 1938–1939*
Counts in cells per liter; from Morozova-Vodyanitskaya (1941)

	Month:					
	VIII	XI	I	III	V	VII
Diatomeae	8,665	77,077	93,235	2,141,783	20,204,560	27,300
Dinoflagellata	45,405	16,325	3,213	332	8,440	25,800
Silicoflagellata	583	1,340	465	130	100	100
Others	1,667	1,110	1,550	600	500	2,600
	56,320	95,852	98,463	2,142,845	20,213,600	55,500

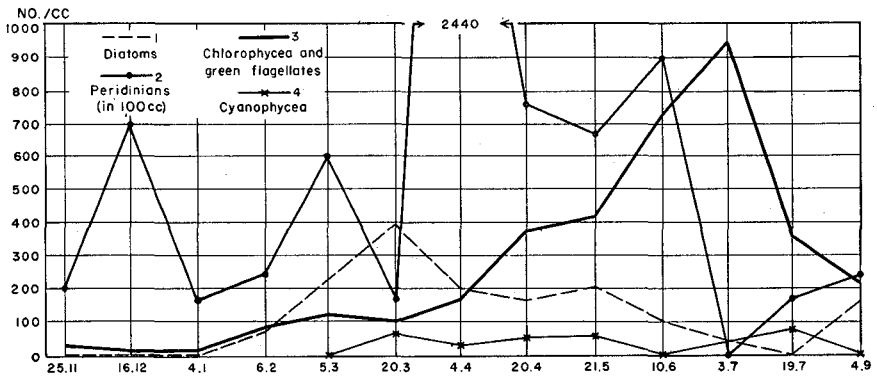

FIGURE 18.—*Average quantity of phytoplankton per cc (peridinians per 100 cc) in Varna Bay, 1940*
1, Diatoms; 2, Peridinians; 3, Chlorophycea and green flagellates; 4, Cyanophycea. From Caspers (1951a).

Thalassionema nitzschioides. Table 13 presents the averages for the plankton for the years 1938–1939.

There are especially large increases in the phytoplankton in the near-shore zones, particularly in the larger bays. Morozova-Vodyanitskaya gives the average counts of cells per liter near Sevastopol, from 0 to 25 m depth, at 255 m off the coast as 11,000 in July, 17,000 in October, and in the bay as 37,000 in July and 107,000 in October. In the spring peak there may be up to 31,000,000 cells per liter in this bay.

Paspalev (1942) has investigated the annual cycle of the phytoplankton in the Gulf of Varna (Bulgarian coast). The diatoms in that area reach their maximum in March, the peridinians in April, and the chlorophyceans and green flagellates in July (Fig. 18). The maximum of the phytoplankton at Varna is correlated with the summer decrease in salinity (from the inflow of fertile continental waters) and the higher temperature. The plankton is accordingly most abundant in the surface layers and is sharply reduced even at 10 m (Caspers, 1951a, p. 14–15).

ZOOPLANKTON

According to the available information, there are about 70 species of zooplankton organisms (Table 14).

The number of species is surprisingly small, especially as compared with the fauna

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TABLE 14.—*Number of zooplankton species in the Black Sea (Zenkevich, 1947)*

		Per cent			Per cent
Tintinnoidea	16	(22.6)	Cladocera	12	(17.0)
Hydromedusae	7	(10.0)	Copepoda	15	(20.6)
Scyphomedusae	2	2.8)	Isopoda	1	(1.4)
Ctenophora	1	(1.4)	Chaetognatha	2	(2.9)
Rotatoria	14	(19.9)	Appendicularia	6	(1.4)

of the Mediterranean. For example, there is one ctenophore against 16, and 15 copepods against 304.

The most important of the zooplankters are:

Cystoflagellata:	*Noctiluca miliaris*
Tintinnoidea:	*Cyttarocyeis helix, C. ehrenbergi, Tintinnopsis campanula, T. ventricosa, T. tubulosa, Tintinnum mediterranea, T. subulatus*
Scyphomedusae:	*Aurelia aurita, Pilema pulmo*
Ctenophora:	*Pleurobrachia pileus*
Copepoda:	*Oithona nana, O. similis, Paracalanus parvus, Acartia clausi, Calanus helgolandicus, Pseudocalanus elongatus, Centropages kroyeri*
Cladocera:	*Evadne nordmanni, E. spinifera, Podon polyphemoides.*
Chaetognatha:	*Sagitta setosa*
Isopoda:	*Idothea algerica* (at some places in considerable numbers)

The improverishment of the Black Sea plankton is associated with the low salinity of the surface waters as compared with the oceanic salinities of the Mediterranean. This influences the phytoplankton only slightly, but has a strong effect on the zooplankton, which lacks coccolithophorids, radiolarians, siphonophores, salps, pteropods, and many typical larvae of benthic animals. Only at a point just opposite the opening into the Bosporus are these forms to be found, at depths of 50–60 m (Demir, 1954). Contrary to Ullyott's ideas (Section II), Demir showed that at this point the waters close to the bottom have a higher salinity than in corresponding depths in the other areas of the Black Sea; his investigations were made in the summer months and in calm weather (or with a light north wind). At this level, Mediterranean plankters, otherwise absent in the Black Sea, have been brought in by the bottom counter current of the Bosporus. The forms in question are the siphonophore *Muggiaea konchi*, the tunicate *Doliolum denticulatum*, the crustaceans *Calocalanus*, *Rhincalanus nasutus*, *Corycaeus furcifer*, and *Oncea mediterranea* (+ polychaetes). Presumably these forms are limited to a small region near the opening of the Bosporus, and that they die off when they are carried farther.

The seasonal changes of the zooplankton have been studied by Nikitin. Through the oxygenated zone *Oithona nana* and most of the copepod species (especially *Acartia clausi, Paracalanus parvus*) and *Oikopleura dioica* occur the year round. *Noctiluca miliaris* declines in numbers in winter, in contrast with its mass abundance in summer. *Centropages kroyeri, Evadne nordmanni, E. spinifera*, and *Podon polyphemoides* are confined to the uppermost zones and occur only in summer. The cold stenothermic *Calanus helgolandicus, Pseudocalanus elongatus, Oithona similis, Sagitta euxina*, and *Pleurobrachius pileus* are present throughout the oxygenated zone in winter, whereas in summer they are found only at depths below 50 m; their upper temperature limit lies between 10° and 14°C. These

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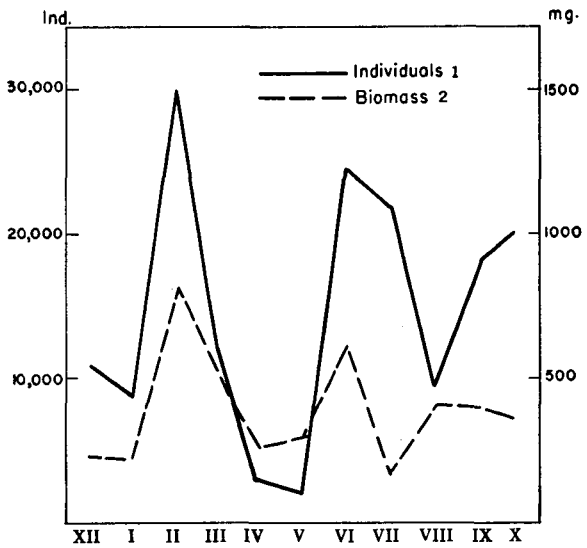

FIGURE 19.—*Annual changes in the abundance and biomass of zooplankton in Novorossiisk Bay, in a water column 21 meters deep x 0.1 m.*[2]
From Zenkevich (1947)

species accordingly migrate vertically according to the seasonal variation in temperature. Below 50 m, where the oxygen content is 4 per cent or less, the species regularly found are *Calanus helogolandicus*, *Pseudocalanus elongatus*, and various forms of polychaetes; the occasional forms are *Oithona similis*, *Oikopleura dioica*, and *Sagitta euxina*. Nikitin and Mal'm (1927) have demonstrated the low-oxygen requirement of these forms in the laboratory.

A variety of forms, especially *Calanus helgolandicus* and *Sagitta euxina*, undergo vertical diurnal migration. At Batum such migrations are made by *Pseudocalanus elongatus*, *Oithona similis*, *Centropages kroyeri*, and *Sagitta setosa*, and to a less marked degree by *Acartia clausi*, *Paracalanus parvus*, *Tintinnopsis ventricosa*, and *Tintinnum mediterranea* (Chokhuri, 1939).

The development of the zooplankton, like that of the phytoplankton, is increased in near-shore zones and in bays and gulfs, especially in the northern regions of the Black Sea. Kosyakina (1937; 1940) has investigated the fluctuations of the zooplankton in the Bay of Novorossiisk. There were three maxima (Fig. 19). The copepods are most important in winter; in the summer there is a marked rise of numbers of bivalve larvae. The same seasonal relations were found in the Bay of Batum by Nikitin, and the species composition was similar.

VERTICAL DISTRIBUTION OF THE PLANKTON

In addition to the diurnal and seasonal vertical migrations, the vertical distribution of the plankton is governed to a very large degree by the very special peculiarities of the hydrographic zonation. It has been pointed out that below the depth of 50 m, with an oxygen content of only 4 per cent, only four plankters are regularly present.

On the basis of the transects made by the Hydrographic Administration and the Biological Station of Sevastopol (166 stations) Nikitin has published a series of

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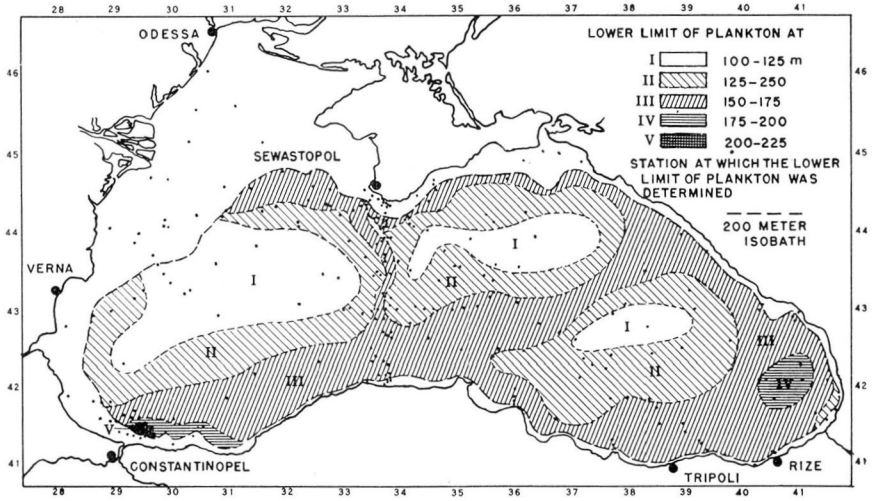

FIGURE 20.—*Chart showing Russian hydrobiological stations in the Black Sea, 1923–1927, and the distribution of the lower limit of plankton*
Modified from Nikitin (1931)

papers on the lower limits of the plankton. He was able to take a comprehensive view of the surface of the Black Sea and to draw the parallel between the results from the plankton and the hydrographic measurements. The general results are shown in Figure 20. The limit of the plankton coincides, for practical purposes, with the oxygenated surface zone.

In correspondence with the upward doming of the lower surface of the zone, in the central parts of the sea, the limits of plankton are at 100–125 m, whereas closer to the shore, both north and south, the limits are at 150–175 m. Along the Crimean coast, the zone with plankton reaching to 175 m occupies a band 10–20 nautical miles wide. This is continued along the Caucasian coast and becomes considerably wider in the southeastern part of the sea. At the center of this region, 20 miles off Poti, there is a small area in which the lower plankton limit drops to 175–200 m; and between Poti and Batum, within a band about 8 miles wide, the lower plankton limit rises to 150–125 m. Toward the west, along the Anatolian coast, the plankton limit is at 150–175 m. At Samsum this band is about 10 nautical miles wide, and west of Sinop it widens to 40 miles. In the western part of the sea the limit of 0_2 is at a higher level, which is conditioned by the strong freshening of the surface waters. The plankton limit lies at the corresponding high level, lying at 100–125 m off the Rumanian and South Ukrainian coast, and at 150 m off the Bulgarian coast.

In the central part of the Black Sea are two troughs in which the plankton descends to 150–175 m. One extends from the Crimea southward to the Anatolian coast, the other from the Caucasian coast southwestward to the southern coast. This is also in accord with the hydrographic system of surface currents. The Black Sea basin is accordingly divided into three parts, in the centers of which the lower plankton limits lie at 1225–100 m, and even at a lesser depth. This area is especially broad in the western part of the sea. Toward the Rumanian coast, the otherwise general lowering of the plankton limit does not appear, and the region with 125–100 m passes directly into the shallow shore zone.

On the whole, the lower limit of the plankton lies at a higher level in the western than in the eastern part of the sea; a rough section shows a decline in this direction of about 50 m.

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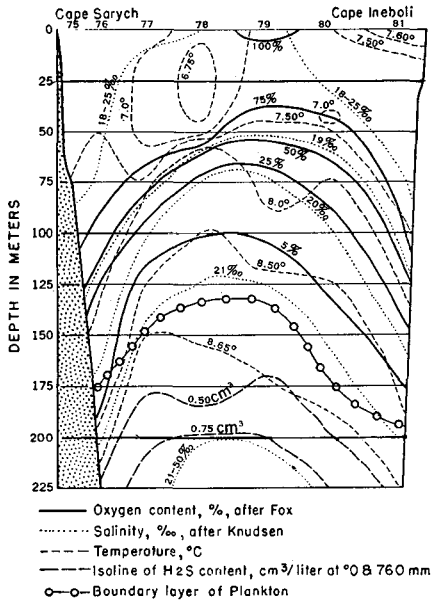

FIGURE 21.—*Hydrobiological section and lower limit of plankton from the south coast of Crimea (Cape Sarych) to the Anatolian coast (Cape Ineboli), February 1925*
From Nikitin (1931)

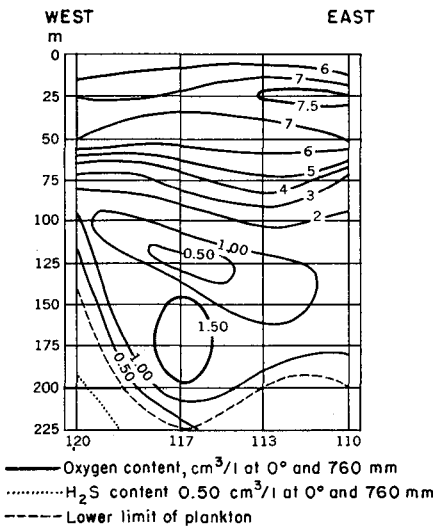

FIGURE 22.—*Hydrobiological section and lower limit of plankton from east to west at the Bosporus, July 1925*
Modified from Nikitin (1931)

The raised level of the plankton boundary toward the central parts of the sea appears also in the north-south profile. Figure 21 shows such a section from the south coast of the Crimea to the Anatolian coast together with the isolines of temperature, O_2, and H_2S. These relations occur throughout the year.

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The depth limit sinks to 225 m off the Bosporus, conditioned by the inflow of highly saline and oxygen-rich waters from the Sea of Marmara. Figure 22 shows a hydrographic section extending east and west at a distance of 15–17 nautical miles from the Bosporus. Station 117 lies directly opposite the entrance to the Bosporus. The amount of oxygen, diminishing rapidly with depth, uses again below 125 m to 1.50 cm^3 per liter, and declines again only below 200 m to the H_2S zone. The lower limit of the plankton is correspondingly depressed.

BIOMASS OF THE PLANKTON

In recent years Russians have investigated the total biomass. Malyatsky (1940b) has determined the biomass of the phytoplankton in the central part of the sea, off the Crimean and Caucasian coasts, at depths of 0 to 75 m (in the photosynthetic zone) (Fig. 23). In May-June a concentration off the Strait of Kerch can be demonstrated, whereas from August on the greatest concentration appears in the central parts of the sea. Figure 24 shows the distribution of the plankton biomass in the

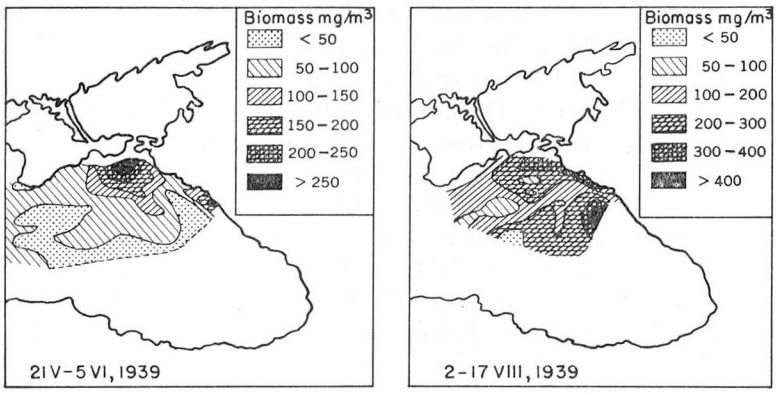

FIGURE 23.—*Distribution of phytoplankton biomass (mg/m³) in the Black Sea*
From Zenkevich (1947)

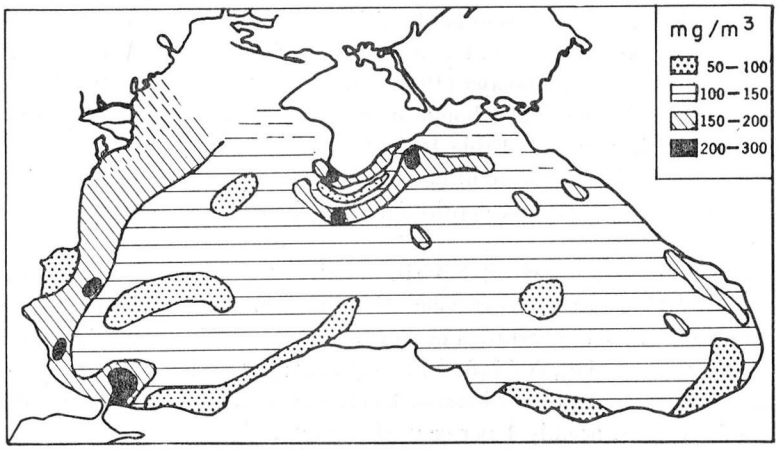

FIGURE 24.—*Horizontal distribution of plankton biomass in the 0–100 meter layer in the Black Sea*
From Zenkevich (1947)

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TABLE 15.—*Average plankton biomass (mg/m³) in the Black Sea*

After Nikitin, from Zenkevich (1947)

Depth, m	V	VI	VII	VIII–IX	X–XI	II
0–25	120	266	278	298	200	95
25–50	120	162	202	125	140	133
50–75	130	136	159	110	113	80
75–100	109	80	70	88	92	64
100–125	68	86	80	193 (?)	67	48
125–150	79 (?)	51	50	58	50	34
150–175	39	33	36	36	43	40
0–175	95	116	125	130	101	71

whole sea. The biomass is relatively uniform in the upper 100 m; it ranges from 100 to 150 mg/m³. Off the Crimea and in the western parts of the sea it rises to 150–200, in a few zones even to 300 mg/m³. In the region of the Crimean coast this increase results from the inflow of food materials from the Sea of Azov, and there may be an effect of a vertical current. The increase in the western part of the sea depends on the fertilization by the large rivers—the Danube, the Dnieper, and the Bug.

Off the Anatolian coast there is a lowering of the plankton density (100 to 50 mg/m³) on account of the lack of fertilization by rivers. In a narrowly limited area off the Bosporus the plankton content may rise to 300 mg/m³. At the depth level of 150–175 m, most areas are without living plankton, except in the region of the Anatolian coastal current and the hydrographically determined currents in the central and eastern part of the sea, where there is a biomass of less than 25 mg/m³. In limited area, the maximum may be 100 mg/m³.

Whereas there is a strong increase in the plankton in the upper water layers in summer, such seasonal fluctuations level out at greater depths, as shown in Table 15.

Nikitin's results are derived from hauls with the Nansen net. They are accordingly representative for the zooplankton but miss a part of the nannoplankton and microplankton. Morozova-Vodyanitskaya (1941) and Konoplev (1937; 1938) have worked with the sedimentation method (though only for a limited coastal area) and arrive at considerably higher values (Table 16).

Zenkevich (1947) gives an account of investigations by Nikitin (1949) on the total biomass of plankton at various depths for the whole of the pelagic region of the Black Sea.

In the first 25 meters (0–25 m) Nikitin found 2,160,690 metric tons, or 31.1 per cent of the total biomass; the next zone, 25–50 m, contained 1,440,000 tons or 20.7 per cent; at 50–75 m 1,172,880 tons or 17.0 per cent; at 75–100 m, 774,984 tons or 11.2 per cent; at 100–125 m, 767,776 or 12.5 per cent; at 125–150 m. there was 453,276 tons or 6.5 per cent of the total biomass. In the lowest depth zone, from 150–175 m, there was 67,108 tons, or only 1 per cent of the total biomass.

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TABLE 16.—*Plankton abundances per m³ in the Black Sea comparing the net hauls by Nikitin with counts by Morozova-Vodyanitskaya and Konoplev (sedimentation method)*

From Zenkevich (1947)

	(a) Batum Bay			(b) Odessa Bay	(c) Sevastopol Bay
	September 1933–1934 (average) Nikitin net haul	September 1939 Morozova-Vodyanitskaya net haul	September 1939 Morozova-Vodyanitskaya Sediment.	September 1935 Konoplev Sediment.	August 1938 Morozova-Vodyanitskaya Sediment.
Phytoplankton					
Diatomeae	15,369	31,920	39,515,000	3,272,000	8,665,000
Peridineae	804	3,280	8,390,000	4,300,000	45,405,000
Silicoflagellata	58	80	1,645,000		583,000
Total	16,231	35,280	49,550,000	7,572,000	54,653,000
Zooplankton					
Copepoda (adult)	3,270	7,776	43,000	19,000	54,653,000
Copepoda (naupl.)	675	5,184	217,000	18,000	
Others	3,595	800	360,000	662,000	
Total	7,540	13,760	620,000	699,000	
Zoo-Phytoplankton total	23,771	49,040	50,170,000	8,271,000	

VI. THE BENTHOS

The main problems of the benthos of the Black Sea concern the composition and distribution in depth of the species. These problems are brought together by discussion of the biocoenoses and their distribution.[13] The occurrence of relict forms is dealt with in Section VIII.

PHYTOBENTHOS

The most important recent works on the Russian coasts are those of Morozova-Vodyanitskaya (1927; 1936a; 1936b; 1936c; 1937; 1941) and of Zinova (1934) for the region of Novorossiisk; the work of Celan (1935) is most important for the Rumanian region; and the papers of Petkow (1905; 1919; 1932) deal with the Bulgarian area.

Among the green algae, the most important are *Chaetomorpha chlorotica*, *Enteromorpha intestinalis*, certain species of *Cladophora*, and *Ulva lactuca*; the important brown algae are *Cystoseira barbata* and *Scytosiphon lamentarius*; the significant red algae are *Phyllophora rubens* var. *nervosa*, *Ceramium rubrum* and *C. diaphanum*, *Polysiphonia subulifera*, *variegata*, *elongata*, and *opaca*, and *Laurencia obtusa*. The

[13] In addition, summarizing my own investigations, I have attempted to review the faunistic data from Russian, Rumanian, and Bulgarian sources, and to bring the nomenclature into agreement. For certain species this is impossible without re-identification of the original specimens, and in these cases the names applied by the authors in question have been used.

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TABLE 17.—*Species composition of the algal floras of the Mediterranean, Black Sea, and Sea of Azov*

After Morozova-Vodyantskaya and Volkov, from Zenkevich (1947)

	Mediterranean		Black Sea		Sea of Azov	
	Genera	Species	Genera	Species	Genera	Species
Green Algae	27	63	23	54	7	10
Brown Algae	56	93	41	64	3	4
Red Algae	126	267	43	103	5	10

complete list of algae includes 221 species, as against 423 species in the Mediterranean. The transition to the Sea of Azov involves a much greater reduction of both genera and species (Table 17).

There are no endemic forms among the algae of the Black Sea, and the flora is accordingly an impoverished Mediterranean one. The size of individuals is reduced. The kelp reaches a length of 10 to 35 cm., and *Cystoseira* grows to 120 cm.

A schematic arrangement of the algae according to depth is:

Meters	
0–2	*Cladophora, Chaetomorpha*
0–23	*Cystoseira barbata*
4–35	*Gracilaria, Polysiphonia elongata, Zanardinia*
25–35	*Phyllophora rubens*

There are also meadows of eelgrass, especially in the northwestern part of the sea, where extensive stands of *Zostera marina* and *Zostera nana* occur on sandy clay bottom at 0.5–6 m. (Fig. 25). According to Russian calculations, the biomass may reach 4 kg/m² in that area; the average is 1.5 kg/m². Vodyanitsky (1941) estimated the total eelgrass biomass of Karkinitsky Bay at 200,000 tons and the total biomass of the Black Sea as a million metric tons. In addition to the more extensive meadows, eelgrasses colonize bays and sheltered stretches of coast, as in Varna Bay (Caspers, 1951a). In some places the eelgrass is intermixed with *Ruppia* and *Potamogeton*. In some areas, a few *Zostera* plants may grow as deep as 15–20 m.

The red alga *Phyllophora rubens* var. *nervosa* is also quantitatively significant. It occurs on all coasts of the Black Sea, but especially in the northwestern region, where it inhabits an area of 10,000 km² (Fig. 25). Zernov called this the Phyllophora Sea. The biomass of *Phyllophora* amounts to 1.7 kg/m², but in special cases may rise to 13 kg. The total biomass of this region may be estimated at 10 million tons. Yakubova (1935) believes that these areas are now displaced southward, as compared with Zernov's picture, so that the principal occurrence now lies at depths of 40–65 m, in a zone otherwise very little grown with algae. Zenkevich (1947) believes that this is the greatest occurrence of macrophytes in all seas.[14] Borcea (1927) states that the

[14] K. Meier (1937) suggests that the masses of *Phyllophora* have been concentrated in that region by the currents and have accumulated on the bottom. His comparison with the Sargasso Sea seems forced. In any case, the dense algal growth has arisen here in place by vegetative growth. The deepest fields (below 30 m) must certainly owe their origin to the action of currents.

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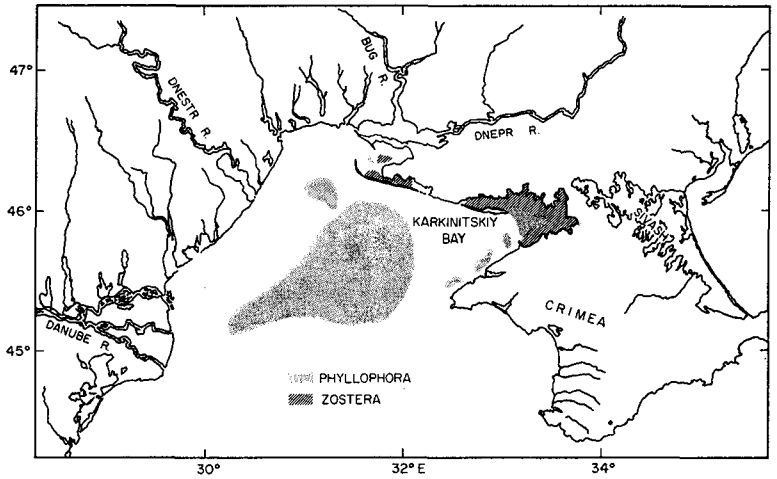

FIGURE 25.—*Distribution of* Zostera *and* Phyllophora *meadows in the northwestern part of the Black Sea*
From Morozova-Vodyanitskaya, after Zenkevich (1947)

predominant algae in the extensive fields off the Rumanian coast are *Dictyota*, *Enteromorpha*, *Ectocarpus*, *Nemalion*, *Delesseria*, *Callithamnion*, and *Padina pavonia* (Teodoresco, 1907; Celan, 1935). The principal growth on the rocks to a depth of 4 m in Varna Bay is formed by *Cystoseira*. It is accompanied by extensive fields of *Dictyota*. For a list of the algae in the region *see* Caspers (1951a, 25–26).

ZOOBENTHOS

There is also a strong reduction in species of the zoobenthos as compared with the corresponding fauna in the Mediterranean. A number of groups are absent, and only a few representatives of others have penetrated to the Black Sea (Table 18). There is a still greater and pronounced reduction from the Black Sea to the Sea of Azov.

After the opening of the Bosporus (*see* Section I), only euryhaline species could enter the Black Sea or maintain themselves there. Zenkevich (1938a) notes that a large number of the invertebrates of the Black Sea are hypertonic in relation to the water in which they live. It is true that a whole series of stenohaline species from the Mediterranean now enter the Black Sea via the Bosporus current. These include *Sternaspis scutata*, *Virgularia mirabilis*, *Ophiothrix echinata*, and *Cyclonassa brisinai* (Nikitin, 1931). They maintain themselves, however, only in a limited area in the vicinity of the Black Sea opening of the Bosporus. More extended dispersal into the Black Sea is prevented by the rapid transition to reduced salinity in the surface water. Ostroumov (1893; 1896a; 1896b; 1896c) showed that the upper 20 m of the Bosporus waters have the fauna of the Black Sea, whereas the deeper zone contains a fauna determined by the inflowing Mediterranean water. On the shore of the Bosporus he found 60 species that also occur in the Black Sea. Of 153 Mediterranean bivalves, there are 103 in the Sea of Marmara at the entrance to the Bosporus, 86 in the upper Bosporus, and 56 in the Black Sea.

Near the Princes Islands in the Sea of Marmara, Demir (1954b) dredged 417 species of invertebrate bottom animals (macrofauna), of which a number occur within the

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TABLE 18.—*Comparison of Zoobenthos in Mediterranean and Black Sea*

	Mediterranean	Black Sea	% of species Bl. Sea to Med.
Planuloidea	10	?	?
Porifera	>110	42	<40
Coelenterata	192	43	15
Hydrozoa	109	35	38
Schyphozoa	36	3	8
Anthozoa	47	5	11
Ctenophora	16	1	6
Platyhelminthes	279	152	55
Nemertea	65	18	28
Nematoda	156	84	15
Kinorhyncha	17	9	53
Acanthocephala	25	5	20
Gephyrea	29	1	3
Annelida	516	126	24
Arthropoda	1201	286	24
Ostracoda	125	25	20
Copepoda	304	77	25
Cirripedia	43	4	9
Cladocera	5	6	120
Leptostraca	2	0	—
Amphipoda	223	70	31
Isopoda	159	32	20
Cumacea	22	12	55
Schizopoda	40	22	55
Decapoda	251	35	14
Pantopoda	27	3	10
Mollusca	1457	125	9
Amphineura	22	2	9
Scaphopoda	14	0	—
Gastropoda	965	74	8
Pteropoda	26	0	—
Pelecypoda	358	49	14
Cephalopoda	72	0	—
Tentaculata ("Molluscoidea")	341	14	4
Phoronida	1	1	100
Bryozoa	306	12	4
Kamptozoa	11	1	9
Brachiopoda	23	0	—
Enteropneusta	3	0	—
Echinoderma	100	2	2
Crinoidea	4	0	—
Asteroidea	24	0	—
Ophiuroidea	21	1	5
Echinoidea	21	0	—
Holothurioidea	30	1	3
Chaetognatha	6	2	3
Tunicata	200	16	8
Acrania	1	1	100
Vertebrata	557	184	33
Pisces	549	180	33
Reptilia	3	0	—
Mammalia	5	4	80
Totals	5281	1111	Ave. 21

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Bosporus itself. Further collections should add to this list. Caspers made quantitative bottom-fauna studies in the Bosporus current and found that the great bulk of the Mediterranean fauna reached its limit of distribution there. The salinity of the deep current of the Bosporus should make possible penetration into the Bosporus, but the strong current does not permit fine sediment to settle, and the coarse sand and mussel bottom is not a good environment for most of the Mediterranean bottom organisms. A rich Mediterranean benthos occurs in small basins where fine sediment settles. In the Golden Horn, a side arm of the Bosporus near the city of Istanbul, there are dense *Cardium* communities in the soft mud of the front zones; in the back regions the influence of the city is evidenced by oxygen deficiency and disappearance of the fauna (Caspers 1957 Ms).

At the present time the forms of Mediterranean origin are most abundant in both species and individuals. Accompanying them is a relict fauna of special zoogeographic interest (Section VIII). There is an extensive literature concerning the extent of the differentiation of the forms in the Black Sea derived from the Mediterranean. Sovinsky (1904) lists 194 out of 680 immigrants from the Mediterranean that exhibit taxonomic distinctness in the Black Sea populations. A large number of these are fishes, which have been intensively investigated with special reference to such distinctions. It appears that taxonomic subdivision has been carried too far in many cases.

Pora (1938a; 1938b; 1938c; 1938d; 1939) has experimented with the physiological capacity for resistance to salinity variation in Black Sea animals. He showed that a large number of the forms of Mediteranean origin are so adjusted to the salinity conditions along the Rumanian coast that they could no longer live in sea water of 35 ‰ salinity. Thus the mysid *Gastrosaccus sanctus* has its optimum at about 18 ‰ and dies if suddenly placed in water of 35 ‰. *Palaemon squilla*, in the Rumanian area, lives at 8–20 ‰. *Balanus improvisus* can live in salinities as low as 3 ‰ (Pora and Rosca, 1955). *Nereis diversicolor* withstands reductions from 24 to 13 ‰ (Pora and Rosca, 1944; 1952).[15] Among fishes, *Trachurus* withstands 15–24 ‰, juveniles 18–26 ‰ (Pora *et al.*, 1952); *Syngnathus nigricollis*, *S. typhla*, and *Hippocampus* live in water of 9–27 ‰. Fishes of the Black Sea are in general highly euryhaline (Pora and Pora, 1950). *Blennius* and *Crenilabrus*, fishes of Mediterranean origin, are adapted to 19 ‰ on the Rumanian coast; *Crenilabrus* in this region withstands 14–23 ‰, *Blennius* 14–30 ‰ (Pora and Stefan, 1952). Pora believes that there must be a number of physiological races of such species. The amphipod *Pontogammarus maeoticus* is found in both fresh and salt water; the fresh-water individuals are smaller, those in the Black Sea live at salinities from 5 to 20 ‰. *Pachygrapsus* seems to be a rather new entrant into the Black Sea. This crab has spread almost everywhere and is absent only off the mouth of the Danube and in the northwesternmost parts of the sea. It withstands salinities from 10 to 30 ‰.

The lower limit of colonization of the bottom is related to the hydrographic factors and differs accordingly in the different regions of the sea (Fig. 26). There are broad parallels with the extent in depth of the living plankton. Off the west coast this limit is at 125 m, in the northwestern region at 115–124 m, off the Crimea it is at 127–135 m, off the Caucasus at 135–165 m, and off the south coast at 130–135 m. Off the Bosporus, and only there, the limit drops to 170–200 m, but this is over an area of only 2900 km^2. In this region Caspers (1957, Ms) found benthic animals at 210 m in H_2S-free mud, the deepest record for such animals in the Black Sea. The

[15] *N. diversicolor* occurs in the Baltic at salinities of 2.66–6.21‰ (R. I. Smith, Biol. Bull. vol. 108, no. 3, pp. 326–345, 1955).

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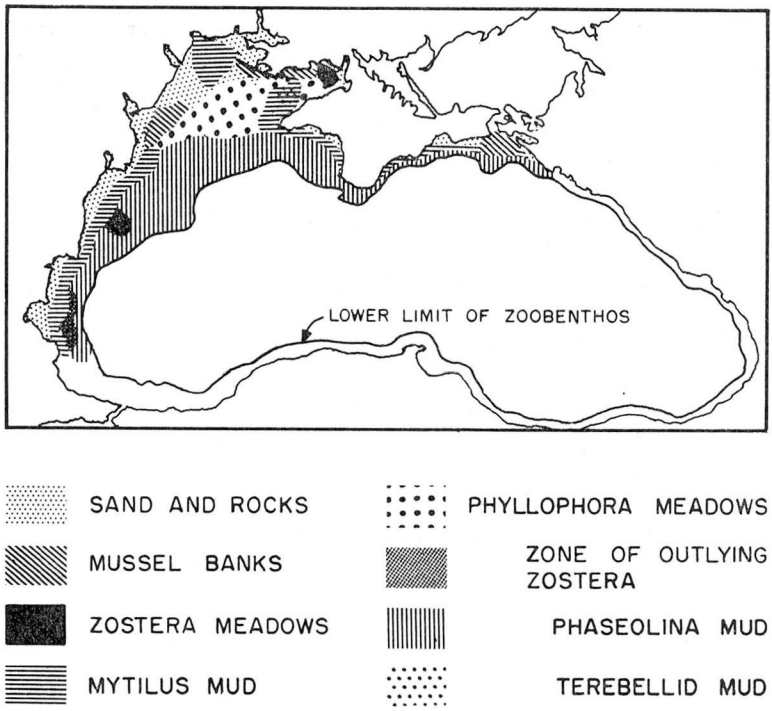

FIGURE 26.—*Distribution of benthic complexes in the northern Black Sea*
According to Zernov (1913); lower limit of benthos in the Black Sea, after Nikitin.

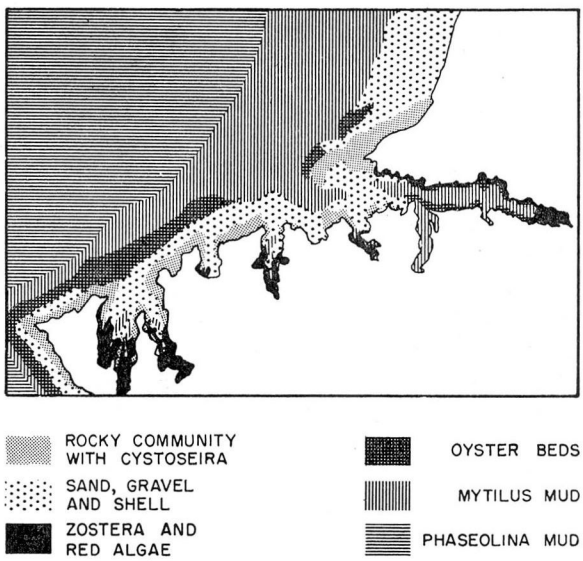

FIGURE 27.—*Distribution of bottom biocoenoses in the vicinity of Sebastopol*
According to Zernov (1913)

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greatest area is in the northwest, where it covers 57,600 km². Along the steep coasts elsewhere the inhabitable benthic zone is small. The total inhabited benthic region is 95,300 km², which is little more than 23 per cent of the total area.

The lower limits of distribution of species that extend below 100 m is as follows (Yakubova, 1935):

to 125 m *Eugyra adriatica, Suberites domuncula*
to 130 m *Terebillides stroemi*
Syndosmya alba, Cardium simile, Mytilus gallo provincialis, Phoronis
to 160 m *Nephtys hombergi*
Cerianthus vestitus
Melinna palmata
to 165 m *Amphiura chiajei* (*-Stepanova*)
to 180 m *Modiolus phaseolinus*

The first quantitative study of the benthic communities was made by Zernov (1913). He subdivided the benthos in the northwest, and his investigations form the basis for all subsequent faunistic studies (Figs. 26–27). The writer's arrangement, diverging somewhat from that of Zernov, is as follows:

1. The strand zone
2. Shallow zones with sand or rock bottom adjacent to the coast
3. Ooze zones close to shore
4. *Zostera* meadows
5. Bivalve reefs
6. *Phyllophora* meadows
7. The outlying areas of *Zostera*
8. The phaseolinid ooze
9. The terebellid ooze

These zones or formations are first characterized faunistically, followed by an attempt at a biocoenotic arrangement according to the available bonitations.

1. Strand Zone

There are long stretches of rocky coast in the Black Sea. The spray zone of such areas is grown with *Scytosiphon Ceramium, Enteromorpha, Corallina*, and other algae, with *Bangia* and *Ralfsia* at the highest level. The upper zone is inhabited by *Littorina neritoides* and *Patella pontica*. There is a fairly continuous zone of barnacles, mostly *Chthamalus stellatus*. Among decapod Crustacea *Pachygrapsus marmoratus* predominates, followed by *Eriphia spinifrons*. At the water level there is a *Mytilus* zone, frequently intermixed with corallines. Zernov notes that on the Russian coast the sessile rock fauna of the intertidal zone dies off to a great extent in the fall, including all the *Mytilus*, whose empty shells are later torn loose by the storms. These are renewed in the spring. Rocky coast appears on the Bulgarian shores at the end of the Balkan range, at Cape Emine, and at the south (Caspers, 1951a). At these places, including Varna Bay and Cape Kaliakra, there is a broad zone of *Chthamalus stellatus* with *Balanus improvisus*.

At some places there may be enormous numbers of *Spirorbis* tubes among the rocks, with coarse sand at the bottom, overgrown by *Enteromorpha*. In the pools are many Isopoda (*Sphaeroma pulchellum*), small polychaetes (*Grubea clavata*), various nematodes, many copepods (*Parastenhelia forficula litoralis, Mesochra heldti, Nitrocra typica*), together with amphipods (*Corophium bonelli*). The amphipod *Hyale prevosti* and the copepod *Tisbe dilatata* were found on the lower sides of small stones on the bottoms of the pools. Above the barnacle zone there are numerous small *Littorina neritoides*. In the dry crevices above the spray zone there are great numbers of the isopod *Ligia italica*. On the sides turned away from the waves, in hollows and crevices, the rocks of the surf zone have a growth of filamentous algae, which grows more luxuriantly at especially protected places and acquires a cushionlike character. The thickness of these cushions is conditioned on one hand by the locality and on the other by the time of year. They are reduced in winter, but their fauna declines as early as fall in some places. In fall the cushion growth is also frequently overgrown with *Enteromorpha*. Sedentary polychaetes do not contribute to the formation of these cushions, and their deposit of ooze is correspondingly less. Nevertheless, as these algal pads develop, a rich "infauna", consisting primarily of copepods, mainly harpactoids, but

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also including amphipods, ostracods, mites, etc., inhabits them. Within these algal cushions there are the interwoven byssus threads of small mussels (*Mytilus gallo-provincialis* and *M. minimus*). In the intertidal zone of the Bulgarian coast they reach a length of at most 1 cm and are then replaced by smaller ones, from the extensive colonies below low-water level; large specimens develop only in deeper waters.

The development of these algal cushions is weaker on the rock coast of South Bulgaria than farther north. There is a strong growth of algae, but the deposit of mud, on account of the strong surf, develops at only a few places. The south Bulgarian infauna is accordingly distinctly less rich in individuals; the number of species seems to be even greater than that of Varna Bay. The tangle of algae beneath the water is inhabited by numerous prawns (*Leander squilla* var. *elegans*), with *Diogenes pugilator*, and with hosts of small individuals of *Pachygrapsus marmoratus*. An interesting element of the fauna of the algal tangle in the intertidal zone consists of chironomid larvae, especially *Clunio marinus* (Caspers 1951d), together with *Trichocladius vitripennis* and *Thalassomyia frauenfeldi*.

Wooden piles are attacked by *Teredo* and *Limnoria*. *Teredo* causes considerable damage along the Russian coast. Piles are thickly encrusted externally with sponges (especially *Halichondria*), barnacles, and *Mytilus*, with dense growths of the tunicate *Botryllus*. In contrast with the Mediterranean, *Bugula* and *Spirographis* are absent. *Cione*, in further contrast with the Mediterranean, is limited to deeper water. Zernov reports the vagile worms found between the clumps of *Mytilus* on piles as nereids, *Phyllodoce*, *Eulalia*, together with the elongate nemertean *Emplectonema gracilis* (= *Eunemertes gracilis*).

The sandy and gravelly shore has been investigated in the Bulgarian region by Caspers (1951a; 1951b) and on the Crimean coast by Mokievsky (1949). A fauna extremely rich in individuals appears in the spray zone. On the Bulgarian coast the dominant creature in these stretches of sand, present in enormous numbers, is the amphipod *Orchestia bottae* (with the addition of *O. gammarella* and *O. montagui*). The population varies with the extent of the beach and the amount of moisture in the sand. In south Bulgaria there is an additional species, *Talorchestia brito*. The damp sand is the habitat of a number of salt-tolerant beetles, with *Bembidium varium* in first place, followed by other species of *Bembidium*, species of *Cafius* and *Troglophaeus*, and the tenebrionid *Phaleria bimaculata*. The "pill bug" *Sphaeroma pulchellum* occurs in the damp sand zone. The dry sand beach is inhabited by tiger beetles, spiders, and ants (for example *Formica rufibarbis* and *Myrmecocystis viaticus*), some of which penetrate the spray zone. The land isopods (for example *Porcellio lamellatus*) live on the dry sand. The beach dunes have a rich insect fauna, exemplified at Mesemvria on the Bulgarian coast (Caspers, 1951b).

There is a rich community of *Donacilla* (a bivalve) and the beach worm *Ophelia* in the sublittoral sand on the Crimean coast; the abundant amphipod of these sands is *Pontogammarus*. The supralittoral fauna is similar to that reported by Caspers.

The beach reptiles of this zone are worthy of mention. On the dry beach of the Bulgarian coast one finds *Lacerta muralis* and *L. viridis* in search of insects. The water snake *Natrix tessellata* was observed actually in the sea (Caspers, 1915b). Popovici (1936b) reported a sea turtle *Caretta caretta* from Cape Kaliakra, undoubtedly a specimen that had wandered in from the Mediterranean.

2. Coastal Shallow Zone with Sand or Rock Bottom

The shore zone, ecologically characterized by shallow water, usually extends to about 15 meters, in places to 28. In bays the extent of the area with sand bottom is usually limited to a few meters, since mud deposits begin at a relatively high level. This is the benthic zone richest in species of any marine habitat, associated with the variety of the bottom and with an adequate supply of oxygen.

The rocks beneath the water are usually thickly beset with the mussel *Mytilus galloprovincialis*, intermixed with *Cystoseira*, *Ulva*, and *Enteromorpha*. This growth provides cover for various snails (*Rissoa*, *Nassa reticulata*, and *Trochus*); crustaceans (*Xantho rivulosus*, *Hippolyte varians*, *Leander squilla*, with amphipods and isopods); and polychaetes. Growths of sponges, hydrozoans, and bryozoans (especially *Membranipora*) are present.

In the Varna Bay rock bottom extends to depths of 6–10 meters (Fig. 30). For a description of the fauna of this bay, *see* Caspers (1951a). Off the Rumanian coast rocky reefs may extend 500 to 1000 m seaward to depths of 10 to 20 m. Borcea (1927b) reports their fauna as entirely like that of the rocks near shore.

The sand zones vary in the degree to which they are inhabited according to the grain size and the amount of admixture of detritus. The coarsest sands, subject to the strongest displacement, are referred to by Zernov as *Saccocirrus* sands, from the archiannelid *Saccocirrus papillocercus*, with which *Protodrilus flavocapitatus* may be associated. In general these coarse sands are inhabited by vagile worms, such as turbellarians (*Procerodes lobata*, *Cercyra papillosa*), polychaetes (*Nerine*, *Spio ornatus*), nemertines (*Lineus lacteus*, *Eunemertes gracilis*, *Borlasia vivipara*), and nematodes. Among Crustacea, amphipods and hermit crabs (*Diogenes varians*) and in some places isopods (*Sphaeroma*, *Idothea*) may be abundant. The gastropods, including *Nassa reticulata* and *Rissoa*, occur in the coarse sand community in the Bay of Varna.

In certain places in the Black Sea there are typical *Polygordius* and *Amphioxus* sands, with *Polygordius ponticus* and *Branchiostoma lanceolata*. *Branchiostoma lanceolata* occurs extensively at depths from 5 to 30 m off the Crimean coast. Zernov (1913, p. 74 ff.) describes Amphioxus sands in the region of Sebastopol and from a few places off South Crimea, where it occurs with *Polygordius*, *Ophelia*, *Glycera*, *Synapta*, and *Ammodytes*. *Branchiostoma* is rare on the Bulgarian coast and has been reported only from the bays of Varna and Burgas (Caspers, 1951a).

The bivalves reported from the fine sands of the Russian region are: *Cardium*, *Syndosmya*, *Loripes*, *Venus gallina*, *Gouldia minima*, *Divaricella divaricata*, *Merethrix rudis*, *Calyptraea chinensis*, *Mactrasubtruncata*, *Tapes proclivis*, *Mytilus galloprovincialis*, and *Cardium exiguum*. The most abundant crustacean is *Portunus holsatus*. It cannot be discerned how much admixture of mud is present. In Varna Bay the hard fine sand, present at depths of 3 to 10m, is characterized by the mass development of the little bivalve *Corbula mediterranea*, though the population varies with depth and time of year. Other bivalves include *Divaricella divaricata*, *Angulus exiguus*, *Abra ovata*, *Cardium exiguum*, and the less abundant *Pecten glaber*. *Nassa neritea* is the common snail. Among polychaetes, *Nepthys* is abundant, but *Nerenides tridentata* is especially characteristic. A similar fauna is described from the Rumanian coast, at 6 to 15 m depth, by Borcea (1927b). He states that the crustacean *Portunus arcuatus* is especially abundant.

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3. Mud Zones near Shore

The mud zones of the shallower waters near the coast, with more or less admixture of fine sand, constitute this category. These muds are rich in detritus, lie between depths of 15 to 25 m, with a rich development of the contained fauna. The most important mollusks are *Cardium*, *Syndosmya*, *Loripes*, and *Nassa*. The most characteristic forms are the decapod *Upogebia litoralis* and the polychaete *Melinna palmata*. Both forms vary strongly in numbers, but are regularly present everywhere in this mud zone. In Varna Bay (Capsers, 1951a) the polychaetes *Nereis*, *Nephthys*, and *Glycera* are represented, together with *Capitella capitata*. The hermit crab *Diogenes*, living mainly in shells of *Nassa*, occurs with *Brachynotus lucasi* and *Portunus depuratur*, and with amphipods. Borcea (1927b) reports that stretches of sandy mud are sacrce off the Rumanian coast. They are colonized by *Cardium*, with *Syndesmya*, *Nereis*, and *Pectinaria*. *Upogebia* is abundant at depths of 8 to 15 m (Popovici, 1940b). This crustacean may be killed out in masses by severe low temperatures in extreme winters, when they are washed ashore by storms in great numbers, in part still alive, together with *Cardium*, and *Mytilus* (Borcea, 1929; Popovici, 1940a).

4. The *Zostera* Meadows

The extensive eelgrass meadows in bays and other sheltered areas harbor a characteristic benthic fauna. Zernov emphasizes the presence of masses of mysids, amphipods, isopods, shrimps, needle fishes (and other fishes). *Rissoa*, *Cerithiolum*, *Tergipes*, and *Trochus* are present in great numbers. The turbellarian fauna is rich. *Lepralia* and *Membranipora* encrust the leaves. The bottom mud is inhabited by amphiurans, *Rhynchobolus*, *Upogebia*, and *Callianassa*. Zernov reports *Syndosmya* and *Cardium* as especially abundant, together with the polychaetes *Nereis*, *Nephthys*, *Glycera*, *Arenicola*, and *Pectinaria*. Borcea (1927b) reports only isolated areas of eelgrass along the Rumanian coast. For details of the fauna *see* Motas (1938).

In eelgrass meadows in Varna Bay there were considerable variations in the amounts of *Zostera*, which are strongly reflected in the fauna (Caspers, 1951a). In dense stands of *Zostera* the bottom is so filled with the network of roots that the amount of animal life is reduced. *Upogebia*, for example, is unable to dig its burrows. Decay reduces the oxygen in the substrata. In intermediate zones with less-developed stands of *Zostera*, and in years with a less flourishing growth in general, the endobiosis is sharply increased and resembles that of the mud areas without *Zostera* at corresponding depths.

5. Bivalve Reefs

As Zernov shows, reefs are formed by bivalves in depths at which the force of currents is so reduced that sand is not deposited, while adequate detritus and plankton is still brought in. In quiet bays such banks may develop even at the depth of 8 m. On open coasts they may extend down to 65 m. There are some extensive reefs, for example off the Ukrainian and Crimean coasts (Figs. 26–27). In general there are four regions: off the Kerch Peninsula; from Tarhankut to Bakkala; off the coast at Tendrovsk; and off the mouth of the Danube. As a rule these banks are formed by *Mytilus*, with an admixture of varying numbers of oysters (*Ostrea edulis*, varieties *sublamellosa* and *taurica*). Zenkevich points out that *Mytilus* banks occur to a greater depth in the Black Sea than in any other part of the world. A special form, *Mytilus galloprovincialis* var. *frequens*, has been described for the Black Sea populations. Borcea (1927a, 1931a) describes the *Mytilus* banks off the Rumanian coast as lying at a depth of 20 to 25 m., occasionally extending downward to 65 m. Nechaev (1936) has described these banks off the Bulgarian coast. Broken into a few larger and several smaller banks, they occur in the region of the "Devil's Current" at 30 to 40 m, extending at some points to 90 m, and in this region overlie the mud zone. The fauna of the bivalve banks on the Rumanian coast is described by Borcea (1927a; 1928; 1931a).

There are banks on which the oyster component is sufficiently predominant to permit economic use. Such oyster banks occur off the Kerch Peninsula and off Sebastopol. Like the reefs composed mainly of *Mytilus*, these oyster banks are also overgrown with *Phyllophora*. Off the Bulgarian coast *Ostrea* develops considerable banks in the Bay of Burgas (Nechaev and Chernev, 1940–1941b). Nikitin (1934a) describes an oyster bank in the Eastern Black Sea at Gudaut, at depths from 10 to 30 m. On this bank *Ostrea* composes about 17%, *Mytilus* 47%, *Pecten ponticus* 19%, and *Modiola adriatica* 17%. Nikitin gives a list of the species that live with and upon the bivalves. The forms associated with the oyster banks off the Crimea are enumerated by Zernov. In addition to *Mytilus*, *Pecten*, and *Modiola*, there are *Tapes rugatus*, *Venus gallina*, *Cardium edule*, *C. exiguum*, *Meretrix rudis*, *Calyptraea chinensis*, *Nassa reticulata*, *Gouldia minima*. Of crustaceans there are *Porcellana*, *Athanas*, *Portunus*, *Diogenes*, and *Balanus improvisus*. Then there are many polychaetes (with the tubes of *Centrocorone*, *Vermilia*, and *Pomatoceros*), sponges (various species; *Spongilia*, with *Reniera* and *Petrosia*, shells are often bored by *Clione*), bryozoans (*Lepralia* and *Membranipora*), hydroids, and *Phoronis*. Considered quantitatively as well as qualitatively, these *Ostrea-Mytilus* banks appear to be the richest zones of the Black Sea benthos.

A soft mud, in which shell is embedded, lies between the *Mytilus* banks. Such bottom extends downward to depths of 48 to 55 m in the open sea, and has a rather rich infauna. Zernov lists as characteristic animals the mollusks *Cardium simile*, *Meretrix rudis*, *Tapes*; the polychaetes *Melinna palmata* and *Terebellides stroemi*; and the echinoderm *Amphiura*. The surface life is composed of large colonies of hydrozoans (*Sertularia polyzonias*) and ascidians (*Ascidiella aspersa*, *Ciona intestinalis*, *Botryllus schlosseri*, and *Eugyra adriatica*). Among crustaceans, *Crangon crangon* is abundant. As Zernov remarks, this *Mytilus* mud extends upward to the shallow zones, to 9–11 m, even to 1 m in the Bay of Odessa. At such places it is identical with the zone characterized above as inshore mud bottom, in which *Melinna* is characteristic together with *Cardium* and *Upogebia*.

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6. *Phyllophora* Meadows

Phyllophora meadows (Fig. 25) form benthic areas dominated by rooted algae, interspersed among the *Mytilus* muds. The fauna of these areas is poor. Crustaceans dominate the fauna, with amphipods, isopods, and *Portunus arcuatus*. For the Rumanian coasts Borcea reports (1927): *Portunus, Terebellides, Syndosmya, Cardium, Modiola, Cerithiolum, Trophonopsis*, and *Retusa*.

7. Zone of Deposited *Zostera*

Areas of deposited *Zostera* are found mainly in bays, at depths of 35 to 45 m, in which the large *Zostera* complexes are developed. Their boundaries are ill-defined and variable. Zernov names as abundant amphipods, mysids, decapods' mollusks, and turbellarians.

8. *Phaseolina* Muds

The *Phaseolina* mud is the deepest zone of benthic life in the Black Sea. It begins in association with the bivalve banks of depths of 55 to 65 m. In some places it may begin at no more than 40 m. The extreme depth to which this zone extends is from 180 to 185 m. The most characteristic faunal element is the bivalve *Modiolus phaseolinus*. Zernov interprets this form as a northern type, rare in the Mediterranean, where it appears to be a relict (See Yakubova, 1948). The remaining animals of this zone are less characteristic; they tend to be euryokous mud-dwelling forms, which accordingly are present also in the shallow-water muds. Borcea (1936b) emphasizes the fact that the animals of this zone are mainly small forms, such as *Syndosmya alba, Cardium simile, C. exiguum*, and *Trophon breviatus*.

BIOCOENOTIC CLASSIFICATION OF THE BENTHOS

The basis for a biocoenotic classification is supplied by Zernov's descriptive classification on the one hand and on the other by Caspers' biocoenotic arrangement of the elements on the Bay of Varna and along the Bulgarian coast (1951a; 1951b). According to the data available, the main faunistic subdivisions in the Black Sea appear to be relatively uniform, so that a general regional and biocoenotic arrangement seems justified. A general discussion of the classification of the marine benthos appears in Chapter 17; *see* also Caspers (1950a). The names derived from the substrate are followed by those of index forms.

A. The Shore Community—the Pachygrapsus Biocoenosis. (The intertidal and Spray Zones, equal to Zernov's Strand Zone)
   a. The Enteromorpha—Idotea Zone. Secondary index forms are the isopods *Idotea* and *Sphaeroma*, the polychaete *Fabriciola*, and larvae of tendipedids.
   b. Surf Zone—*Chthamalus*
   c. Spray Zone—*Littorina-Ligia* variation
   d. Sand beach Zone—*Orchestia variation*
      Secondary index forms are the amphipods of the genus *Orchestia*, halophilic staphylinid beetles (*e.g.*, *Cafius xantholoma*) and other kelp beetles and flies.

B. The Sand Community—The *Venus gallina* and *Corbula* Biocoenosis
   a. Find sands with *Corbula*, *Venus gallina*, and the polychaete *Nerinides*
   b. Coarse sands
      1. *Saccocirrus* sand, with *S. papillocercus*, *Protodrilus*, and *Nerine*
      2. *Amphioxus* sand, with *Branchiostoma*
      3. *Polygordius* sand, with *P. ponticus*
      4. *Sabellaria* sand (with colonies also on rock)

C. The Mud Community—The *Melinna* Biocoenosis
   a. Shallow sand-mud zones, the *Upogebia* variation
   b. The Phytobenthal variation
      1. *Zostera* meadows
      2. *Phyllophora* meadows
   c. The Epibiotic variation, the *Mytilus-Ostrea* banks
      1. *Mytilus* banks
      2. *Ostrea* banks
   d. Deep-sea mud. The *Modiolus phaseolinus* variation

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The shore community is clearly marked throughout its extent, and its ecological characterization is also distinct. *Pachygrapsus* ideally fulfills the requirements for an index form of primary rank. It is present in great numbers from the rock crevices under water to the highest points on the rock, but is absent in deeper water. In the sand-beach community it is present among algae and beneath the drift material cast on the beach. This zone is small in vertical extent, since the Black Sea is essentially without tides. The variations b, c, and d are contrasted with the *Enteromorpha-Idotea* zone as "moist zones". They have many forms in common, such as the apterygote *Anurida*. In the sand-beach variation index forms of secondary importance are the terrestrial halophilic species (*cf.* Caspers, 1951a; 1951b).

The sand community is quite sharply distinguished on the one hand from the strand community and on the other from that of the mud. Index forms, however, are less easily designated. The terminology is derived from the writer's studies in the Bay of Varna. Suitable *quantitative* evaluations are not yet available for other regions. Zernov's *Saccocirrus*, *Amphioxus*, and *Polygordius* sands are grouped together as coarse sands. It is with some reservations that the *Sabellaria* colonies are placed with the sand communities, since they depend on the sand element for their origin. In the Bay of Varna they were restricted to rock bottom at depths of 6–10 m, but they also colonize hard sand.

These two communities are developed in shallow water. The mud community extends vertically over a much more extended zone, down to the lower limit of existence of life. A review of the sampling of the mud zone shows relatively little variation in its living component. The primary index form, the polychaete *Melinna*, adequately characterizes the community as a whole. The zones closer to shore, with a larger component of sand, have as a secondary index form the decapod *Upogebia*. The *Zostera* and *Phyllophora* meadows, discussed in detail by Zernov, are referred to as "phytobenthal variations" and arranged with the mud community. This variation is raised from the substrate by the development of the plant growth, which forms the feeding ground for a rich fauna of epibiotic animals. As the fauna of the Bay of Varna (Caspers, 1951a) is shown, the endobiotic fauna beneath the plant growth is reduced though it is developed in its typical form in interspersed areas free from plant growth.

The most difficult question of arrangement involves the placing of the shell banks in the mud community, especially as the concept of the biocoenosis was developed by Moebius in 1877 on the basis of studies of the oyster banks in the North Sea. The shell banks are everywhere intermixed with mud, and their development is ecologically so closely connected with the surrounding mud zone, from which a host of vagile forms enters the banks, that for the larger classification from the biocoenotic aspect this seems to be the best solution. Their characterization as an epibiotic variation seems to convey the typical nature of these banks.

The geographical distribution of these communities is indicated in Zernov's maps, Figure 26 for the Black Sea as a whole and Figure 27 for the region near Sebastopol; Figure 28 shows their distribution in Varna Bay.

VII. THE LIMANS AND THE COASTAL LAGOONS (including the Sea of Azov)

The limans of the Black Sea region are the drowned estuaries of rivers. Their present-day connections with the sea vary greatly, according to situation and current,

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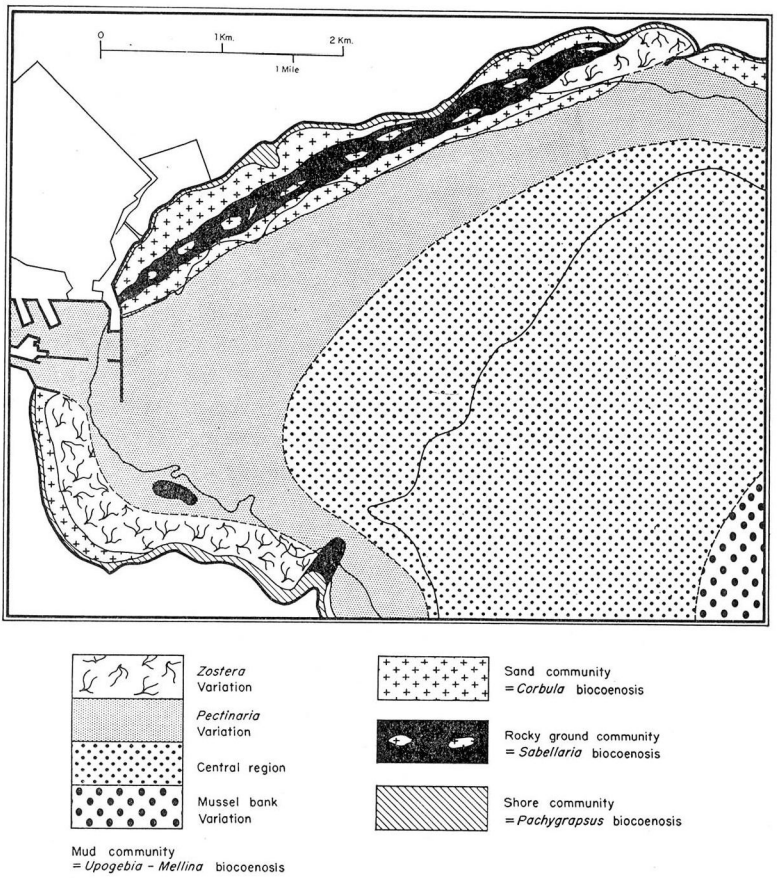

FIGURE 28.—*Distribution of principal bottom communities in Varna Bay* Caspers, (1951a)

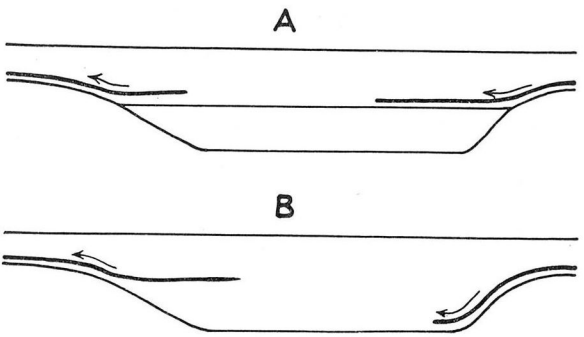

FIGURE 29.—*Schematic diagram of influx of salt water from the Black Sea into Varna Lake* *A*, in summer; *B*, in winter. From Valkanov (1942) and Caspers (1951a).

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and have been subject to variation in the most recent geological times. Only a small number of the limans have been well investigated biologically. One of the best-known examples is Varna Lake, on the Bulgarian coast, which is described in detail elsewhere (Caspers, 1951a). The limans are of especial interest as refuges for relict elements of the Sarmatian fauna (Section VIII).

The Sea of Azov is in many respects like the true limans and is discussed in Section 5 below.

1. BULGARIAN COASTAL LIMANS AND LAGOONS

a) Varna Lake (Fig. 31)

This liman, formerly called Djevinski Liman and for a few recent years known as Stalin Lake, lies north of the Balkan Mountain range and represents a former extension of the Gulf of Varna. It belongs to the Provadia, and Devna river system, which has other lakes farther inland, some of them now silted up or dried out. Varna Lake is an elongate oval 14.7 km long, with a greatest depth of 11.5 m. After a period in which the liman was broadly connected with the sea, it was cut off about 3000 years ago by a sand bar that is still growing. This barrier almost completely separated it from the Black Sea, and the water level reached a height of +1.40 m. The building of a navigable canal in 1907 again equalized the level of water in liman and sea and permitted a renewed inflow of salt water. Since that time the liman has been a catohaline basin, in which the surface salinity varies from 7 to 10.5‰, and the bottom from 11 to 15‰.

The inflow of fresh water is 4 m³/sec. in the shallow western part of the lagoon, which lowers the salinity as much as 2–5.‰ The influx of water from the sea that compensates for outflow and evaporation flows to the deepest zones of the basin and to the western area in winter, whereas in summer and autumn the salt water flows in over the denser water at the bottom and occupies a zone between 8 and 10 m (Fig. 29). Thus a mesohaline stratification is formed, which is upset only in late fall. In the winter there is complete isohalinity below 14 m (between 12.3–13.4‰; 14.6‰). The summer stratification strongly affects the temperature, which may be up to 28.9°C. at the surface, and only 7.5° at the bottom. With the spring stagnation, the bottom water is considerably lowered in oxygen content at greater depths, so that by July there is no oxygen below 14 m. In September–October the lower limit for oxygen is 8–9 m (Fig. 30), and hydrogen sulfide occurs in the whole of the deeper basin below 10–12 m.

Most of the limnetic plankton of the inflowing surface water dies out at a concentration of 7‰ Cl. The dinoflagellates *Gonyaulax polyedra, Prorocentrum micans, Dinophysis sacculus, Peridinium divergens, Ceratium furca,* regarded by Stundl (1937) as typical brackish-water forms, are distributed through the entire liman. *Synedra acus* and *Biddulphia* extend into the eastern part from the sea. In general, the populations are reduced toward Varna Bay. In the middle of the liman diatoms predominate in March, Cyanophycea in April, and Chlorophycea and green Flagellata in July (Paspalev, 1942). There are two phytoplankton maxima during the year, the first in March, the second at the beginning of September. Whereas the early peak is produced by the increase in diatoms, all the groups of phytoplankton are involved in the later maximum, and there appears to be no relation with salinity and temperature changes, as was the case in Varna Bay. Paspalev explains this as the result of the stagnation of the deeper waters, of the strongly increased temperature, and of the freshening of the water in summer, which produces a strong current. The plankton is absent in the deep zone, where there is stagnation and hydrogen sulfide accumulation in summer. Thus there is a reduction of the total mass of plankton as only the species of the upper layers can undergo mass development in summer. The oxybiontic plankton of the upper zone is replaced in the deeper zone in summer by sapropelic ciliates, and these enter the higher-water layers with the rise of the upper level of the H_2S zone; individual species react distinctively to the partial pressures of H_2S and O_2 and accordingly exhibit zonation (Valkanov, 1941–1942). Oxybiont plankton is brought in

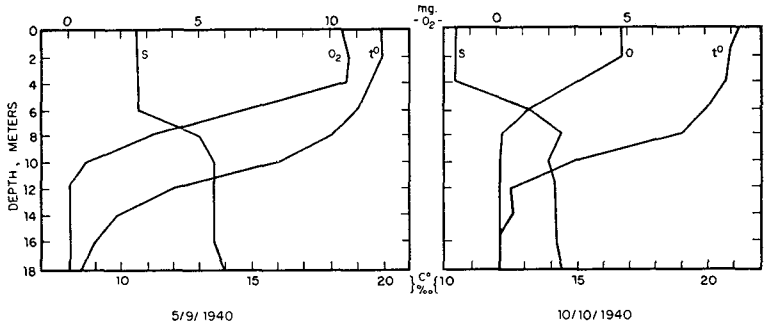

FIGURE 30.—*Salinity, temperature, and oxygen from 0 to 18 meters in the middle part of Varna Lake* From Paspalev (1942) and Caspers (1951a)

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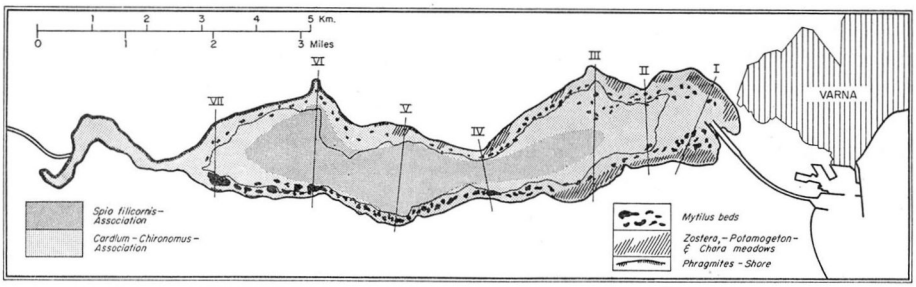

FIGURE 31.—*Chart of bottom associations in Varna Lake*
Caspers, (1951a)

by the bottom current, so that there may be a vertical alternation of oxybiont and saproplankton.

The bottom of the liman is covered in the main by a very soft mud, filled with organic remains. Only a narrow bordering strip, down to 10 m depth, is covered with sand, of which the grain size has been determined (Caspers, 1951a). From summer to late fall the mud is permeated by hydrogen sulfide.

The bottom communities of Varna Lake are indicated in Figure 31. The shallow zones above the level of the summer thermocline are covered by extensive beds of *Mytilus galloprovincialis*, and associated organisms are also very dense colonies of *Cardium edule*.

Because of the rich food supply and abundant oxygen the bottom of the connecting canal to the sea supports a dense population of bivalves. These colonies vary from place to place and from year to year, according to the supply of larvae in the stage for attachment. The western extension of the liman is avoided by *Mytilus*, *Cardium*, and other marine bivalves, and there the dominant animals are chironomid larvae, cf. *Chironomus salinarius*. These appear throughout the basin in shallow water, but

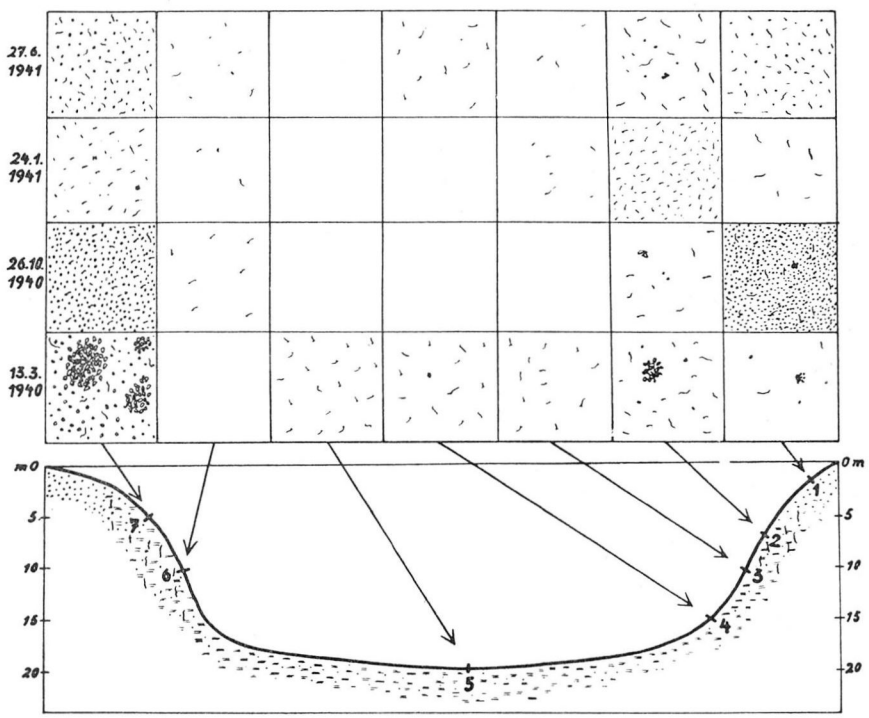

FIGURE 32.—*Profile of the narrowest part of Varna Lake*
Showing seven bottom-sampling stations (1/10m²), with contents of the samples at the indicated dates, of section IV of Figure 31. (Caspers, 1951a)

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their abundance increases with reduction in salinity. In the westernmost part of the lagoon there are also larvae of cf. *Chironomus halophilus*.

Zostera meadows are present in the eastern portion of the liman, with a rich fauna that includes *Idotea baltica*, *Sphaeroma pulchellum*, *Gammarus locusta*, and *Nereis succinea*, with *Membranipora pilosa* and *Balanus improvisus* on the leaves. *Hippocampus* and ascidians, characteristic of the bay, do not enter the liman, and the bivalve fauna, especially *Cardium*, is strongly reduced in the middle section. In the middle section of the liman there are *Potamogeton* and *Chara* meadows.

The Phragmites strip broadens toward the west. Most of the algae are from the sea; they include *Dictyota* and *Enteromorpha*. The fresh-water chlorophycean *Tetraspora explanata* is most dense in the western section, but extends into the middle section and there overlies the strongly H_2S-filled muck at median depths.

The polychaete *Nereis succinea* ranges into the deep zone where there is only a weak concentration of H_2S; it is also present in the brackish western section, where it is associated with *Nephthys hombergi*. The spionid *Spio filicornis* has a special place in the liman, for it is the characteristic form in the H_2S-filled deep zone. In late spring the entire deep zone is occupied; this population disappears in median depths in summer and fall (Fig. 32). Whereas this polychaete is very rare in the muddy zones of the Gulf, it reaches a concentration of 45 per .1 m^2 in the liman.

In general marine forms now predominate over those of fresh water in the liman, both in numbers of species and of individuals. Caspers (1951a) characterizes the faunal community, in relation to the classification of the biocoenoses of the Varna Bay, as the *"Chironomus"—Spio filicornis* variation of the muck community of the Gulf. Because of the extreme conditions presented by the liman, the index forms *Melinna* and *Upogebia* (of the bay) are excluded.

Typical Sarmation relicts are absent in Varna Lake, since it was too long separated from the sea and had been completely a body of fresh water for some time.

b) Other Bulgarian Coastal Lagoons

The remaining lagoons on the Bulgarian coast are mostly not true limans. All are characterized by having a narrow connection with the sea. Very few of them have been studied.

Mandra Lagoon, a few km southwest of Burgas, has been investigated by Nechaev and Chernev (1937c). This is a long narrow basin of only 5 m maximum depth. Connection with the sea is by means of two natural canals, about 30 m long, through which salt water is driven into the basin when the wind is from the east. The salinity then rises to 15.7‰. During periods of west winds the lagoon becomes almost fresh. The fish fauna is composed of fresh-water and salt-water species. *Cyprinus carpio* withstands a salinity of 13‰. *Lucioperca sandra* and mullets are additional forms of economic importance.

Anchialo Lagoon (= Lake Pomorie) is almost completely separated from the sea. Salt water filters in through a sand barrier, and by evaporation the lagoon becomes hypersaline, reaching a concentration of 83‰. After the melting of the snow in spring, the salinity falls below 36.5‰. A periodically opened canal permits the entry of mullets (especially *Mugil auratus*), which thrive in spite of the high salinity (Nechaev and Chernev, 1938; Caspers, 1952). Salt manufacturing is carried on adjacent to the lagoon, and the connection with the sea is kept closed for most of the year to avoid lowering of the salinity.

c) Bulgarian Marine Salt Works (Salterns)

The salterns north of Burgas at Solnitzi and Anchialo (in addition to those at Pomorie) occupy a total of 2,422,000 sq m and have been in operation from antiquity. The salinity is first increased to about 90‰ in shallow basins, and the further concentration and crystallization of common salt is by evaporation from adjacent connecting evaporation flats. The residual solution, with potassium and magnesium salts, has fresh stocks of water of high salinity added to it from the fore tanks. The salt is promptly removed, to protect it from rain. The first stage of evaporation is carried out in tanks of 100 to 200 sq m with a depth of 20 to 30 cm, and these afford a favorable environment for halobiontic species (Caspers, 1952).

The open water of these ponds is inhabited by *Artemia salina*, and there are various parallels with the hypersaline part of the Sivash Lagoon on the west coast of the Sea of Azov (Chapter 23). The massively developed clumps of *Cladophora glomerata* on the borders of the ponds at Anchialo contain vast numbers of larvae and pupae of the salt fly *Ephydra macellaria*; the transformed flies keep strictly to the borders of the salt ponds. Larvae of *Eristalis* and of chironomids are present (*Halliella caspersi*, Strenzke, 1950, and *Chironomus salinarius*, Kieff). The hydrophiid beetle *Paracymus aeneus* and the dytiscids *Deronectes cerisyi*, *Enochrus bicolor*, and *Ochthebius* have been found, and copepods and nematodes are present (Caspers, 1952). The maximum biomass is reached at salinity of 70 to 90‰. At 280‰ only *Halliella* and *Ephydra* larvae and *Artemia* remain. In general, the fauna is identical with that of highly saline pools of the Mediterranean coast. Coastal forms of the Black Sea enter the hypersaline pools only in small proportions; *Gammarus locusta* goes farthest, but even it dies out at 50‰ salinity. The Black Sea fauna is, in general, adapted to lower salinity, and even its euryhaline forms do not range as widely as various Mediterranean forms. The hypersaline salt-work tanks are accordingly colonized by highly specialized Mediterranean elements, species that have had their origin elsewhere and have then spread—by means unknown—to the exact habitats to which they are adjusted.

2. RUMANIAN LIMANS

Detailed studies of the biology of the Rumanian coastal lagoons have been presented by Bujor (1900; 1904; 1912; 1928). There are in all 28 such bodies of water, among them 11 near the mouth of the Dniester, 4 near Tulcea, 6 near Constanza, and 4 near Caliacra. All seem to be true limans. They were formerly in open connection with the sea, as attested by numerous remains of bivalves.

The largest of these lagoons are the Sasic (or Conduc), with 20,350 ha, and the Razelm with 23,406 (1 hectare = 2.47 acres). Both are connected with the sea by a canal. The best-studied lagoon is the Tekirghiol, with an extent of 1270 ha and a greatest depth of 10 m. It is separated from the sea by a narrow strip of dune. The bottom of this

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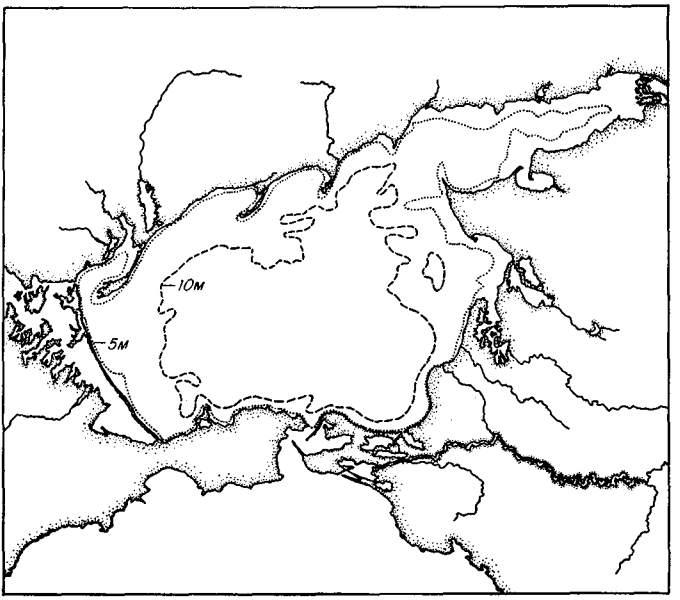

FIGURE 33.—*Chart of the Sea of Azov*
With 5- and 10-meter depth contours; 1 inch = 09.70 miles. From Knipovich

lagoon consists of a black muck that contains H_2S. The organic material originates mainly from the floating branches of *Cladophora cristallina*.[16]

Like the Tekirghiol, most of the other lagoons are hypersaline. The fauna is characterized by the mass development of *Artemia salina*. *Gammarus locusta* and *Orchestia littoria* are the principal amphipods in the clumps of algae (*see* Bujor, 1928, for complete list). Bujor gives an account also of the sulfur bacteria of the liman-bottom muck.

3. RUSSIAN LIMANS[17] (for the Sivash, *See* Chapter 23)

The animal life of the salt-lake limans at Odessa has been studied by Buchinsky (1897a; 1897b; 1900) for the lagoons of Chadjikej and Kujalnitzkij. At times their salt content is very high, and with its increase faunal impoverishment proceeds by stages. In general, the fauna varies greatly in both species composition and numbers of individuals. The crustaceans, especially *Artemia salina*, withstand the highest salt concentrations. (Chernovsky, 1949) describes the mass appearance of the chironomid *Halliella taurica* in the salt lakes of the southern Crimea.

Lubyanov (1953) provides a faunal review of certain coastal lagoons of the southeastern Ukraine, which are characterized by Caspian elements. These shallow bodies, which are to be regarded to some extent as relict lakes, with depths usually from 2 to 6 m, maximally 12 m, are now fresh, with strong H_2S formation in summer (pH 8.0–8.6). Lubyanov characterizes the fauna as a "liman-Black Sea complex of Caspian type," reckoning 17 species as Caspian (Section VIII).

4. SEA OF AZOV

Since the Sea of Azov is of especial importance for its fisheries, there is an exhaustive Russian literature devoted to it. The writer's summary is based upon Zenkevich (1947).

The Sea of Azov is a shallow basin connected with the Black Sea by the Strait of Kerch (Fig. 33). Its hydrography is controlled by the inflowing waters of the Don. The elongated estuary of the Don, the Bay of Taganrog, forms a liman in the northeastern part of the Sea. Farther southeast the Kuban enters. The Sea of Azov occupies a total area of 37,600 sq km, of which the Bay of Taganrog amounts to 5640 sq km. On the western coast is an extensive area of shallow bordering swamps, the Sivash, of 2630 sq km. The greatest depth of the sea is 13.2 m, the average depth 7.2 m, 4–7 m in the Bay of Taganrog; 50.2 per cent of the area has a depth greater than 10 m, 42.7 per cent a depth of 5 to 10 m.

There is a continuous current from the Bay of Taganrog to the Strait of Kerch. Knipovich (1932) has demonstrated, in addition, a circular current along the coasts. The annual inflow of fresh water amounts to 56.4 cubic km, 28.5 from the Don, 11.0 from the Kuban, 14.78, a fourth of the total, from surface rainfall. The surplus water flows through the Straight of Kerch into the Black Sea. However, a deep

[16] May this be the same as *Cladophora glomerata* reported from the Bulgarian salt works?

[17] The complete literature on the Russian limans has not been available to the writer.

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TABLE 19.—*Salinity (‰) in the Sea of Azov*
After Knipovich, from Zenkevich (1947)

Depth	Taganrog Bay			Sea of Azov	
	East	West	Central	Kossa Berdynskaya-Kossa Obitochna	Ostrov Biryuchii
0 m mean	0.29	6.73	10.66	9.85	10.35
max.	1.65	10.34	10.70	11.20	10.70
min.	0.009	1.94	8.89	7.59	9.78
5 m mean	—	7.57	10.79	9.99	10.39
max.	—	11.28	12.50	11.28	10.70
min.	—	5.16	8.93	8.82	9.80
Bottom mean	0.43	7.72	11.42	9.98	10.41
max.	1.67	11.28	15.07	11.29	10.70
min.	0.045	5.37	9.85	9.06	9.96

counter current brings salt water into the Azov basin from the Black Sea. The exact relations of the water equilibrium in this respect are not known, especially as there is considerable seasonal variation.

The average salinity of the Sea of Azov is 11.2‰; opposite the Strait of Kerch, it is 17.5‰ at the bottom, essentially that of the northern Black Sea. The greatest salinity occurs in winter, followed by a rapid decrease in spring with the melting of the snow. In the eastern part of Taganrog Bay the water may be nearly fresh; in the western part the salinity is 4–5‰ (Table 19).

There is a wide annual range of water temperature in the Sea of Azov. Extensive areas are often covered by ice in winter, and the bottom temperature is then +1.67°C (salinity 6‰). In severe winters the ice may last 4 to 5 months, with a thickness of 9 to 10 cm. The summer average temperature is 11.28°C. in the Bay of Taganrog, and 12.4° at Temryuk. The highest summer temperature at Taganrog is 29.6°C. Cooling in the fall is often very rapid, and homothermy then usually develops. The oxygen content is usually adequate in the upper water layer. During the periods of rapid development of phytoplankton it undergoes a significant increase of from 92–114 per cent. An oxygen deficit may develop in the water near the bottom from the consumption of the organic muck deposits and on account of the high summer temperatures (may be August). When the weather is calm the oxygen content near the bottom may fall almost to 0 in many areas.

There may be, correspondingly, an enormous concentration of bacteria in certain bottom zones. *Desulfovibrio aestuarii* reaches a concentration of 56 millions per gram of bottom. This is accompanied by considerable poisoning of the bottom by H_2S during the summer months. Nitrates are found in considerable amounts beginning in August. In September–October they amount to 30 mg/m³; in November to 90 mg/m³; and in the Bay of Taganrog to 150–200 mg/m³. This supply is then completely consumed by the phytoplankton production in spring and falls to 8 mg/m³ in the Bay of Taganrog. The ammonia content may rise to 100 mg/m³ after the phytoplankton bloom dies out. Phosphates are present in relatively small amounts; they are periodically almost used up in the surface zones. The amounts in the southern area, from spring to July, are 4–12 mg/m³, in September–October as much as 40 mg/m³, and reduce in November–December to 9 mg/m³. Near the bottom, the amount is 30 mg/m³ in spring, up to 200–300 mg/m³ in July, and reduced to 40–50 mg/m³ in August.

With continuing temperature stratification the bottom fauna is killed out by oxygen deficiency over wide areas of the bottom. Large amounts of nitrates and phosphates are then stored up, and these do not become available until fall, when the vertical circulation again makes them available for organic growth. The quantities of these nutrient salts are associated with the rapid growth of plankton.

The sediments in the Sea of Azov are quite uniformly distributed. In the central region and in the deeper parts of the Taganrog Bay there is a fine clayey muck (more than 50 per cent of less than 0.01 mm. particles), whereas near the shores a larger amount of sand is mixed with the muck, and the amount less than 0.01 mm. may drop to 30 per cent. In the deepest zone, below 3.5–4.5 m, the soft muck contains large numbers of ostracod shells. Mordukhai-Boltovskoi (1937) estimates the number of living ostracods in those area at 50,000 to 100,000 per square meter.

Phytoplankton

The phytoplankton varies considerably during the year, but changes in zooplankton are less conspicuous (Fig. 34).

Usachev (1927) enumerated 183 species of phytoplankton, of which 22 undergo mass development. The biomass consists mainly of diatoms (55%) and peridineans (41.2%). The Cyanophyceae may amount to 13% in summer, but only from 4% to 2% in the yearly average. Diatom growth has a maximum in spring (March–April), with *Skeletonema costatum* and the species of *Coscinodiscus*, amounting to 7 g/m³, and a smaller one of 2 g/m³ in the fall (October–November) produced by *Rhizosolenia calcar-avis*, *Leptocylindrus danicus*, *Ditylium brightwelli*, *Skeletonema costatum*, *Thalassionema nitzschioides*, *Thalassiosira nana*, and various species of *Chaetoceras* and *Coscinodiscus*. The diatoms produce 90–98% of the biomass in the phytoplankton, and there is sometimes an enormous development of diatoms. Usachev determined the biomass in October 1924

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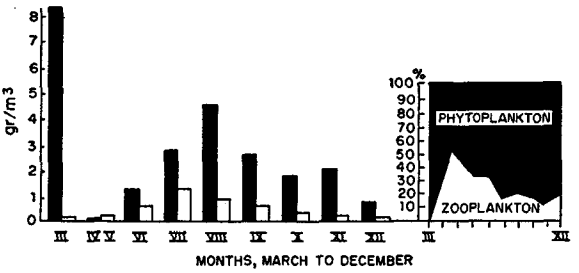

FIGURE 34.—*Comparative abundance of phyto- and zooplankton at various times of the year in the Sea of Azov*
From Okul, after Zenkevich (1947)

TABLE 20.—*Plankton stratification in the Sea of Azov and Bay of Taganrog, June 6, 1924*
After Usachev (1927)

Sea of Azov			Bay of Taganrog		
	0 m	5 m		0 m	5 m
Thalassiosira nana	300,000	5,300,000	*Aphanizomenon* and *Anabaena* chains	500,000	21,000
Prorocentrum micans	12,000	11,000	*Microcystis* colonies	300,000	18,000
Other dinoflagellates	171,000	304,000	Diatoms Chaetoceras, etc.	248,000	310,000

as 106 g/m³ and in August 1925 as 270 g/m³, consisting almost entirely of *Rhizosolenia calcar-avis*. The summer maximum of the peridineans of 3.5 g/m³ is produced mainly by *Exuviella cordata, Gonyaulax polyedra, G. tricantha, Prorocentrum micans, Peridinium knipowitschi*, and others. *Volvox* and green algae appear mostly in the most strongly freshened areas. The phytoplankton biomass in summer in Taganrog Bay is determined by *Microcystis* and *Aphanizomenon* (up to 85–93%). In general, there are no periods of nutrient salt deficits in the Sea of Azov, because of the shallow water and the rapidity of mineralization (Knipovich, 1932).

A well-developed stratification of the plankton is indicated by the abundance of certain index forms (Table 20).

There may be 5.5 million chains of *Aphanizomenon* in a cubic meter, each chain consisting of 100 to 150 cells; the combined count of dinoflagellates and diatoms may be as high as 4,500,000 per cubic meter.

Zooplankton

According to Pauli (1927), there are 155 species in the zooplankton, to which must be added the larvae of benthic animals. Pauli arranges the zooplankton as follows:

I. Euxinian relicts; these are especially in Taganrog Bay. They include *Evadne trigona, Cercopages pengoi, Heterocope caspia, Calanipeda aquae dulcis* and others.
II. Mediterranean immigrants; these are mainly copepods: *Acartia clausi, Paracartia latisetosa, Centropages kröyeri, Labidocera brunescens*, and *Oithona nana*. The tintinnids are *Tintinnopsis menneri, T. parvula, T. tubulosa*, and *Leprotintinnus bolnicus*. There is one cladoceran, *Podon polyphemoides*.
III. The fresh-water cladocerans and rotifers in the fresh water areas: *Leptodora, Asplanchna*, and others.

Special mass development is shown by *Calanipeda aquae dulcis, Evadne trigona, Brachionus bakeri, B. mülleri*, and *Pedalion oxyuris*. In the outer parts of Taganrog Bay *Heterocope* and *Cercopagis* appear in masses, as do rotifers, cladocerans, and cyclopids in the inner region where the water is most completely fresh.

The biomass of the zooplankton is calculated by Mordukhai-Boltovskoi (1938) and Okul (1940), (Fig. 35). The leading role is played by *Acartia clausi, Paracartia latisetosa, Centropages kroyeri*, and *Calanipeda aquae dulcis*, which forms may compose more than 50% of the biomass; in the Taganrog Bay, with *Calanipeda* especially, up to 70% (1500 mg/m³). The maximum for the copepods is in July–August; *Paracartia* and *Centropages* are limited to the summer months. In June cirripede larvae compose 42% of the zoo-biomass. Tintinnids may have a larger share, amounting to 9.6%, in July to 16.8%, of the total zooplankton. There may be 50,000,000 specimens in a cubic meter of water (= 1 g.). Barnacle larvae and tintinnids are fewer in the Bay of Tagonrog. The rotifers *Brachionus mülleri, Synchaeta, Pierodina, Pedalion oxyuris* form 25% of the zooplankton biomass, and up to 80–90% in spring. Purely fresh-water forms like *Anuraea cochlearis, A. aculeata, Triarthra longiseta*, and others are contributed from the Bay of Taganrog. Mollusk larvae are present in the Sea of Azov through most of the year. They compose 14.5% of the zooplankton biomass in June, amounting to 94 mg/m³. The mysid *Macropsis slabberi* has 152 mg of mass in a water column of 1 m², and in Taganrog Bay this rises to 1835 mg. *Mesomysis helleri* reaches 57 mg; and in Taganrog Bay *Mesomysis kowalewskyi* has 254 in the same space.

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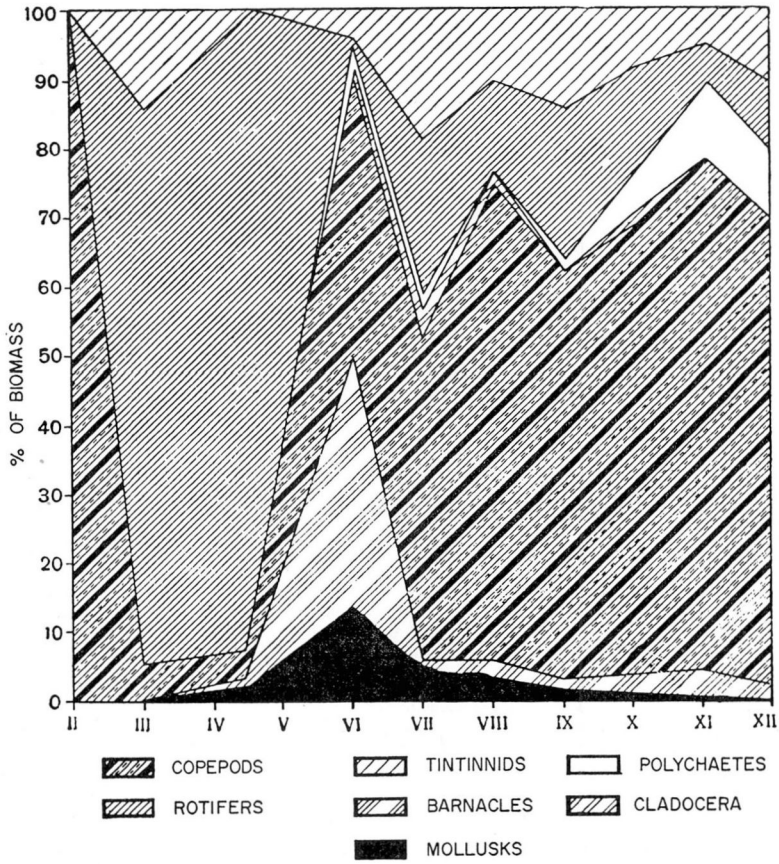

FIGURE 35.—*Yearly changes in the biomass of zooplankton groups in the Sea of Azov (in per cent)* From Okul, after Zenkevich (1947)

Benthos

Benthic algae occupy only a narrow strip of coast. The most widely distributed red algae are *Ceramium diaphanum, Polysiphonia opaca, P. spinosa;* of the green algae *Enteromorpha* and *Cladophora* are most widespread. Other plants are *Zostera marina, Z. nana, Zanichellia palustria,* and *Potamogeton marinus,* but they do not occur in large masses.

The zoobenthos thus far known consists of 128 species; the arthropods predominate in numbers of species, the mollusks in biomass (Table 21).

The general aspect of the fauna of the Sea of Azov is that of a reduced Black Sea fauna, in correspondence with the extreme hydrographic features. Zenkevich points out that certain Mediterranean forms exhibit mass development in the Sea of Azov. To these are to be added the relict forms. These, according to Mordukhai-Boltovskoi and Vorob'ev (cited from Zenkevich), are: *Dreissena, Monodacna, Hypaniola,* and a few species of *Corophium* and *Pontogammarus.* The Mediterranean elements are *Cardium, Syndosmya, Mytilaster, Corbula, Hydrobia, Balanus, Nereis, Sphaeroma,* and *Pectinaria.* The principal distribution of the more important elements and the total biomass are shown in figure 36.

The bottom fauna of the Sea of Azov is divided by Russian scientists into seven communities or "Complexes" (these do not exactly correspond to the biocoenoses of Figure 36, which includes two facies of the Cardium Complex, No. 5):

Community 1: *Dreissena polymorpha* and *Monodacna colorata,* with the unionids *Unio pictorum, U. tumidus,* and *Pseudanodonta complanata* (No. 6 in Fig. 36). These bivalves occur in the most nearly salt-free areas, in the inner part of Taganrog Bay, and in part off the mouth of the Don. The biomass amounts to 13 g/m², of which 11.6 g are of *Dreissena.*

Other forms in these areas are the cumaceans *Pterocuma sowinskyi, Stenocuma tenuicauda,* and *Schizorhynchus* sp.; the mysids *Metamysis strauchi* and *Mesomysis kowalewskyi;* the amphipods *Corophium curvispinum, Pontogammarus abbreviatus,* and *Gmelina* sp., together with tubificids and

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TABLE 21.—*Zoobenthos in the Sea of Azov*
Numbers of individuals and average biomass per m². After Vorob'ev in Zenkevich (1947)

	Average number of individuals		Average biomass	
	per m²	%	per m² in g.	%
Mollusks	971	6.3	98.50	74.2
Crustaceans	11,345	74.0	15.26	11.6
Worms	1,939	12.6	7.50	5.8
Others	911	7.1	10.74	8.4
Totals	15,166	100.0	132.00	100.0

chironomids. These collateral elements produced 10.7% of the total biomass. In deep water the ostracod *Cyprideis littoralis* is abundant, up to 15,000 specimens per m².

Community 2: *Nereis diversicolor* and Ostracoda (No. 5 in Fig. 36). This faunal group is developed in the southern part ot Taganrog Bay on soft black muck. The average biomass is 9.12 g/m². Fresh-water elements like *Tanypus* larvae and tubificids are reduced. The benthos of the central part of Taganrog Bay is dominated by ostracods, especially *Cyprideis littoralis*, which appear in astonishing numbers. The average number is 40,000/m³ (= 7.6 g, or 58% of the biomass).

In the adjoining liman of Yejsk, tubificids predominate (27.54 g/m²), with ostracods (150,000 m², about 40% of the biomass) and *Corophium volutator* (6000/m², 26% of the biomass). Other forms are *Hypaniola kowalewekyi* (to 40,000/m²), *Nereis diversicolor*, *Balanus improvisus*, *Cardium edule*, and *Monodacna colorata*.

Community 3: *Nereis succinea* (No. 7 in Fig. 36). The *Nereis succinea* formation develops in shallow water close to the shores in the Sea of Azov, where there is a muck bottom. Its distribution is not clearly delimited from the *Cardium—Syndosmya* group. There are strong seasonal variations in the populations, with large increase of size in individuals and numbers toward autumn. According to Russian sources *Cardium* enters this zone from greater depths. The *Nereis* areas are of great importance as feeding grounds for fishes.

Community 4: *Pontogammarus maeoticus*. This relict amphipod may appear at times in the sandy shore zones up to the spray zone, in great numbers when there is a certain amount of admixture of detritus. The populations vary but may amount to 80,000 specimens per m² (642 g/m²). A few *Nereis succinea* are present in this community. In winter these crustaceans move to deeper water

Community 5: *Cardium edule-Syndosmya ovata* (No. 2 of Fig. 36). The *Cardium* beds take up the largest amount of space in the open zones of the Sea of Azov, 10,000 to 12,000 km², where they find favorable conditions for mass development, insofar as they avoid the oxygen-poor depths. Plankton in excess is available to these ciliary feeders. The biomass of *Cardium* may amount to 2 kg/m². The greatest numbers are found at depths of 6–10 m; *Syndosmya* goes somewhat deeper. In very soft muck *Mytilaster* appears. In the sandy shallow zones above 4 m. *Corbula* predominates.

Cardium may live more than 5 years, by which time they have attained a diameter of 21–24 mm. Compared with other regions, their growth is slow, which Zenkevich ascribes to the periodically inadequate supply of oxygen, the reduced salinity, and also to the early sexual maturity that results from the high summer temperature of the water. The writer believes the high density produces biological competition—*i.e.*, competition for space and food among the individuals of *Cardium*, *Mytilaster*, and

TABLE 22.—Cardium edule *communities in the Sea of Azov*
After Zenkevich (1947)

Community	Spring			Autumn		
	No. of species	Biomass g/m²	Average no. individuals	No. of species	Biomass g/m²	Average no. individuals
Cardium—Syndosmya	17	330	3046	25	1100	6408
Cardium—Balanus	15	323	2500	25	558	3276
Cardium—Nereis	15	180	720	25	444	1586
Cardium—Hydrobia	9	87	8106	15	1741	22991
Cardium—Mytilaster	16	256	5640	7	809	6635

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Balanus. Russian zoologists distinguish *Cardium edule* var. *maeotica*, in the Sea of Azov, from var. *picta* in the limans.

Cardium is associated in distinctive ways with other benthic animals, forming several facies or associations (Table 22). The most extensive of these facies is that of *Cardium-Syndosmya* on muck bottom at depths of 8–10 m, where it includes *Mytilaster*, *Balanus*, *Corbula*, *Hydrobia* (with mass increase in autumn), *Nereis*, *Nephthys*, and *Brachynotus*.

In shallower waters (5–8 m.) there are variant facies, *Cardium-Balanus improvisus* and *Cardium-Nereis succinea*. There are also well-defined communities of *Cardium-Hydrobia*, in which up to 15,000 snails may be present on 1 m^2.

The epibiosis produced by *Balanus improvisus* is most richly developed in depths of 6–8 m (No. 4 of Fig. 36). The barnacles form a dense overgrowth on the shells of living and dead bivalves. The population at greater depths is reduced in summer in consequence of the decrease in oxygenation (Table 23).

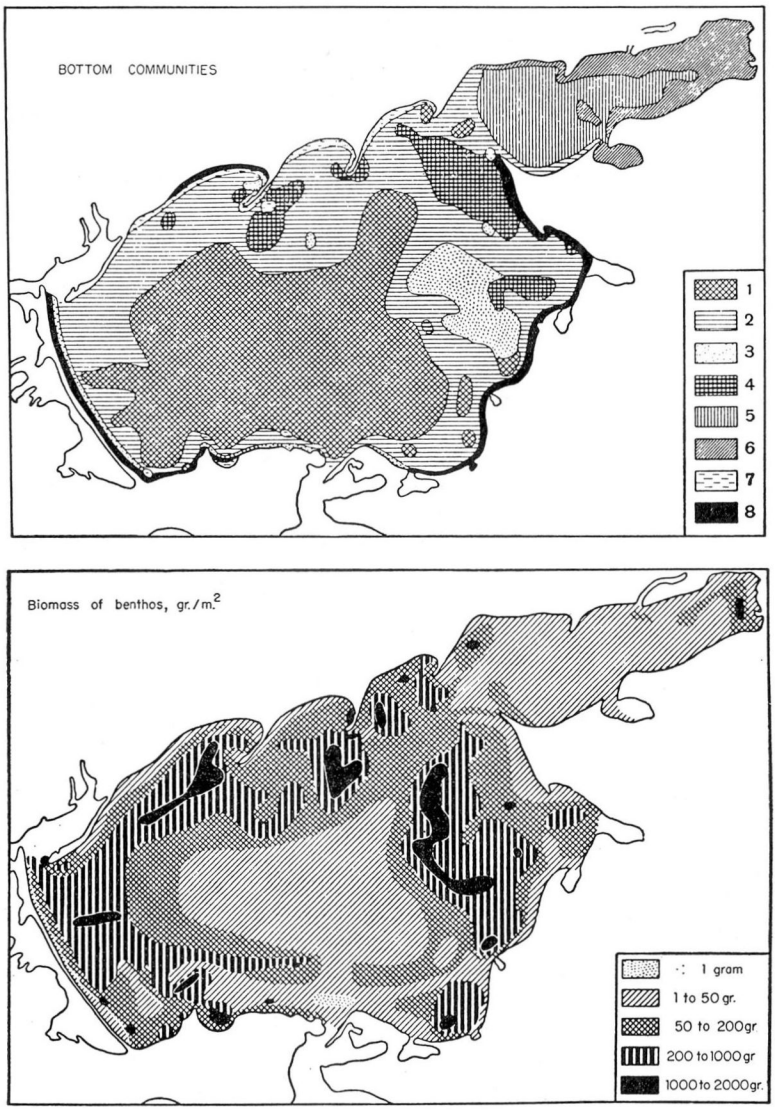

FIGURE 36.—*Distribution of benthic associations in the Sea of Azov*

Upper: Bottom communities in autumn. 1, *Syndosmya-Hydrobia;* 2, *Cardium;* 3, *Mytilaster;* 4, *Balanus;* 5, *Nereis*-Ostracoda; 6, *Monodacna-Dreissena;* 7, *Nereis;* 8, *Corbulomya*

Lower: Biomass of benthos in summer. (From Vorob'ev, after Zenkevich (1947)).

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TABLE 23.—Cardium edule–Hydrobia ventrosa *community in the Sea of Azov*
Average population per m², number of individuals and biomass. After Zenkevich (1947)

	Numbers/m²	Biomass g/m²g.
Cardium edule	467	151.5
Syndesmya ovata	2740	151.3
Hydrobia ventrosa	14321	14.85
Nephthys hombergi	45	1.69
Nereis succinea	54	2.14
Balanus improvisus	30	2.20
Ostracoda	1563	0.16
Corbula maeotica	10	1.46
Others	19	0.96
Total	19249	326.26

The *Cardium-Mytilaster lineatus* community is found in limited areas on hard bottom below a depth of 7–8 m. (No. 3 of Fig. 36). These areas are less muddy and have good oxygenation produced by the current. On the Jelesinki Bank this facies occupies an area of 1470 km². The population is more than twice as large in the fall as in spring, but is in general more constant than the other *Cardium* facies. The spring community consists of 1 year-old (4900/m²) and 2 year-old (375/m²) individuals. In the fall the O-group is added (7800/m²), and the population of 1- and 2-year old individuals is strongly reduced, mainly by fishes (to 2890 + 108/m²). The important associated forms are *Balanus* and *Nereis succinea*, with the amphipod *Ampelisca diadema* and the mollusks *Mytilus galloprovincialis* and *Hydrobia ventrosa*.

Community 6: *Syndosmya ovata* (No. 1 of Fig. 36). This bivalve is next in importance to *Cardium* in the Sea of Azov. It lives on muck and sandy-muck bottom at depths of 1–13 m. The maximum lies below the *Cardium* community, in 10 to 11 m. But in even a muddy sand at 4–6 m, *i.e.*, above the *Cardium* beds, this community is well represented.

Pure *Syndosmya* communities are found below the *Cardium* zone in 11-12 m depth. Whereas *Cardium* drops out, *Hydrobia* is well represented in individuals, and this form predominates in the deepest zones (12–13 m). At 9–10 m *Syndosmya* and *Cardium* are present in about equal numbers. These two bivalves are in rather strong competition for the food supply in this zone.

Syndosmya is very euryhaline. Its densest populations are at 9–12‰ salinity, but it is present in Taganrog Bay where the salinity is 5.5–7‰, and also in the bordering hypersaline lagoons, with salinities up to 55‰. The breeding period extends from the end of April to the end of September, with a June and an August–September maximum of larvae. In their third year these bivalves reach a size of 17–22 mm.

In the central deepest zones of the Sea of Azov (11–13 m) there is a community in which the index forms are *Hydrobia-Nephthys-Syndosmya*. The total number of species amounts only to 16; in addition to *Hydrobia ventrosa*, *Nephthys hombergi*, and *Syndosmya*, the only moderately abundant forms are *Nereis succinea* and *Corbula maeotica*. With the disappearance of oxygen in summer there is a strong reduction in the mollusk populations; *Cardium* is said to emigrate to the shallower waters.

Community 7: *Corbula maeotica*[18] (No. 8 of Fig. 36). The small bivalve designated as *Corbula maeotica* is most abundant at depths of 2–4 m and occurs from 1 to 6 m, when there is clean sand or at least sand with only a little mud in the coastal zones. The number of individuals per m² is high. Other mollusks present are *Cardium edule* (mainly in the deeper areas) and *Syndosmya*, *Mytilaster*, and *Hydrobia*.

Among crustaceans those with considerable numbers are the amphipods *Pontogammarus maeoticus* and *Ampelisca diadema*, the cumacean *Epinöe serrata*,[19] and the isopod *Sphaeroma serrata*. *Nereis succinea* is abundant. In the autumn the numbers of crustaceans and worms increase, and those of *Hydrobia* are reduced.

The same faunal complexes are, in general, encountered in the liman of Utlyutskij. There are in addition many Black Sea species, which are constantly present on account of the higher salinity. Such forms are: *Cerithiolum reticulatum*, *Pectinaria koreni*, *Cardium exiguum*, *Rissoa euxinica*, *R. venusta*, and others.

Biocoenotic Classification

Supplementing the purely descriptive review of the benthos of the Sea of Azov of the Russian authors, the writer attempts a biocoenotic arrangement corresponding to that of the Black Sea, and attempt to relate the faunal types of the two seas.

The special difficulty of such a synecological identifica-

[18] *Corbula (Corbulomya)* is represented in the Black Sea only in certain areas. The form occurring in the Varna Bay was determined by Jaeckel (1954) as *Corbula mediterranea* Costa. Jaeckel doubts the validity of the species *C. maeotica* established for the Black Sea forms by Milashevich. The writer follows current Russian usage, in which these bivalves are designated as *Corbula (Corbulomya) maeotica*.

[19] The form of *Ephinöe serrata* in the Sea of Azov is the variety *maeotica*.

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tion arises from the fact that the species in the Sea of Azov are those that have relatively weak biocoenotic connections (being euryoekous) and are thus unsuitable as index forms of biocoenotic types. Nevertheless, the attempted synecological identification is justified by the common occurrence of many of the species.

1. The shore community.

Pachygrapsus, the characteristic form of this community in the Black Sea, seems to be unrepresented in the Sea of Azov. The Russian authors emphasize the mass occurrence of the amphipod *Pontogammarus maeoticus* in the corresponding shore zone as their complex 4. Thus we may consider this as the index species of the shore community in question in the Sea of Azov, and regard this as an Azov Variation. This is accordingly to be added to the list of variations of the shore community of the Black Sea as:

e. The sandy shore community variation = the *Pontogammarus maeoticus* Variation.

This follows the *Orchestia* Variation of the Black Sea, also characterized by an amphipod.

2. The sand community (= the *Venus-Corbula* biocoenosis of the Black Sea).

This community is distinctly developed in the Sea of Azov in its fine-sand variety and is characterized by the mass development of *Corbula*. *Venus* is wanting. Its distribution corresponds to that of "Complex 7" of the Russian authors. This Azov community facies may be designated as:

c. The Azov fine-sand Variation = the *Corbula maeotica* Variation.

With some reservation a further community of the Sea of Azov may be included in this biocoenosis. This is "Complex 1" of the Russian authors, in the innermost portion of Taganrog Bay. The shallow sandy bottoms of this region of the mouth of the Don support a *Dreissena-Monodacna*-unionid community with associated cumaceans, mysids, amphipods, tubificids, and chironomid larvae. The faunal group involved is determined by the extensive freshening of the region, in which relict forms have a strong share. It may be justified to relate this to the fine-sand biocoenosis of the Black Sea as:

d. The Taganrog-fine-sand Variation = the *Dreissena-Monodacna*-unionid Variation.

3. The mud community (= the *Melinna* biocoenosis of the Black Sea).

The whole of the deep zone of the Sea of Azov must be placed in this biocoenosis. *Melinna* seems to be absent, but we may nevertheless regard the Azov mud fauna as a variation of the *Melinna* biocoenosis of the Black Sea, and thus characterize the Sea of Azov as an impoverished bordering sea of the pontic basin. The four "Variations" set up for this community in the Black Sea cannot be clearly recognized in the Sea of Azov, and its mud community must accordingly be regarded as a further, fifth Variation:

e. Azov Variation = the *Hydrobia ventrosa* Variation.

Hydrobia may be regarded as the index form of the extensive bottom life variation in the Sea of Azov. This snail undergoes mass development and colonizes the deep zones. Complexes 3, 5, and 6 of the Russian scheme are to be included in this category. The differences in abundance of the individual components corresponding to depths and nature of the bottom permit further subdivision, which might well go beyond the "complexes" of the Russian authors.

Another faunistic specialization is exhibited by the mud bottom of Taganrog Bay, "Complex 2" of the Russian arrangement. In it *Nereis diversicolor* plays an important role, but this variation is characterized mainly by ostracods and by *Corophium volutator*. This community may accordingly be designated as the Taganrog Variation of the mud community of the Black Sea.

f. Taganrog-Variation = the *Corophium volutator*-ostracod-*Nereis diversicolor* Variation.

VII. THE SARMATIAN RELICT FAUNA AND MEDITERRANEAN IMMIGRANTS

The Sarmatian fauna, once the richest brackish-water fauna in the world, is represented today by relict forms in the bays and limans of the Black Sea and, especially, in the Caspian Sea. In addition to the brackish forms of the Sarmatian inland sea there was a fresh-water element in weakly saline lagoons and bays. This inland basin was separated into the Black Sea and Aralo-Caspian basins in Mid-Pliocene times. This was followed by the Quaternary connection between the Mediterranean and Black seas and a resulting increase in salinity of the Black Sea. As a result, there was an invasion of Mediterranean forms and a reduction in the original brackish-water fauna, which was forced into weakly saline refuge areas.[20] A number of recent Russian investigators (Birshtein, 1935; 1946; Mordukhai-Boltovskoi, 1939b; 1945; 1946; 1953) consider a series of species occurring in the Sea of Azov and in the Black Sea proper to be of Caspian rather than Sarmatian origin and refer to a "Caspian fauna".

[20] Certain euryhaline Mediterranean fishes apparently entered the Sarmatian Sea at an earlier time, via the Bosporus-Hellespont stream before it became a marine strait. Two species now occurring in the Caspian and Black seas, *Syngnathus nigrolineatus* and *Atherina mochon*, evidently entered from the Mediterranean before the separation of the original Sarmatian basin (Kosswig, 1943).

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FISHES

The zoogeography of the Sarmatian fish fauna is discussed by Kosswig (1943, and later papers). According to Kosswig the Sarmatian element includes a large number of true, anadromous fresh-water fishes that enter the least saline parts of the Black Sea and spawn in rivers and limans (especially the Sea of Azov). The Sarmatian element proper, fishes that live only in the least saline areas and do not occur in the Black Sea, includes the gobies *Caspiosoma*, *Benthophilus*, *Knipowitschia*, and *Mesogobius gymnotrachelus* and *Gobius platyrostris*, and *Percarina*.

Because of the close relation of the region of the Bosporus with the Sarmatian basin before the opening of the Bosporus as a marine strait, the preservation of Sarmatian elements in the nonmarine fauna of fresh and brackish waters of the Bosporus region is to be expected. Kosswig found a surprising wealth of such fishes in northwestern Anatolia; many of these are not endemically Sarmatian but of a wider, Arctogaean distribution. Of 35 species in the fresh waters of northwestern Anatolia, 33 per cent are considered to be Sarmatian, and 12 per cent are more recent immigrants from the Mediterranean:

Sarmatian	Distribution	Mediteranean immigrants	Distribution
Clupeonella muhlisi	L. Apulyont	*Cyprinodon fasciatus*	Eu. side of: Bosporus, Küçük, Çekmece
Caspialosa tanaica	L. Manyas		
Caspialosa maeotica	L. Sapanca	*Syngnathus nigrolineatus*	L. Sapanca, L. Abulyont
Rutilus frisii	L. Iznik	*Blennius fluviatillis*	L. Iznik
Chalcaburneus chalcoides	L. Sapanca		
Pungitus platygaster	Anatolia; Black Sea region		
Proteorhinus marmoratus	L. Iznik, Manyas, Apulyont, Sapanca		
Gobius fluviatilis	L. Manyas, Sapanca		
Gobius melanostomus	L. Sapanca		
Mesogobius gymnotrachelus	L. Sapanca		
Bubyr caucasicus	L. Manyas		

The zoogeography of the fish faunas of the four large lakes on the Asiatic side of the Sea of Marmara (see Fig. 3), lakes Sapanca, Iznik (Nicaea), Manyas, and Apulyont (Apollonia) is discussed at length by Kosswig (1954; 1955a; 1955b). These lakes occupy graben formed during the Günz period; when the Bursa plain was raised about 100 m above sea level during Würm I, Lake Iznik was raised about 85 m, Lake Sapanca 34 and Lakes Apulyont and Manyas barely 10 m above sea level. Since that time, about 100,000 years ago, the only changes in the region have been the eustatic changes in sea level; in Würm I sea level was 90 m lower, and during the postglacial warm period was 3 m higher than today. The advance of the glaciers pushed the Euxine fauna south, and the rising sea level during interglacial periods forced the fauna into refuge areas. In view of their history the occurrence of central European and Sarmatian fishes in lakes Iznik, Manyas, Sapanca, and Apulyont is not unexpected. Lake Iznik, however, now lies at a much higher level than the other lakes and was separated from the Sea of Marmara at an earlier date. At present it has no stream outlet to the Sea of Marmara; its principal contribution to stream flow is by seepage. Nevertheless Lake Iznik contains fishes of Mediterranean and central European origin as well as Sarmatian forms. According to Pfannenstiel (1944) Lake Iznik was originally a bay of the Sea of Marmara that has been secondarily separated by and raised by epeirogenic activity. This would mean that it received its

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marine elements before Würm I or even earlier. On the other hand Luahn (1948) considers the lake to be an independent basin that was never connected with the Sea of Marmara. The immigration of marine fishes must then have taken place via surface drainages in earlier periods. Lakes Manyas and Apulyont are certainly of late origin and have become relict lakes only in postglacial time. There are several Sarmatian fishes, but the only Mediterranean representative is *Syngnathus*, a genus common in fresh water; the species in Lake Abulyont is considered by Kosswig to be distinct from the Sarmatian form.

Lake Sapanca has had a somewhat different history. It was an arm of the sea in Tyrrhenian II, a continuation of the modern Gulf of Ismit (Nicomedia), which extended into the Black Sea before the Bosporus connection was formed. With the return of the sea, Lake Sapanca, which had by then become isolated, was drawn into the Euxenian region. The Sarmatian fishes include four gobies and a Caspialosa; *Gobius melanostoma* is dwarfed as compared with brackish-water populations (Sözer, 1941). There are also a number of Sarmatian invertebrates: *Dikerogammarus haemobaphes*, *Corophium robustum*, and large populations of the supposedly Sarmatian *Dreissena polymorpha* (Neu, 1937), as well as the mysids of the genera *Mesomysis* and *Paramysis*. Entrants from the Mediterranean are *Atherina mochon* (in a special form) and *Syngnathus abaster*.[21]

CASPIAN FAUNA

According to some Russian authors, 119 species occurring in the Azov-Black Sea basin are derived from the Caspian Sea in comparatively recent (post-Pleistocene) times via the Manych depression.[22] The relict fauna of the Black Sea is not, therefore, directly derived from a Sarmatian Sea whose autochthonous fauna became separated by geological processes into two large regions, but represents a reinvasion from a previously isolated region. This Caspian element consists of 3 hydroids, 1 turbellarian, 1 cestode, 2 nematodes, 2 polychaetes, 1 leech, 1 tardigrade, 4 bivalves, 6 gastropods, 4 cladocerans, 3 copepods, 33 amphipods (Gammaridae and Corophiidae), 8 mysids, 10 cumaceans, 3 decapods, 1 isopod, 1 hydrocarid, and 30 fishes (especially sturgeons and clupeids). Only 8 or 10 of these can be considered Azov-Black Sea endemics; the others are identical with, or at best geographical races of, Caspian species. This "Caspian fauna" is about 39 per cent of the autochthonous Caspian fauna, which consists of 300–305 species.[23] The origins and relationships of the fauna of the Caspian Sea are discussed in the next chapter.

As evidence in favor of their theory of Caspian origin for the fauna in the Azov region (as summarized by Mordukhai-Boltovskoi, 1953), Russian biologists stress the ecological peculiarities of the fauna, especially its salinity and oxygen relationships:

> Only 18 Caspian species occur in the open Black Sea (18‰), and these are primarily fishes. In the more saline (less freshened) parts of the open Sea of Azov (10–11‰), there are 30 forms, of which 10 are invertebrates. The number of Caspian elements is distinctly higher in the zones outside the river mouths in both the Black Sea and the Sea of Azov where salinity is further reduced. All these forms occur in the oligohaline zones of the estuaries of the large rivers: the Don, the Kuban, the

[21] The systematic position of *Syngnathus abaster* is discussed by Kosswig (1954). The population in Lake Sapanca is so variable that characteristics of several species may be combined in a single specimen; in addition, new features appear, not known from any Mediterranean form of the genus. The probability is that we have to do with a varied mixture of hybrids, a "hybrid swarm" in which at least two species of *Syngnathus* have hybridized, and more probably three or four, though the characteristics of *abaster* predominates. The development of this variety or form is the more remarkable when compared with the great uniformity of a species like *Blennius vulgaris*, which lives in the circum-Mediterranean fresh waters, in which populations that have been separated since the Pliocene, accordingly for a million years, yet still belong to the same species as far as systematics is concerned.

[22] Mordukhai-Boltovskoi postulates a period of salinity increase during a "Chwalinskian transgression".

[23] Zenkevich, (*see* Chapter 26), gives the number as 350 species.

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Dnieper-Bug, the Dniester, and the Danube (42 species in the Kuban estuary, 91 in that of the Dnieper-Bug). Of the total species of the Caspian element, 95 are found only in water less than 15‰. Only 20 species can be reckoned as mesohaline. The optimum salinity for these species is 3‰ to 15‰; examples are *Cordylophora*, the medusa *Ostroumovia*, the polychaete *Hypaniola*, the gammarids *Cardiophilus* and *Gmelina pusilla*, and certain clupeid fishes. The 60 to 62 oligohaline species must be regarded ecologically as fresh-water forms, occurring in salinities of 1 to 3‰, and never entering more saline water. Finally, 14 species are euryhaline (so far as the Black Sea standard is concerned); they can inhabit river water of less than 0.5‰ to salinities of 17–19‰ and are ubiquitous. Such forms include primarily fishes: six gobies (for example *Gobius fluviatilis* and *G. melanostomus*), *Pungitius*, sturgeons, and clupeids. Some of them, like *Huso huso*, three gobies that occur in the Sea of Marmara, and *Cordylophora* can withstand still higher salinity. About 65 per cent of the Caspian species are oligohaline. In addition, the mesohaline forms tend to inhabit waters of lessened salinity rather than toward more saline regions. Thus, most, if not all, of the Caspian elements in the region of the Sea of Azov and Black Sea can be designated as oligohaline. Most of the Mediterranean species in the same region are polyhaline, a large number euryhaline, and none oligohaline. The Caspian fauna of the Azov-Black Sea basin is a typical river-mouth fauna.

In the Caspian Sea itself, the fauna lives in regions with much higher salinity, primarily 12–13‰. There is a parallel further penetration of the fauna into more saline areas than is the case in the Sea of Azov and Black Sea. Conversely, Caspian forms found in the Azov-Black Sea rivers (like *Monodacna*, *Corophium robustum*, and *Stenocuma tenuicauda*) never enter river mouths in the Caspian basin. Experimental investigations by Karpevich (1940) show, however, that Caspian monodacnas and dreissenas can be adjusted to life in pure fresh water if the salinity is gradually lowered.

The Caspian species in the Black Sea-Azov Basin that have become more resistant to loss of salinity are now beginning to adapt themselves to the concentration of the Black Sea as well. Certain sturgeons may be named as examples. The spread of *Pontogammarus maeoticus* in the last 50 years along the Black Sea coasts is similarly interpreted.

The Caspian fauna, in the Azov region, especially the benthic species, is not adjusted to oxygen decrease. About 55 per cent of the Caspian species living in and off the Don estuary require hard or sandy bottom, which is correlated with higher-oxygen requirements. Forty-five per cent live on soft bottom with a rich food supply, but avoid oxygen-deficient areas, which are colonized entirely by Mediterranean elements. This high-oxygen requirement also limits the Caspian element in both the Pontic-Azov area and the Caspian Sea itself to the epifaunal habitat, true "infauna" species being absent, except for the cardiid *Adacna*, which lives only half buried in mud. There is a corresponding concentration of the Caspian element in the Black Sea–Sea of Azov region in the shore zones rich in oxygen, in river mouths, on plant growth, and on shell banks. In the rivers themselves, the Caspian forms are distinctively rheophilic.[24]

Experiments have shown that the Caspian mysids of the Volga and Danube systems require a minimum of 4 to 5 cm^3/l of oxygen, and that only *Limnomysis*, *Paramysis*, and *Mesomysis kowalewskii* can live in somewhat smaller oxygen concentrations, but not less that 2.5 to 3 cm^3/l. For the gammarids *Pontogammarus maeoticus*,

[24] The limitation to zones rich in oxygen has the further consequence that only arctic and fresh-water forms are found in the Caspian Sea at depths of 300 to 400 m, with the exception of *Hypania* and a single fish.

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Chaetogammarus ischnus, and *Dikerogammarus villosus* oxygen concentration of less than 1 cm^3/l was lethal.

The biocoenotic position of this Caspian fauna corresponds to its ecological peculiarities. Only the upper horizons are occupied in the mesohaline zones; in the oligohaline and fresh-water regions the hard and sandy bottoms have a predominantly Caspian fauna, which is indicated by a mass development that is not found even among the autochthonous forms in the Caspian Sea itself. In the Dnieper and Don there are distinctive *Corophium* bottoms. Birshtein and Mordukhai-Boltovskoi oppose the interpretation of Zenkevich and others, who maintain that the Caspian fauna in the Azov-Black Sea region exhibits a general biological inferiority, accompanied by ecological displacement. The great mass of these Caspian elements is developed in the lower courses and estuaries of the rivers where the major concentration of cardiids, gastropods, polychaetes, and the majority of gammarids and mysids is found. Their mass development, resulting from rich food, forms the basis for the rich development of the food fishes; for example, the mysids are the food of the sturgeons, and the amphipods and cumaceans supply the benthic fishes. Mordukhai-Boltovskoi states that experiments have been made to increase the food-supply base for fishes, by transplanting Caspian forms to other areas with impoverished fisheries. The introduction of *Paramysis* in the coastal waters of the Ukraine is said to have had effects of economic importance in a relatively short time. (For a discussion of the converse experiment, the transplantation of species from the Sea of Azov to the Caspian Sea, see the next chapter.)

On the whole, as far as the available literature is concerned, the Russian case for a "Caspian fauna" does not seem to be very convincing. The more traditional concept of a widely distributed Sarmatian fauna, now isolated in relict basins, is strongly supported by Kosswig's study of fish distribution in Anatolian lakes, especially of the elevated Lake Iznik, whose isolation may have antedated the separation of the Caspian basin from the Azov-Black Sea basin, or at least coincided with it.

IX. FISHERIES AND PRODUCTIVITY OF THE BLACK SEA AND SEA OF AZOV

According to Slastenenko (1939; 1941) there are 171 species of fish (plus 7 subspecies) in the Black Sea, representing 107 genera and 52 families. Of these 31 are considered Pontic relicts, and 103 (plus 7 subspecies) are Mediterranean immigrants. The remainder consists of fresh-water species found in the brackish-water zones of estuaries and limans.

For a summary of the Black Sea and Sea of Azov fish faunas *see* Slastenenko (1936, 1939), Nikitin (1934b), and Vodyanitsky (1930); for the Turkish coast (with keys) *see* Aksiray (1954). There are numerous accounts of the biology of Black Sea fishes. Bibliographic summaries are provided by Maksimov (1913), Nikitin (1934b; 1939b), and Romanov (1955). Among the more recent contributions are those of Malyatsky (1938; 1940a; 1940b), Lebedev (1936), Antonio-Murgoci (1938), Tomazo (1938), Smirnov (1938), Moskvin (1940), and Vodyanitsky (1940; 1941). The most recent investigations are reported in volume 28 of "Trudy VNIRO" (Berdichevsky and Chugunova, 1954). For the Rumanian area *see* Antipa (1905; 1928; 1931; 1933; 1936), Borcea (1934; 1936a); 1936c), and Popovici (1938; 1939; 1940c). For the Bulgarian coast *see* Maksimov (1914a), Drensky (1921; 1923; 1924; 1925), Nechaev (1929), Boshkov, Morov, Zascher, and Nechaev (1935), Grosev and Nechaev (1930), Paspalev (1934), and Caspers (1951c).

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Twenty per cent of the fishes of the Black Sea are of economic use. Several of the most valuable commercial fishes, which support most of the fisheries, are migratory. Some of these migrations are via the Bosporus to the Sea of Marmara, others are through Kerch Strait to the Sea of Azov. In the spring great schools of *Engraulis*, *Scomber*, *Sarda*, *Pomatomus*, *Thunnus*, *Spratella*, *Sardina*, and a few other species enter the Black Sea via the Bosporus. *Scomber* does not breed in the Black Sea, but enters only to feed.[25]

In addition to these migrations into and out of the Sea of Marmara, there are extensive movements of fishes within the Black Sea itself, especially between the southern region and the northwestern area. There is an intensive migration through the Kerch Strait into the Sea of Azov by species of *Engraulis*, *Caspialosa*, *Harengula*, *Mugil*, and *Mullus*. When these schools leave the Sea of Azov in winter, they spread out along the coasts of Crimea and the Caucasus (Malyatsky, 1938; 1940a; 1940b). The catch of migrant fishes from the Bosporus along the Bulgarian and Rumanian coasts is considerable.

As examples we shall consider briefly the biology of three migrant species:

(1) The mackerel (*Scomber scombrus*) breeds in spring in the Sea of Marmara, and its schools enter the Black Sea via the Bosporus in summer; spreading as far as Odessa—*i.e.*, to the northwestern region. The first schools appear on the Bulgarian coast in early April, and the height of the migration is between May 10 and May 25 (Nechaev, 1941; Caspers, 1951c). After a very cold spring the migration may be delayed from 2 weeks to a month. The feeding period produces an increase in length of from 10 to 15 cm and an increase in weight of 30 to 35 per cent. The return migration begins in October; the maximum catch on the Bulgarian coast is from about November 20 to December 10. In January, most of the mackerels migrate into the Sea of Marmara, but some schools remain in the southern part of the Black Sea.

(2) The spring migration of the bonito (*Sarda sarda*) into the Black Sea is divided into two groups, an eastern and a western. Nümann (1955a) has investigated the appearance of these fishes in the Turkish region. Marking experiments and the analysis of the age group and length measurements showed that the bonitos of the whole of the Black Sea and the waters connecting with the northeastern region form a uniform population. In May and June they move through the Bosporus into the Black Sea, where they spawn.[26] For several months they remain away from the Anatolian coast, in the northern part of the sea where they are attracted by good feeding grounds. Their probable migration routes in the Black Sea are shown by Nümann (1955a) (Fig. 37). They seem to be closely related to the current system. At the end of May and in June eggs and larvae are found in both the western and eastern parts of the sea, but primarily along the Caucasian coast (Fig. 37). In the southern Black Sea the young bonitos of the length group 15–20 cm form two groups, one off the Bosporus and the other in the area off Sinop at the middle of the Anatolian coast (Nümann, 1955a). The young fishes that appear off the Bosporus have a length of 24–27 cm. From the end of August to the beginning of October they pass the Bosporus, Marmara, and the Dardanelles at a rate of about 50 km per day. As Nümann assumes, the mass of distinctly variable numbers of the outward-migrating bonitos is not dependent on external factors, or on the number of spawning fishes or eggs, but on the conditions under which the eggs have developed into larvae in the unstable hydrographic system of the Black Sea. Along with the young fishes, the adult bonitos also migrate through the Bosporus back into the Sea of Marmara. Whole schools, to be sure, over-winter in the Black Sea.

(3) *Trachurus mediterraneus* spawns along the entire northern coast of the Black Sea (Aleev, 1952; Ambroz, 1954; Nümann, 1956, map, p. 32). Along the Anatolian coast these fish move from east to west in July (Nümann, 1956). The 2-year and older fish of the Marmara-Bosporus region move through the Bosporus in May and June and along the Bulgarian coast to the spawning places on the

[25] Reports of breeding of *Scomber* in the Black Sea are unconfirmed; *see* Krotov (1940; 1954).

[26] The records of spawning of the bonito in the Sea of Marmara prove to be erroneous.

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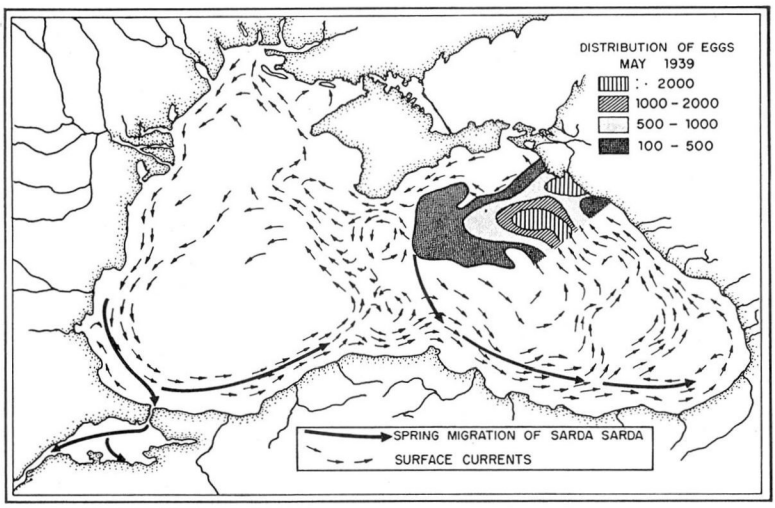

FIGURE 37.—*Bonito* (Sarda sarda) *in the Black Sea*
Spring migration, from Nümann (1955); distribution of eggs according to Malatsky, from Zenkevich (1947).

Russian coast; the year-old fish follow the older ones somewhat later—June to mid-July. At least some of the older fish then remain in the Black Sea and grow to large size there. There has been a displacement of the principal fisheries grounds in the Black Sea in recent years. Along the north coast this is progressively westward (Ambroz, 1954).

On the Anatolian coast of the Black Sea large *trachurus* first appeared in numbers about 1942, in the Trabzon-Tirebolu district, from where they first spread slowly eastward and more rapidly westward, first appearing in the Bosporus in 1954. In addition to this gradual displacement the fishes on the Anatolian coast undergo an annual migration. During the winter they live at greater depths and approach the surface in May, as a result of which they reappear westward in the Ordu region; by September the movement is slowly toward the east again. Nümann (1956) considers it possible that the movements of *Trachurus* are directly related to those of *Engraulis*. There is a parallel movement along the Crimean coast and opposite parts of the Anatolian coast and from there similarly toward the east; the stomach contents of large *Trachurus* are predominantly *Engraulis* (Fortunatora, 1949).

According to Zenkevich's data (1947) the Russian catch of fishes for 1950 in the Black Sea amounted to 500,000 hundred weight. To this must be added 360,000 hundred weight for the other countries. In the Russian fishery, 38% is composed of *Engraulis* and *Spratella*, 11% of *Vimbra*, *Abramis*, *Cyprinus*, and *Pelecus*, 6% of *Mugil*, and 5% of gobiids. In the over-all picture of the Russian fisheries in the Black Sea region, 38% is from the rivers and limans, 45% from the coastal fisheries, and only 14% from the open sea. Of this 15%, the porpoise catch makes up 90%. On the Bulgarian coast, 50–60% of the total catch is made up of *Scomber* and *Sarda* (Caspers, 1951c).

THE SEA OF AZOV

The fish fauna of the Sea of Azov consists of 79 species of which 20 are wholly or partly migratory; 13 are fresh-water species.

As a result of the high eutrophic level of the Sea of Azov (Pauli, 1939) and of its rich food supply, production of fish is high. According to Zenkevich (1947) the Sea

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of Azov (including the Kerch Peninsula) produces about 250,000 tons per year, or about 72 to 82 kg/ha. In 1937 the catch was composed as follows (in tons):

Harengula	81,900	*Cyprinus*	1,200
Lucioperca	72,100	Acipenseridae	7,500
Engraulis	50,400	*Caspialosa*	6,200
Abramis	34,100	Gobiids	4,400
Vimba	3,900	Others	11,900
Pelecus	3,900		
			277,500

The high production is associated with the similarly large supply of plankton and benthonic food. In the plankton, the copepods are of primary importance. They compose 85% of the food in *Harengula*, 40% in *Engraulis* (up to 70% in August), 56% in *Atherina*, and 20 to 30% in *Caspialosa*.

PORPOISES AND SEALS

Three porpoises occur in the Black Sea: *Delphinus delphis*, *Tursiops truncatus*, *Phocaena phocaena*;[27] only *Delphinus* is commercially taken. This porpoise (or dolphin) frequently appears in large schools that follow the schools of fishes, especially those of the smaller species like *Engraulis* and *Clupeonella*; *Scomber* is taken only when the porpoises are very hungry.[28] The population is estimated at one million individuals.

The principal commercial porpoise fisheries are along the coasts of Crimea and Caucasus, and Anatolia; in addition the mouth of the Danube (Kravchenko, 1932); for the catch on the Bulgarian coast *see* Caspers (1951). The Russians employ nets to catch them, in order not to injure the skins; off Bulgaria they are shot; on the Anatolian coast they are either shot or netted. Inividual porpoises may have a weight of 500 kg at a length of 2.5 cm. Most specimens are considerably smaller. According to the Russian reports the annual catch in the Black Sea amounts to nearly 120,000 individuals, USSR 75,000, Turkey 40,000, Rumania 5,000, and Bulgaria 2,000–3,000 (Caspers, 1951c).

The occurrence of the monk seal, *Monachus monachus* in the Black Sea is noteworthy. This species was formerly widely distributed along the Russian coasts (Zernov, 1913), but there is now only a remnant population at Cape Kaliakra (Caspers, 1950b; Krotov, 1952), although it persists on the Anatolian coast.[29]

QUANTITATIVE ASPECTS OF THE BIOLOGICAL PRODUCTIVITY OF THE BLACK SEA

The biological productivity of the Black Sea and related problems are examined by Vodyanitsky (1941; 1945; 1954). The most recent paper is based on original investigations of the pelagic region and a thorough review of the literature. Questions concerning economic use and the increase of useful productivity are also discussed. Vodyanitsky emphasizes that a final statement is not yet possible because of the lack of agreement of figures from various investigations and the still-unresolved contro-

[27] *See* Kleinenberg (1956) for a detailed account of these species in the Black Sea. *Phocaena relicta* Abel is not considered a distinct form (Tsalkin, 1840, Kleinenberg, 1956). It is thought that *Phocaena phocaena* has entered the Black Sea in Recent times, so that even subspecific recognition is questionable.

[28] Tsalkin (1940) estimated the annual consumption of fishes by porpoises as 1.5 to 3 million CWT (300 kg. per porpoise)-which is about one and a half times greater than the estimated annual catch of fishes. Vodyanitsky considers Tsalkin's estimates too low. Although Il'in (1946) considers the supply of pelagic fishes practically inexhaustible, Vodyanitsky and others conclude that the porpoise population must be reduced to a minimum if the fisheries are to be increased.

[29] According to a personal communication from Dr. Nümann, there is supposed to be a colony at Cape Sinop. *Monachus* may also be seen in the Bosporus. In the Mediterranean these seals are almost extinct (*see* Caspers, 1950b). For a recent systematic summary of the monk seals, *see* King, (1956).

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versies among investigators. There is a tendency to abandon the idea of high productivity for the Black Sea (*see* also Kusmorskaya, 1950).[30]

On the basis of the fisheries expeditions in the Sea of Azov and the Black Sea from 1920 to 1930, Knipovich correlated the production of fishes with the quantity and distribution of pelagic eggs, larvae, and juvenile fishes. Only those Mediterranean fishes passing all their developmental stages in the upper surface layers or near shore could become established in the Black Sea. Species developing in deeper water are absent (Vodyanitsky, 1930; Kosyakina, 1937; 1940; Pchelina, 1936; 1940). According to several workers (Malyatsky, 1931; 1933; 1934; 1938; 1940; Golenchenko, 1940; 1948; Krotov, 1938; 1949; 1951) there are still considerable populations of fishes, principally adult pelamids, that are not yet exploited commercially. Other workers have shown that the phyto- and zooplankton masses are greater than had been supposed (Morozova-Vodyanitskaya, 1927; 1941; Galadyiev, 1948; Arnoldi, 1941; 1948; 1949; Nikitin, 1946; 1949; 1950). According to a map of the bathymetric distribution of the plankton biomass compiled by Malyatsky (1940b) the highest values are in the middle regions. The principal food chain of the pelagic region has been established as:

$$\text{Plankton} \rightarrow \frac{\text{Engraulis}}{\text{Clupeidae}} \rightarrow \text{Dolphins.}$$

(*see* also Tsalkin, 1940). The porpoises, at least in some periods, are competitors of the pelamids.

Earlier views of the comparatively low productivity of the Black Sea as compared with the Sea of Azov (and the Mediterranean) have been modified by Vodyanitsky, who points out that the populations of fishes in the Sea of Azov are to a considerable extent dependent on the Black Sea, for the most abundant fishes are migratory and spend part of their lives in the Black Sea. In the Black Sea the larger fishes and predatory animals, especially porpoises, continually reduce the populations of pelagic fishes. This does not occur in the Sea of Azov.

The productivity of the Black Sea must be considered in the light of its chemical characteristics. The content of nitrates, phosphates, and ammonia is higher in the upper zones than in most oceans or in the Mediterranean Sea. Earlier comparisons of these nutrients were misleading because the concentration of nitrates, for example, was compared with the total concentration of ocean waters including the deeper zones. The rivers contribute 160 mg of phosphates per m^2 per year, from which about 100 g of phytoplankton per m^2 are produced annually. According to Vodyanitsky the contribution of nutrients from the rivers is supplemented by a considerable supply from the deeper zones of the Black Sea itself by the recycling of nutrient salts. This supply increases during dry periods as the result of increased vertical circulation and consequent downward extension of the oxygenated upper zone. This transport is even more pronounced during periods or years with cold winters, when the vertical circulation involves the deeper zones. Plankton production increases considerably following such periods. This vertical supply of phosphates is estimated at 300–400 mg/m^3, which is notably greater than the annual supply from the rivers.[31] According

[30] Vodyanitsky emphases the inadequacy of the "biomass" concept for the characterization of the composition of plants and animals, although "biomass" is widely used in Russian hydrobiological literature. It is essential that data on weight be supplemented by data on the numbers of organisms, as done by Morozova-Vodyanitskaya in her recent work. Bruevich (1950) uses the coefficient P.B. (productivity/increase) on a seasonal basis—*i.e.*, the "biomass." *See* the discussion in Chapter 3 and the papers cited therein, especially Macfadyen, 1948.

[31] Vodyanitsky regards the present high nitrogen and phosphorus content of the surface zones of the Black Sea as the result of a recent increase associated with present climatic conditions. This view is opposed by Lebedev (1953). According to Vodyanitsky (1948) there has been a stabilization of the salinity of the deeper zones during the last 60 years as a result of the general and continuing vertical exchange of water masses. He estimates that an average of 3000 km^3 of water per year have been transferred to the upper layers from the deep zones.

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TABLE 24.—*Plankton biomass of the Black Sea, 1939*
Malyatsky (1940, from Vodyanitsky, 1954)

	May–June			August		
	Min.	Max.	Mean	Min.	Max.	Mean
Total biomass (g/m² of surface)	2.3	39.9	13.8	3.4	20	10.18
Calanus (individuals m² of surface)	10	19,600	2,578	10	6,928	1,779
Chaetognaths (individuals m² of surface)	1	3,524	756	2	1,650	235
Phytoplankton (mg/m³)	34	6,620	85.0	31	4,780	198.0

to Datsko the total production of animal life in the Black Sea is too high to be accounted for on the basis of phytoplankton productivity alone. He suggests that autotrophic bacteria must play a considerable role in this productivity and that they are based on the nutrient supplies of the depths. According to this view the deep zones do not merely accumulate nutrients, but return part of them to the upper zone.

Because of the winter supply of nutrients from deeper waters the plankton can develop in winter and spring, and the seasonal differences in plankton productivity are accordingly less pronounced, as compared with other seas. The average phytoplankton content in a square meter column of water in winter is 35 to 40 g; since this is limited to the upper 100 meters, the concentration is about 0.3 to 0.4 g/m³. In regions of stable salinity during the summer the plankton content does not exceed 17 g beneath a square meter of surface. Nearer shore the mass development of diatoms may bring the value up to 120 g.; in the summer of 1937 there was 20–24 g per m² of surface off the south coast of the Crimea and in Karkinitsky Bay.[32] The values given for Black Sea plankton are according to Malyatsky (1940), who considers them conservative (Table 24).

On the basis of expeditions during 1946 and 1948 the average biomass of the open regions in the eastern part of the Black Sea in September is estimated as 11.6 g (range 5 to 20 g) for a 100-m water column beneath a square meter of surface (Morozova-Vodyanitskaya, 1950). In the coastal zones to depths of 10 m the concentration rises to 400–500 mg/m³. The total phytoplankton biomass (wet weight) of the Black Sea in September amounted to 4.8 million metric tons (2.8 million tons without *Rhizosolenia*), of which 3.6 million tons were in the upper 50 m. Winter and spring production of diatoms occurs not only in the bays but out to 10 nautical miles from shore. In the bays during spring the daily production of *Chaetoceros*, *Ceratulina*, and *Leptocylindrus* was 100–120 million cells/m³ (biomass, 250 mg/m³). Pitsyk (1950) agrees with Morozova-Vodyanitskaya that the phytoplankton biomass in areas far from the coast is almost as great. Toward the end of August the concentration was 152 mg/m³, or 11 million cells, 120 nautical miles off the Crimean coast. In these areas dinoflagellates are the principal component, whereas diatoms are preponderant in the coastal zones. In the summer months the average plytoplankton biomass for the upper 100 m is 75 mg/m³, or 10,180,000 cells, and 92 mg/m³ (or 15,000,000 cells) in the upper 25 m. The phytoplankton biomass is 10 times as great in the Sea of Azov but is composed mainly of Rhizosolenia and Cyanophyceae. On this basis the food value of the summer phytoplankton of the Sea of Azov is not as high as that of the Black Sea plankton with its dinoflagellates and diatoms (Pitsyk, 1950; Vodyanitsky, 1954). Vodyanitsky questions the estimates by Stroikina (1940; 1950). These results led Vodyanitsky to

[32] As yet there are no accurate data on the plankton content of shallow coastal zones where there are benthic populations. Vodyanitsky gives a value of 200–400 g per m² of surface for the rich shore regions (to 100-m depth) and 30–50 g for the adjacent Phaseoline region.

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contradict the view of Usachev (1947) and earlier workers that the Black Sea phytoplankton is impoverished (10–20 mg/m³) during the growing season. Basic data for a clear understanding of the relations between plankton distribution and currents are still inadequate, especially in view of the recent investigations indicating a rich plankton development in the central parts of the sea as a consequence of fertilization from the deeper zones.

The distribution of zooplankton corresponds to that of phytoplankton. The summer mass development depends on the spring diatom flowering and the succeeding dinoflagellate development, which constitutes the food base for many fish larvae. The development of *Noctiluca* and *Pleurobrachia* plays a subordinate role in the food supply of higher animals (Kusmorskaya, 1950; Malyatsky, 1940b; Mirinov, 1941; 1954), but on the other hand they are important in the production of detritus. On the south coast of the Crimea the productivity at depths of 10–15 m was as high as 321.4 mg/m³ (Galdyiev, 1948). At the same time the production was five times as great (1642.2 mg/m³, av. 863.3) in Karkinitsky Bay. There is less difference in the minima for these regions, which are 140 and 298 mg/m³ respectively. In the open sea of the Crimea the average is 118 mg/m³. In the shallow Karkinitsky Bay the plankton occurs only to depths of 20–30 m, whereas it extends to depths of 175–200 m in the open regions off Crimea. Galadyiev estimates the plankton of the open zones of the sea at 120 to 130 mg/m³.

The average weight of all organisms, including benthos, but exclusive of fishes, is 150 g per square meter of surface. In the coastal regions with benthic life, up to 120 m, the amount is 200 to 300 g, and in the central regions it falls to 20–30 g. The production of fishes is about 2.5 kg/hectare/year (calculated for the total sea surface). There is a strong seasonal fluctuation, with a spring migration into the Sea of Azov and an autumn movement into the Marmara regions.

Production of pelagic fish is seven times that of the benthic fishes. Predatory fishes and porpoises play a large role. About 200,000 porpoises are caught annually, which is about 20 per cent of the population.

A summary of the standing crop and annual production of the Black Sea as a whole was compiled by Datsko (1951) from various sources (Table 25).

The trophic relationships have been summarized by Vodyanitsky (1954) from various sources with the following rounded figures: Of the total biomass of the summer plankton, which amounts to 150 mg/m³ (or 15 g in a water column beneath a square meter), about 30 per cent, or 5 g, is consumed by zooplankton. The fishes, totalling

TABLE 25.—*Biomasses and annual production of plants and animals in the Black Sea*
From Vodyanitsky (1954, after Datsko, 1951)

	Biomass, metric tons × 1,000		Annual coefficient, P/B*	Annual production metric tons × 1,000		
	Wet weight	Dry weight		Wet weight	Dry weight	% dry weight
Phytoplankton, upper 50 meter layer	3,600	360	300	1,000,000	100,000	10
Bacteria, 0–200 m.	13,500	2,700	250	3,375,000	675,000	20
Zooplankton, 0–10 m.	11,000	1,100	30	330,000	33,000	10
Zoobenthos	15,000	2,250	2.5	37,000	5,550	15
Phytobenthos	20,000	2,400	1	20,000	2,400	12
Fishes:						
Pelagic	5,000	1,500	0.5	2,500	750	30
Benthic	700	310	0.5	350	105	30
Porpoises	50	17	0.35	17	10	35

* Coefficient P/B: Production/Annual increment

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about 5,000,000 tons (125 g/hectare or 15 g/m^2), consume up to about 1.5 per cent of their weight, or about 0.2 g/m^2, which requires about 2 to 3 g/m^2 of zooplankton.[33] The approximately one million porpoises consume at least 6 million kg. of fish per day, equalling 50 kg/ha/year (or about 150 g/ha/day). Datsko estimates the annual production of pelagic fish at 2,500,000 tons, of which 2,000,000 tons, or four-fifths, is consumed by porpoises.

These calculations are the result of the newest methods of Soviet hydrobiologists and fisheries biologists. A study of the literature reveals many uncertainties in the quantitative investigations on which they depend, with various sources of error for the total estimates. Further, much work remains to be done on the theoretical assumptions. Nevertheless, these investigations provide a basis for understanding the magnitude of the biological processes in this isolated body of water.

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Editor's Note: The references to this chapter were submitted in the short style acceptable in many European publications. Circumstances have prevented bringing all the references into conformity with the rest of this volume; the inclusion of page numbers indicates that the reference has been checked by the editor, either against the original or in one of the several abstracting journals. Responsibility for the accuracy of citations without page numbers rests with the author. A German title in brackets indicates a translation by the author; in some cases there may be an English or French summary. Where a Russian or Bulgarian title is followed by a title in brackets in another language, it indicates that there is no summary except in the language of the paper. A title in italics is the title of the summary in that language; usually this is also indicated by the appropriate page numbers in italics. Because of the difficulty of identifying many journals from their abbreviated titles, a list of the full titles of several of the more frequently cited journals precedes the list of references, according to the following system: A transliterated abbreviation, as used in the references, is given, followed by the full Cyrillic title. This is followed by a number in brackets, which is the number given in the World List of Scientific Periodicals (3rd ed., 1952). When known, the alternate title in another language is then given in italics. The last item is the transliterated title as given in the Union List of Serials. From the WL and ULS entries it is possible to determine library holdings in Britain and the United States, although it must be remembered that many of these listings are not up to date. The abbreviations used in this list are not intended to establish any style of citation, but apply only to the list at hand.

Although of great utility, the bibliography of Russian fisheries literature by Romanov (1955) is unfortunately restricted to fish and fisheries, *sensu stricto*, and does not include literature from other countries bordering the Black Sea. Those references included in Romanov's bibliography are designated by his number, in brackets at the end of the reference.

The editor wishes to thank Mrs. Gerda F. Behrens of the General Library, University of California, Berkeley, for assistance in identifying many of the serials and in supplying titles.

J.W.H.

JOURNALS

Bull. Moskva obshch. prirody
Бюллетинь московского общества испытателей природы [5791]
Bulletin de la société [imperiale] des naturalistes de Moscow
Moskovskoe obshchestvo ispytateleĭ prirody
From 1917 on in two sections, (biol.), and (geol.)

[33] This calculation is incorrect, since the daily increase of zooplankton was estimated at only 1.5 g/m^2. Many pelagic fishes, especially juvenile stages, consume phytoplankton directly. Furthermore, the zooplankton may use up to half the phytoplankton biomass daily (Morozova-Vodyanitskaya).

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D. A. N.
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C. R. Acad. Sci. U. R. S. S.
Akademiia nauk USSR. Leningrad Doklady
Although the Doklady nows bears a Moscow imprint, it is listed in ULS under Leningrad: see there also for the bewildering array of other akad. nauk serials.

Raboty Don-Kuban Sta.
Работы Доно-Кубанской научной рыбохозяйственной станции. Ростов на Дону [17546h]
Rostov on Don. Azovsko-chernomorskiĭ nauchno-issledovatel'skiĭ institut morskogo rybnogo khoziaĭstva i okeanografiĭ. Raboty

Trud. Ikhtiol. Sta. Sosopol
Опитна ихтиологична станция, Созополъ.—Трудове ихтиологична София, изд. Министерство на земед. и държ. имоти, Бургасъ, п-ца Котва
Not in WL or ULS; vol. 3, was published in an edition of 500, vol. 4, of 300 copies. Its probable American listing would be:
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Trud. morska. biol. sta. Varna [or Stalin]
Турудове на морската биологична станция в гр. Сталин [1629a]
Varna, Bulgaria. Chernomorska biologichna stantsiia. Trudove
Arbeiten aus der biologischen Meerestation am schwarzen Meer in Varna. Sofia
Library of Congress, 1955: Stalin, Bulgaria. Morska biologichna stantsiia. Trudove. Publications. Sofia
From 1933 to 1942, published under Chernomorska biologichna stantsiia; from 1943 to 1952 under later name. Began with v. 2, 1933; v. 1 as v. 6 no. 1 of Izvestiia prirodonauchni institut, Sofia

Trudy Azov-Chernom. Exp.
Труды Азовско-Черноморской научно-промысловой экспедиции. Всесоюзныи научно-исследовательскии институт морского рыбного хозяйства.
No recognizable listing in WL or ULS; recent reports under this title have appeared as whole numbers of Trudy VNIRO. Nos. 5 and 10 are catalogued at SIO as "Moscow. Institute of Fisheries and Oceanography (Vsesoiuznyi institut morskogo rybnogo khoziaĭstva i okeanografii). Abhandlungen der Wissenschaftlichen Fischerei-Expedition im Asowschen und Schwarzen Meer."

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Novorossiĭsk. Biologicheskai͡a stant͡siia imeni V. M. Arnol'di. Trudy.

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Chapter 26
Caspian and Aral Seas[1]

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I. CASPIAN SEA

The Caspian Sea (Fig. 1), which in olden times was called Khvalynski Sea, is the world's largest land-locked body of water [with an area more than five times that of Lake Superior]. It is a relict sea, with water about one-third the salinity of the ocean (12–13 ‰), populated by the original relict fauna that was much more widely distributed in earlier times and is now preserved in the various marine and fresh-water bodies of Eurasia. In its origin and development, the Caspian Sea has been connected with the fate of sea basins of the South Russian geosyncline. The natural resources of the Caspian Sea are great and very unusual, especially in their composition.

PHYSICO-GEOGRAPHICAL AND HYDROLOGICAL CHARACTERISTICS

The Caspian Sea is 1200 km long and 200 to 550 km wide, extending meridionally; its area is approximately 436,000 square kilometers, its average depth is 184 meters, and its volume is 77,000 cubic kilometers. The Caspian Sea is divided into three natural regions: the northern, very shallow part (not more than 10–12 meters deep); the central part with depths up to 770 meters; and the southern part with much deeper water (up to 1000 meters). The central and southern parts of the Caspian Sea are divided by the shoal at the region of the Apsheron Peninsula. All three regions are almost equal in area, but in their volume they differ substantially: about two-thirds of the water volume belongs to the southern part, about one-third to the central part, and only 0.01 to the northern part.

The distribution of benthic life in the Caspian Sea is correlated with the distribution of the bottom sediments. Silts are the principal sediment of those parts of the sea deeper than 100 meters. Thick deposits of soft silts rich in detritus are also formed in the shallows, very often close to the coastal line in the northern region as a result of the presence of rich plant life and abundant alluvial deposits from the inflowing rivers. Between the shoal-water silts and deep-water silts there are in places vast stretches of sands or immense accumulations of crushed shells with an admixture of silt. The distribution of the bottom sediments, in turn, is correlated with the current system. In the Caspian Sea, as a whole, there is a principal cyclonic (counterclockwise) current breaking into several smaller cyclonic eddies: two in the southern part, a large one in central, and two in the northern part (Fig. 2). Rivers flowing into the Caspian Sea add approximately 350 cubic kilometers of water annually, of which about 76 per cent is contributed by the Volga River alone. If we add

[1] This is a translation by A. S. Loukashkin, California Academy of Sciences, revised and emended by Joel W. Hedgpeth [as indicated by bracketed items], of pages 314–338 of *The Seas of USSR, their Flora and Fauna*. Since this is a summary of an earlier book by Zenkevich, no citations were provided. A guide to the pertinent literature is appended to this translation by the editor. This translation has been corrected by Professor Zenkevich.

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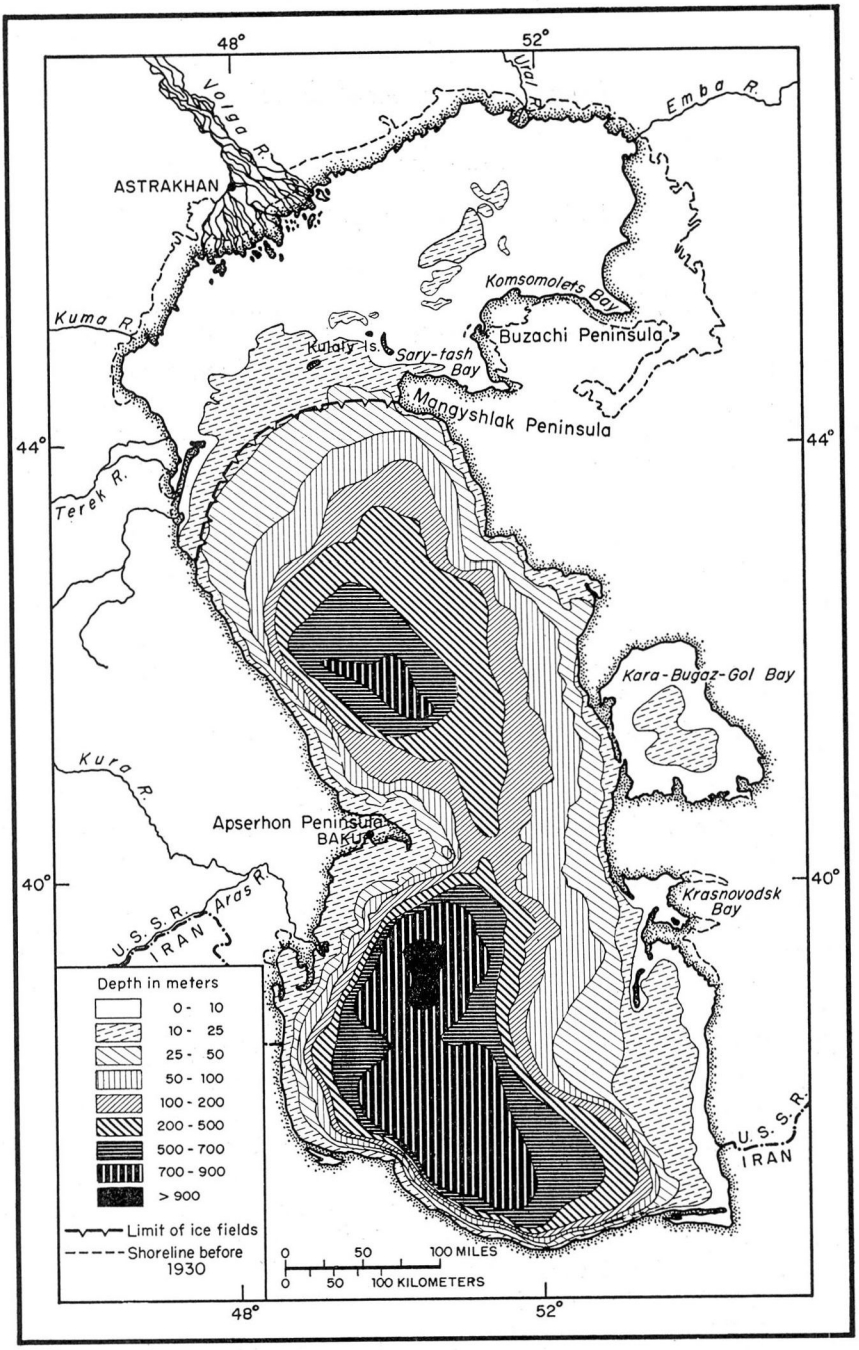

FIGURE 1.—*The Caspian Sea*
Compiled from Zenkevich (1951) and Taskin (1954)

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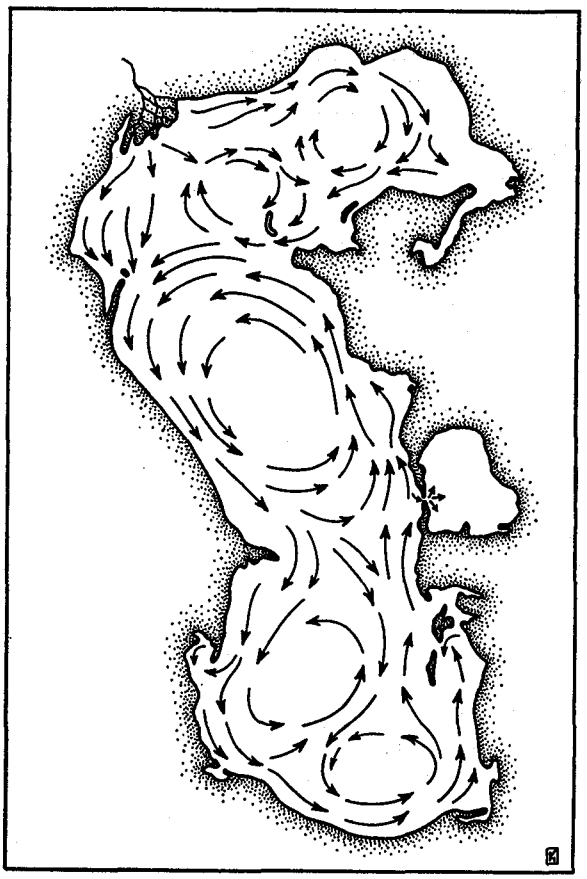

FIGURE 2.—*Surface-current patterns in the Caspian Sea*
Zenkevich (1947)

about 100 cubic kilometers of precipitation falling directly on the sea surface, we obtain approximately 450 cubic kilometers of fresh-water influx per year, or 1/176 of the entire volume of the sea. This amount of water could raise the sea level 125–135 cm in 1 year, and at such a rate the entire Caspian depression would be flooded in 176 years. However, the natural process of evaporation neutralizes the effect of inflow of fresh water and maintains the sea level at relatively the same place (but only relatively because the level of the Caspian Sea at times undergoes considerable fluctuation). At the present time, the level of the Caspian Sea is approximately 28 meters below sea level. The average level of the Caspian Sea from the zero mark of the Baku depth gauge for a century (1830–1929) is 326 cm. The highest sea level was recorded for 1896 at 363 cm. above the zero mark of the Baku depth gauge, and the lowest level has been observed during the past few years. In the last 20 years the sea level has been lowered more than 2 meters. However, it is known that in former centuries there were periods when the sea level was still lower. In several

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places along the coast, especially near Baku, even in the present low-level period, the ancient city buildings still remain under water. These fluctuations of the sea level appear to be the results of fluctuations in volumes of fresh water produced by the inflowing rivers and precipitation minus quantities of water evaporated [Taskin, 1954].

In thermal regime, the northern and southern parts of the Caspian Sea differ greatly from each other. In summer, however, the temperature of the surface water of the whole sea is quite uniform and high: it ranges from 24°C. in the northern to 27°C. in the southern part. In winter the difference in temperature is very sharp: in the open sea of the southern part the surface temperature never goes below 9°C., while in the northern region it drops below zero, accompanied by the formation of ice, mostly as continuous ice fields, from December to March. These differences are in full conformity with the climatic differences of these two regions. The annual mean air temperature near the delta of the Ural River is +7.8°C., in Pehlevi +15.6°C., in Astrabad Bay in certain years +19.5°C. The mean temperature for the month of January near the Ural River Delta is −10.5°, in Pehlevi, +5.9°C.

In the upper water layers above 300 meters the temperature drops sharply, but below 400 meters it remains stable throughout the year (Table 1).

The salinity of the Caspian Sea is almost one-third that of normal oceanic water. The surface salinity in the central and southern regions is quite homogeneous and is 12–13‰. In the northern region the salinity drops considerably. In the central parts the salinity is 5–10‰, and toward the Volga Delta it is even less. The eastern shore receives a negligible volume of river water, and precipitation is slight, while evaporation is very high. As a result, in all the bays along this shore, especially in those which are isolated from the open sea, such as Kaidak, Dead Kultuk (Zaliv Komsomoletz), Kochak, Karabogaz-Gol (Kara-bugaz), and Krasnovodsk, the water becomes more saline, for example, up to 200‰ in the Kara-bugaz Gulf. With cooling of water in winters, quite pure Glaubers salt is precipitated. This salt is an object of local industry.

In the deeper water, the salinity is somewhat higher, but the difference in salinity between the surface and deep waters is insignificant and does not cause vertical

TABLE 1.—*Variation in water temperature (°C), of the Caspian Sea at different depths*

Depth, meters	Central Caspian		Southern Caspian	
	at the end of winter	at the end of summer	at the end of winter	at the end of summer
0	5.94	22.03	9.05	24.18
50	5.78	6.63	8.92	9.58
100	5.62	5.76	7.20	7.11
200	5.27	5.29	6.11	6.14
300	5.07	4.96	5.91	5.96
400	4.88		5.90	
600	4.86		5.93	
800	—		5.96	
900	—		5.94	

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circulation in winter time when the surface water is cooled. Consequently, there is little oxygen below 200–300 meters, and near the bottom the oxygen content may drop to zero, accompanied by the appearance of hydrogen sulfide, but in lesser amounts than in the Black Sea (up to 0.2–0.3 cm^3/l). As in the Black Sea, this hydrogen sulfide is generated by the anaerobic reduction of sulfates as a result of the activity of *Microspira*-type bacteria [*Desulfovibrio*].

The disappearance of oxygen in the near-bottom layer and even the appearance of hydrogen sulfide is observed also in the shallow waters of the northern region, especially in places where soft silts rich in organic matter are abundantly deposited and where the salinity of the surface layer is low. This creates a phenomenon of the weak vertical shift of water masses, accompanied by quick and complete disappearance of oxygen in the near-bottom layer, and sometimes the appearance of hydrogen sulfide. This phenomenon is most characteristic for the southwestern part of the northern region of the Caspian Sea.

Mineral nutrients necessary for development of the phytoplankton in the Caspian Sea occur in mean quantity. Both the phosphates and nitrates accumulate in the deeper layers in sufficient quantities (30–50 and 100–150 mg/m^3 respectively), but in the photosynthetic surface layer in autumn their quantities drop very substantially, sometimes almost to zero.

FLORA AND FAUNA OF THE CASPIAN SEA

The flora and fauna of the Caspian Sea are not rich in number of species and are heterogeneous in origin (Fig. 3). Basically, the fauna is originally a marine Tertiary one which has undergone considerable changes as a result of the changes in the orogenic and hydrologic (mainly salinity) regimes of this water basin. The remnants of the populations of the Sarmatic and Pontic seas are represented by such characteristic Caspian groups as herrings [*Caspialosa*], gobies, "pugolovki" [*Benthophilus*], and possibly the acipenserids; among mollusks various cardids (with the exception of *Cardium edule*), dreissensids, and the majority of gastropods; Bryozoa, ampharetid polychetes, some turbellarians; among decapod crustaceans two species of crayfishes; cumaceans, large numbers of mysids (with the exception of the genus *Mysis*) and gammarids; sponges, the medusa *Moerisia* [*pallasi*], and the hydroid *Cordylophora*.

In addition to this basic faunal component there is a considerable admixture of more recent immigrants from the northern seas (the Arctic complex of Crustacea, Pisces, etc., some 12–15 species altogether), from western seas (The Mediterranean complex, consisting of 20 species of mollusks, fishes, worms, crustaceans and other groups), and, finally, a large number of species of crustaceans, fishes, mollusks, rotifers algae, etc. from fresh waters.

During those phases of the basin's history when salinity had substantially dropped and the water had become almost fresh, the fresh-water fauna penetrated it, and part of it gradually became adapted during the ensuing increase of salinity in the basin. The first to acclimatize were the cyprinids and percids among the fishes; almost all the gastropods, oligochetes, some turbellarians, and many other groups of animals and plants; in the plankton, most of the green and blue-green algae, cladocerans, and many others.

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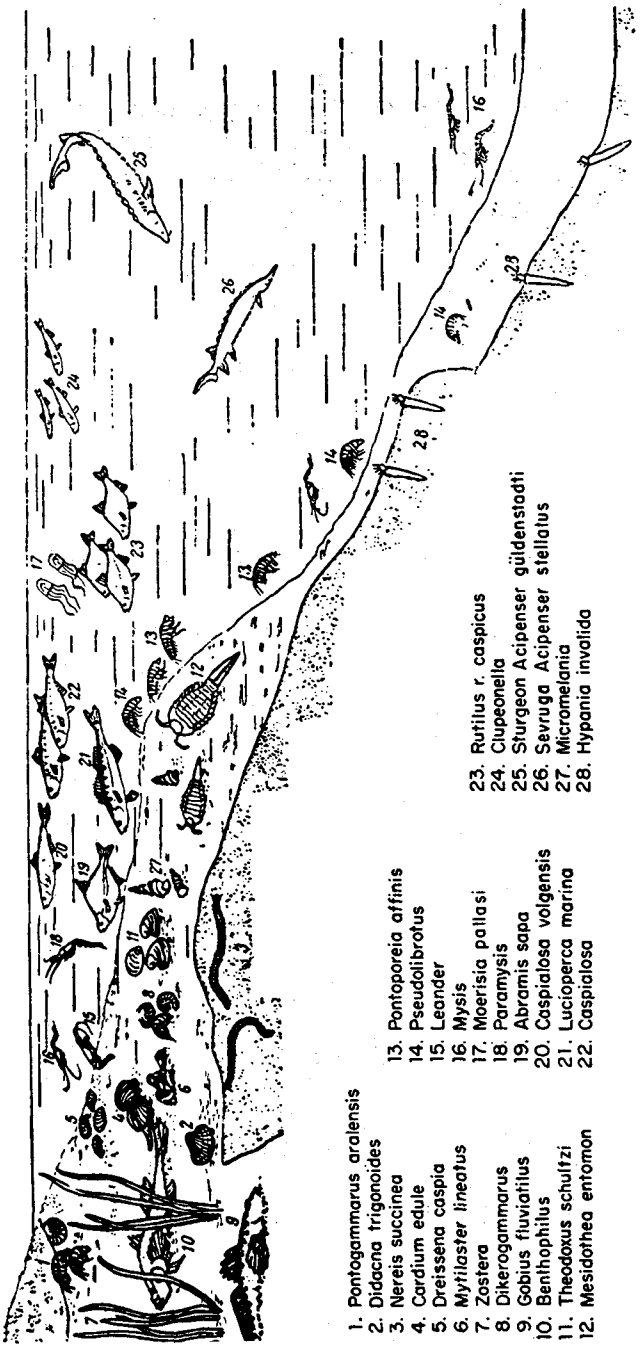

FIGURE 3.—*Characteristic mass forms of the Caspian Sea*
Zenkevich (1951)

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TABLE 2.—*Degree of endemism in the Caspian fauna of different groups of animals*

Group	Total number of species	Endemic species		Species in Black and Azov seas		Occurring outside Black, Azov, and Caspian seas	
		No.	Per cent	No.	Per cent	No.	Per cent
Crustacea	107	70	65.42	30	28.04	7	6.54
Mollusca	47	41	87.23	4	8.51	2	4.26
Pisces	54	33	61.11	19	35.19	2	3.7

It is remarkable that these two basic components of the present Caspian population, originally of marine and fresh-water origin, surviving together the ensuing phases of salinification and freshening, have been merging with each other so that they have acquired similar biological peculiarities and similar distributions. In each of these we find groups that inhabit only the regions of the sea with waters of the highest salinity, or groups that are found only in the parts of the Caspian Sea where salinity is very low, or finally, we find the anadromous or semi-anadromous fishes migrating into rivers for spawning. These two basic divisions of the Caspian fauna have been joined by the recent immigrants from the Arctic seas and Sea of Azov and Black Sea basins.

The absence of a series of typically marine groups produces the so-called negative characteristics of the Caspian fauna. Only the fishes and crustaceans, and to a lesser degree the mollusks, show a comparatively large diversity. The originally marine species in these three groups compose about 60 per cent of all the free-living animals of the Caspian Sea. Another typical feature of the Caspian Sea is the presence of a very large number of endemic forms and groups. Altogether, up to 60 per cent of the entire Caspian fauna are endemics, and the percentage is much higher in some groups (Table 2).

This pronounced endemism is the result of the long isolation of the Caspian Sea and its fauna. The vigorous mass development of the recent immigrants from the Mediterranean fauna that have penetrated the Caspian Sea through the Azov-Black Sea basin is a typical feature of the Caspian Sea.

On the other hand, some of the ancient Caspian aborigines emigrated from the Caspian Sea at different periods of the Tertiary and Quaternary epochs (some in Recent time) and rapidly resettled a vast territory, and in some cases have become cosmopolitan in distribution. In ancient times the river crayfishes emigrated from the Caspian Sea or, more properly, from the pre-existing basin and became widely distributed in Eurasia and North America. The fresh-water Bryozoa, and the medusa *Craspedacusta* [*sowerbyi*] followed the same pattern. The hydroid *Cordylophora* [*caspia=lacustris*], the mollusk *Dreissena* [*polymorpha*], and the amphipod *Corophium* were introduced into the Baltic Sea via the Mariinsky system, and *Cordylophora* has been carried even farther, by ocean-going ships.[2] The Caspian animals, especially

[2 *Note by the Editor:* The Mariinsky system of canals connecting the Caspian and Baltic basins was first opened about 1808 or 1810 with the Mariinsk canal between the Vytegra and Kovzha rivers, flowing into Lake Onega and Lake Beloye respectively; the present system with canals around the southern parts of Lake Onega and Lake Ladoga was completed in 1852. The rates of dispersal postulated for these various organisms by Zenkevich are not excessive in view of the known

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TABLE 3.—*Comparison of qualitative content of the Caspian fauna with fauna of the Mediterranean Sea by the number of species*

Group	Mediterranean Sea		Caspian Sea		
	Total number of species	Per cent of the entire fauna	Total number of species	Per cent of the fauna of the Mediterranean	Per cent of the entire Caspian fauna
Echinodermata	101	1.7	0	0	0
Bryozoa	138	2.3	3	3	0.7
Polychaetes	433	7.2	5	1.2	1.2
Bivalve mollusks	366	6.1	16	4.4	4.0
Gastropoda	937	15.6	26	2.8	6.5
Higher crustaceans	620	10.3	90	14.5	22.5
Fishes	529	8.7	71	14.0	19.0
Fishes and higher crustaceans together	1,149	19	161	14.3	41.5

the fish and crustaceans, emigrate very readily into river systems, and many of them have formed local races in rivers.

The negative characteristics of the Caspian fauna, in comparison with those of the open sea, are determined by the absence of such typically marine types and classes as Radiolaria, calcareous and horny sponges, siphonophores, scyphomedusae and Anthozoa, Ctenophora, Nemertina, Brachiopoda, pantopods, crabs, cephalopods, echinoderms, tunicates; the skates and sharks among fishes; cetaceans are also absent from the Caspian Sea. Fishes and crustaceans in the Caspian fauna present comparatively much greater diversity than in the other sea basins (Table 3). Evidently fishes and crustaceans adapt themselves to existence in brackish waters incomparably better than do the majority of other groups, and they withstand better the subsequent changes in salinity of the basin they occupy. This is explained by the

spread of such organisms as *Eriocheir sinensis* and *Elminius modestus*. (*See* Chapter 23, pp. 786–787.) Whatever the original home of the fresh-water Bryozoa and *Craspedacusta* may have been, the dispersal of their resting stages by wind makes it difficult to prove their region of origin; for *Craspedacusta*, however, a strong case might be built on the basis of the occurrence of both sexes of the medusa in a population; as Russell suggests, the fact that most of the records of *Craspedacusta* are of monosexual swarms indicates colonization by a single hydroid in the resting stage, increasing by asexual budding and hence producing medusae of only one sex. (*See* Russell, F. S., *The Medusae of the British Isles*, Ray Society, 1953, p. 408–417, and biblio, p. 511 ff.) The occurrence of both sexes in the Kentucky River has been cited as evidence for the origin of this medusa in eastern North America by Payne (Biol. Bull., vol. 50, pp. 433–443, 1926). I have no information about the occurrence of both sexes in the Caspian region. The information available to Zenkevich in 1951 strongly supported his view that *Dreissena polymorpha*, a mollusk with pelagic eggs and larva, was of Caspian origin. It was first recorded by Pallas from the Aral region, in 1824. In 1825 it was first observed in the Baltic and by 1860 was found in the Seine and Loire rivers (van Benthem Jutting, *in Flora en Fauna der Zuiderzee*, p. 399, 1922). However, Tesch, in 1951, reported the finding of the species as a Pleistocene fossil in Holland, thus antedating the interlocking of European waters by canals in the early nineteenth century (Tesch, P., Geol. Mijnbouw., vol. 13, no. 4, p. 154, 1951); this record, however, is based on a single specimen (one valve?), in a core, and needs confirmation. While the Caspian region is rich in species of *Corophium*, it would appear, at least from the review of the genus by Crawford (J. Mar. Biol. Ass., vol. 21, no. 2, pp. 589–630, 1937), that only one species, *Corophium curvispinum*, may be suspected of having emigrated from the Caspian in historical times. The Caspian species, of which *C. nobile*, *C. chelicorne*, and *C. curvispinum* are the most abundant, fall into Crawford's group A, which he considers to be among the more primitive members of the genus. Concerning the river crayfishes, on the other hand, Bott (Abh. Senckenber. Naturf. Gesellsch. no. 483, 1950) considers the Caspian-Volga species *Astacus leptodactylus* and *A. pachypus* among the more specialized members of the genus, an opinion that might be cited in favor of the long residence of the genus in the region. See also the discussion of distribution and dispersal in Chapter 13, on biogeography, in this volume.]

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TABLE 4.—*Degree of endemism in the basic groups of the Caspian fauna*

Group	Total number of species	Endemics		Present in Black and Azov seas		Outside Ponto-Aralo-Caspian Basin	
		No.	Per cent	No.	Per cent	No.	Per cent
Crustacea	107	70	65.4	30	28.0	7	6.5
Mollusca	47	41	83.2	4	8.5	2	4.3
Pisces	54	33	61.1	19	35.2	2	3.7

presence of an integument that protects the body from osmotic processes. Also, it is characteristic of the fauna of the Caspian Sea that many forms have undergone a vigorous process of evolution and formed groups of numerous species and forms that have probably originated from relatively few forms, or even from one original form. To this category we refer the herrings, [*Caspialosa*] gobies, and *Benthophilus*, among fishes; amphipods, mysids, and cumaceans among the crustaceans; and cardiids, *Dreissena*, micromelaniids, and others among the mollusks.

In addition, the fauna of the Caspian Sea is characterized by a high degree of endemism. Not less than 60 per cent of all forms inhabiting the Caspian Sea are unknown outside this basin. If we consider this remarkable fauna in broader sense—*i.e.*, with those Caspian forms that also inhabit adjacent basins such as the Black, Azov, and Aral seas, and the river systems, the endemism would rise to 93–96 per cent (Table 4).

The high percentage of endemic genera indicates the great antiquity of the Caspian fauna. For instance, out of nine genera of gastropods, five are found only in the Caspian Sea; out of five genera of the bivalve mollusks four are endemic; two genera of clupeoids are also endemic, etc.[3]

A considerable part of the fauna of the Caspian Sea represents more or less ancient immigration from fresh waters. This immigration took place several times in the history of the Caspian Sea, during its least saline phases. In this respect, the most characteristic are cyprinoid and percoid fishes, and from other groups, cladocera, insect larvae, gastropods, rotifers, green and blue-green algae, etc.

After final separation of the Caspian and Black seas, and the connection of the latter with the Mediterranean and the subsequent population of the Black Sea by elements of the Mediterranean fauna, some forms of the latter penetrated the Caspian Sea via the Kumo-Manych depression and to the Aral Sea through the Usboi. Several millenia ago a number of species followed this route, including the marine plant *Zostera*, the mollusk *Cardium*, such fishes as *Atherina*, *Syngnathus*, and *Pomatoschistus*, and *Fabricia*, a polychaete. *Zostera* and *Cardium* penetrated even farther and now inhabit the Aral Sea.

In addition to these 6 forms, 14 representatives of the Mediterranean fauna have found their way into the Caspian Sea in the past 25 years through human interven-

[3 The endemic genera include the Micromelaniidae (which some consider Hydrobiidae) *Micromelania*, *Clessiniola* (pro *Clessinia*), *Nematurella*, *Caspia*, and *Caspiella* (Thiele considers *Nematurella* and *Caspia* synonymous); the cardiids *Adacna*, *Monodacna*, and *Didacna*; and the clupeoids *Caspialosa* and *Clupeonella*.]

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tion, deliberately or unintentionally. We shall discuss these later in connection with the acclimatization of new forms in the Caspian Sea. Six of these 14 forms have not flourished in the new basin and evidently perished; the other 7 forms have flourished vigorously and at present compose a very considerable part of the population of the Caspian Sea.

The fourth component of the Caspian fauna, the Arctic immigrants from the Arctic Ocean, is by no means the least interesting. About 15 species of crustaceans, fishes, and some other organisms accomplished their remarkable migration 15,000–20,000 years ago when immense water masses from melting glaciers were flowing southward into our southern seas. (The coast line of the Arctic Ocean at that time was situated hundreds of kilometers south of the present shores, and the northern shores of the Caspian Sea were hundreds of kilometers farther north).[4]

Among these immigrants are various biological groups, such as planktonic crustaceans (*Limnocalanus*, *Pontoporeia*, *Mysis*), benthic crustaceans (the isopod *Mesidotea*), several amphipods, several fishes, belorybitsa [*Stenodus leucichthys*], and salmon [*Salmo trutta caspius*], the seal, and some others. It is interesting that the seal carried its acanthocephalan parasite, *Carinosoma*, a typical arctic animal, to the Caspian Sea. Many of these Arctic immigrants have preserved all the peculiarities of cold-water inhabitants up to the present time. The seal propagates in winters on the ice field of the northern region of the Caspian Sea; many crustaceans live in the deeper layers of the sea where water is cold; the salmon and "belorybitsa" spawn in the coldest season of the year, etc. And still it remains amazing that this entire group of very cold-water inhabitants of the Arctic Ocean could have become adapted to this new environment which is so different from that of their aboriginal existence in the north.

The Caspian fauna, having been adapted in the course of historical events to the existence in brackish water easily enters river waters and expands its distributional boundaries along the river systems well above the river deltas. Again fishes, and in particular crustaceans, are far ahead in comparison with the other groups of the Caspian fauna.

The Caspian crustaceans in the Volga basin include 44 species, mainly amphipods, cumaceans, and mysids. Among the genetically marine fishes, not less than 18 species are capable of penetrating fresh waters; among these are the herrings, sturgeons, and gobies. Among the other groups, only a few of the autochthonus Caspian forms can penetrate the fresh waters. [The emigration of certain forms from the Caspian basin in recent times has already been mentioned.]

Strangely enough, the Caspian fauna shows relations with that of some far-distant basins, such as Lake Baikal and Ochrida in particular. For instance, the Caspian sponge (*Metschnikovia*) is closely related to the Ochrid (*Ochridospongia*) and the Baikal *Lubomirskia*. The fresh-water polychaete *Manayunkia* inhabits both the Caspian Sea and Lake Baikal, and a long series of Caspian and Baikal copepods are

[4 Ekman, *Zoogeography of the Sea*, 1953, p. 99, discusses other theories of the manner in which this migration may have occurred. These involve the damming of northern lakes by glacial action, resulting in transgressions of these lakes into the Caspian basin. Ed.]

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TABLE 5.—*Comparison of composition of the phytoplankton of the Caspian Sea with that of other seas in relation to number of species*

Group	Caspian Sea		Barents Sea		Karsk Sea		Azov Sea	
	Total	Per cent	Total	Per cent	Total	Per cent	Total	Per cent
Peridineae	28	16	47	43	84	30	52	28
Other Flagellata	17	10	3	3	15	6	7	4
Green algae	28	16	4	3	16	6	48	26
Diatoms	52	28	56	51	155	56	41	23
Blue-green algae	54	29	—	—	6	2	35	19
Total	179	100	110	100	276	100	183	100

undoubtedly related to each other.[5] All three basins preserve remnants of the ancient Tertiary marine fauna that once had a much broader distribution and which is now limited to a narrow area (relict). The peculiarity, considerable antiquity, and endemism of the Caspian fauna justify its classification as an independent zoogeographical salt-water region, partly marine and partly fresh water in origin.

The phytoplankton of the Caspian Sea is characterized by a considerable predominance of the blue-green and green algae (a result of dilution of salts), a phenomenon that has not been observed in our other seas (Table 5), and by the considerably smaller relative role of the diatoms and peridinians. Among the latter group, *Exuviella cordata*, because of its mass concentration, appears to be a basic food for the plankton invertebrates and plankton-eating fishes, sometimes with a biomass of 4.5–6.5 g/m^3.

Since 1934, *Rhizosolenia*, a diatom, has become an abundant species in the Caspian plankton. How it found its way into the Caspian Sea remains unknown. In some years *Rhizosolenia* has composed 80–99 per cent of the entire mass of the phytoplankton in the Caspian Sea, producing over 6–9 gr. or 10–30 million individuals per cubic meter of water. The mass plankton species are, among the green algae, *Dictiosphaerium*, *Botriococcus*, and others; and among diatoms *Skeletonema*, *Actinocyclus*, and others. Among blue-green algae the most abundant is a fresh-water *Aphanizomenon*.

The zooplankton of the Caspian Sea includes about 100 species, of which about 75 are rotifers and cladocera; only 22 per cent are copepods. Fresh-water forms make up more than half the number of species (Table 6).

The most mass-developing forms among the zooplankton are *Calanipeda aquae dulcis*, *Evadne trigona*, and *Cercopagis gracillima*.

The summer and autumn blooming of the Caspian plankton is far behind that in many other seas, particularly the Barents and Azov seas. In regard to plankton productivity, the Caspian Sea is also behind the Azov Sea. In deeper water the

[5 For a comprehensive review of the fauna of Lake Baikal, *see* J. L. Brooks, *Speciation in ancient lakes*: Quar. Rev. Biol., Vol. 25, Nos. 1 & 2, 1950.]

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TABLE 6.—*Correlation of the species in zooplankton of the Caspian Sea by group and origin*

	Per cent		Per cent
Rotifera	42.2	Fresh-water forms	56.
Cladocera	28.6	Brackish-water forms	7.5
Copepods	21.7	Marine forms	33.8
Others	4.5	Indifferent forms	2.2

TABLE 7.—*Vertical distribution of the plankton biomass in the Caspian Sea (in mg/m³)*

Depth in meters	Biomass in mg/m³		
	Northern Region	Central Region	Southern Region
0– 25	288	182	145
25– 50	—	122	93
50–100	—	103	49
100–300	—	36	36
300–500	—	17	14
500–800	—	0	0

quantity of plankton drops considerably, and below 300–500 meters it is almost zero (Table 7).

There are pronounced vertical migrations of plankton, plankto–benthos, and even benthos, in the Caspian Sea. At night, enormous quantities of crustaceans rise to the surface from depths of 50–100–200–400 meters. The surface water swarms with the masses of these organisms then to such a degree that when illuminated with an electric light the water has a milky color. Twice a day innumerable quantities of planktonic organisms cover distances of several hundred meters, which are great in comparison with their tiny bodies. Some of them accomplish vertical shifts of 80–90 meters in an hour. Therefore, the concentration of plankton in the different layers of the sea is entirely different for day and night (Table 8).

The phytobenthos of the Caspian Sea is characterized, first of all, by a predominance of green algae (25 species). Red and brown algae are consideraly fewer in number. Only three species of brown algae inhabit this basin. The flowering plants, such as *Zostera*, *Ruppia*, *Potamogeton*, etc., are widely distributed in the Caspian Sea, especially along the eastern shores. The biomass of *Zostera* here is as high as

TABLE 8.—*Changes in quantities of the plankton in different water layers of the Caspian Sea during 24 hours, in tons per sq km*

Depth	Central Region		Southern Region	
	Day	Night	Day	Night
0– 50	1.1	9.7	0.7	7.7
50–100	3.0	1.9	0.9	3.4
100–400	16.8	6.0	6.3	1.5

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TABLE 9.—*Qualitative comparison of composition of the faunas of Caspian and Black seas in regard to the number of species*

Groups	In the Black Sea	In the Caspian Sea
Sponges	42	5
Coelenterates	44	3
Polychaeta	123	5
Higher crustaceans	214	98
Bivalve mollusks	49	16
Gastropod mollusks	74	26
Fishes	143	71

1 kg/m². The total resources of this plant compose approximately 700,000 tons in raw weight, and it is utilized commercially.

The zoobenthos of the Caspian Sea does not vary very much, and in this respect it is less than the fauna of the Black Sea (Table 9). Altogether, there are about 350 species of free-living animals in the Caspian Sea. Although some animals reach great depths in the Caspian Sea, animal life even 100–150 meters below the surface is nevertheless very scanty. In the depths above 50 meters the mollusks predominate; in the deeper waters the crustaceans, and still deeper the worms are most abundant.

In the majority of cases the biomass of benthos is less than 100 g/m² and is seldom above this figure in the shallow depths.

The fishes of the Caspian Sea are quite varied, and they represent 14 families, of which 2 were introduced by man (flatfish and mullets) and 2 immigrated at comparatively recent times (*Atherina* and *Syngnathus*). The majority of species are representatives of such families as Gobiidae, Cyprinidae, Clupeidae, and Acipenseridae (Table 10).

We have already pointed out that the Caspian fishes are of different origins, mainly marine and fresh water, and that both groups compose homogeneous biological groups that have been formed as a result of protracted coexistence. Among the Caspian fishes, we can separate first of all a group of anadromous fishes which is richly represented here as well as in the Sea of Azov. Living in the sea, the anadromous fishes enter rivers for spawning, and very often they migrate far upstream. To this group in the Caspian Sea we refer the "vobla" [*Rutilus r. caspicus*] and many other cyprinid fishes; sturgeons, salmons, and some herrings.

To the so-called "semi-anadromous" group, we refer those fishes which frequent

TABLE 10.—*Composition of the Caspian ichthyofauna by family and number of species*

Petromyzonidae	1	Percidae	3
Acipenseridae	5	Gobiidae	30
Clupeidae	9	Osmeridae	1
Salmonidae	2	Syngnathidae	1
Cyprinidae	14	Atherinidae	1
Cobitidae	1	Pleuronectidae	1
Siluridae	1	Mugilidae	2

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the least saline parts of the sea and also migrate into the rivers to spawn. These are as follows: the sterlet [*Acipenser ruthenus*], the "sudak" [*Lucioperca lucioperca*], the bream [*Abramis brama*], and some herrings.

Similarly, among "marine" fishes of the Caspian Sea (those that spend their whole life in the sea) we find species of fresh-water origin as, for example, "marine sudak" [*Lucioperca volgensis*], and those of marine origin such as herrings and sprats. Thus, we find different biological groups even within a single family.

The Caspian herrings perform regular and quite complicated migrations within the basin itself. In winters they concentrate in the southern and middle parts of the sea, in summers they move into northern and middle parts where they forage intensively.

Caspian fishes feed in part on the plankton, in part on the benthos. Some of the fishes are predators in their habits. Many Caspian herrings (*Caspialosa*) and sprats (*Clupeonella*) live on plankton.

Among the fishes feeding upon benthic fauna, one can distinguish the mollusk eaters (such as the "vobla"), the crustacean eaters (many of the gobies, the bream and carp); the worm eaters (such as the sturgeons), and the predators ("beluga" [*Huso huso*], "sudak" [*Lucioperca lucioperca*], and some herrings). The total annual catch of the Caspian fisheries in pre-war years was about 4,500,000 cwt. The major part of the catch was taken in the northern part of the Caspian Sea, which produced an average of 32 kg of fish per hectare. The total annual catch in relation to the entire basin is only about 12 kg/hectare. Thus, the Northern Caspian Sea in its productivity occupies the next place after the Sea of Azov, while the entire Caspian Sea ranks only fifth in production.

The acclimatization problem in the Caspian Sea is theoretically the most interesting, and very important economically. Soviet investigators established the fact that the density of populations of the fauna (biomass) in our southern seas differs considerably. The Sea of Azov was found to be of the highest density. It is the most productive basin in the world. In regard to the annual fisheries catch, the Sea of Azov is more than twice as productive in comparison with the northern part of the Caspian Sea, the North Sea, and Sea of Japan. In some years the catch per hectare in the Sea of Azov is as high as 80 kg. Various fishes find in the Sea of Azov exceptionally favorable conditions for fattening.

If we attempt to characterize the biological productivity of the European south seas by the average quantity of benthic fauna and fisheries production, we obtain the values shown in Table 11.

The considerably higher density of animal life in the Black Sea and Sea of Azov in comparison to that of the Caspian Sea is dependent, of course, on the entire combination of conditions of existence. However, with sufficient degree of probability we can assume that this, to a certain measure, should be referred to the properties of the Mediterranean fauna itself, which evidently is stronger and possesses greater vital stability than the relict fauna of the Caspian Sea. In fact, numerous comparative experimental investigations of the Azov-Black Sea and Caspian faunas showed that many forms of the Azov and Black seas are more stable than those of the Caspian

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TABLE 11.—*Average quantity of benthic fauna (biomass) in grams per 1 square meter of the bottom in different seas and their fisheries productivity in kg/ha.*

Sea	Average biomass of benthic fauna in gr/m²	Fisheries productivity in kg/ha
Mediterranean Sea	5– 20	0.5
Black Sea	100–300	2.0*
Sea of Azov	200–500	80.0
Northern Caspian Sea	25–100	30.0
Aral Sea	20– 25	10.0

* The low value characterizing the fisheries productivity of the Black Sea is because the fisheries are generally maintained along the coast, but computations are made for the entire sea area.

TABLE 12.—*Comparison of nutritive content of worms, crustaceans, and mollusks*

Group	Fats	Albumins	Carbohydrates
Caspian mollusks	1.23	10.16	83.06
Caspian crustaceans	6.47	53.71	25.59
Nereis succinea, the polychaete of the Azov and Black seas	7.73	66.88	13.82

Sea in their ability to survive the fluctuations in salinity, oxygen content, and some other environmental factors.

Also, it was found that the faunas of the Azov and Black seas possess considerably higher nutritive qualities for the fish, mainly because polychaete worms compose the great part of the fish diet. These polychaetes are almost absent in the Caspian Sea. Among the larger groups of animals, at whose expense the fattening of the fishes goes on in the seas—worms, crustaceans and mollusks—the worms possess the highest nutritive qualities in terms of calories (Table 12).

Worms and crustaceans compose, by mass, about one-fourth of the entire animal population in the Sea of Azov but are only one-twentieth in the Caspian Sea. Taking into account the difference in caloric content of the fish diet in the Sea of Azov and the Caspian Sea, we could explain a considerably higher rate of growth of the fishes in the Azov Sea by this same difference. For instance, a bream [*Abramis brama*] of the 8-year class in the northern Caspian Sea is 37 cm in length, the fish of the same age in the Azov Sea is 43 cm long; the 15-year old Caspian sturgeon [*Acipenser güldenstädti*] reaches 123 cm in length, while the same fish in the Azov Sea is 142 cm long; for the 10-year old sevriuga [*Acipenser stellatus*] the respective lengths are known to be 114 and 134 cm, etc. Thus, it was established that sturgeons and bream in Azov and Black seas feed intensively on worms, but in the Caspian Sea, in the absence of this diet, they have to consume mollusks and crustaceans, which are less nutritive food elements.

One more very important factor is clear—namely, that the benthic fauna of the northern part of Caspian Sea is very scarce in relation to the quantities of fishes.

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TABLE 13.—*Relation of the catch of fishes feeding upon benthic fauna to the food quantities in the seas*

Sea Basin	A. Average annual catch in kg/ha	B. Quantities of the benthic population in kg/ha	C. Relation of A to B multiplied 100 times
Northern part of the Caspian Sea	24	417	5.8
Sea of Azov	16.3	3,214	0.5
Barents Sea	0.3	1,600	0.07

TABLE 14.—*Changes in quantities of benthic fauna in the northern part of the Caspian Sea after 1935*

Groups of benthic animals	Average quantities of biomass of benthic fauna in g/m²			
	1935	1937	1938	1940
Mollusks	34.62	7.60	3.99	19.54
Crustaceans	1.90	0.38	0.43	1.37
Oligochaetes	0.18	0.25	0.15	0.70
Others	0.14	0.06	0.17	0.51
Total	36.84	8.29	4.74	22.12

Here, in comparison with the Sea of Azov alone, there is very great competition among the commercially important fishes for the food supply (Table 13).

All these and other facts that have been obtained during the past 20 years have attracted the very keen attention of investigators. Furthermore, quantitative investigations of the benthic fauna have detected some phenomena in the northern part of the Caspian Sea that are taking place and which ultimately should reflect on the fishes of commercial importance. After 1935 the quantity of benthic fauna in the northern part of the Caspian Sea dropped sharply (Table 14), and by 1938 it was 10 times less than in 1935 (Fig. 4). Later the quantity of benthic fauna began to increase.

Thus, the mollusks suffered most, while crustaceans experienced a lesser drop in population density. It is true that by 1940 the quantities of benthos began to show an increase, but a decrease may recur. The sharp changes in the quantities of benthos in the northern part of the Caspian Sea have resulted from the recent changes in the regime of the Caspian Sea mainly in conjunction with the drought period. Reduction in the influx of river waters has caused a sharp drop of the level of the Caspian, an increase in salinity, changes in distribution of currents and sediment deposition, etc.

The regime of the Caspian Sea, as well as of the Azov and Aral seas, may experience further serious changes which certainly will reflect on their fauna and supplies of commercial fishes. In the near future we will witness the extensive reconstruction of our environment with the fulfillment of the 15-year plan to create field-protecting aforestation, and also of the majestic plan to irrigate the Trans-Volga region, the Caspian plains, and other drought-afflicted southern regions. One important part

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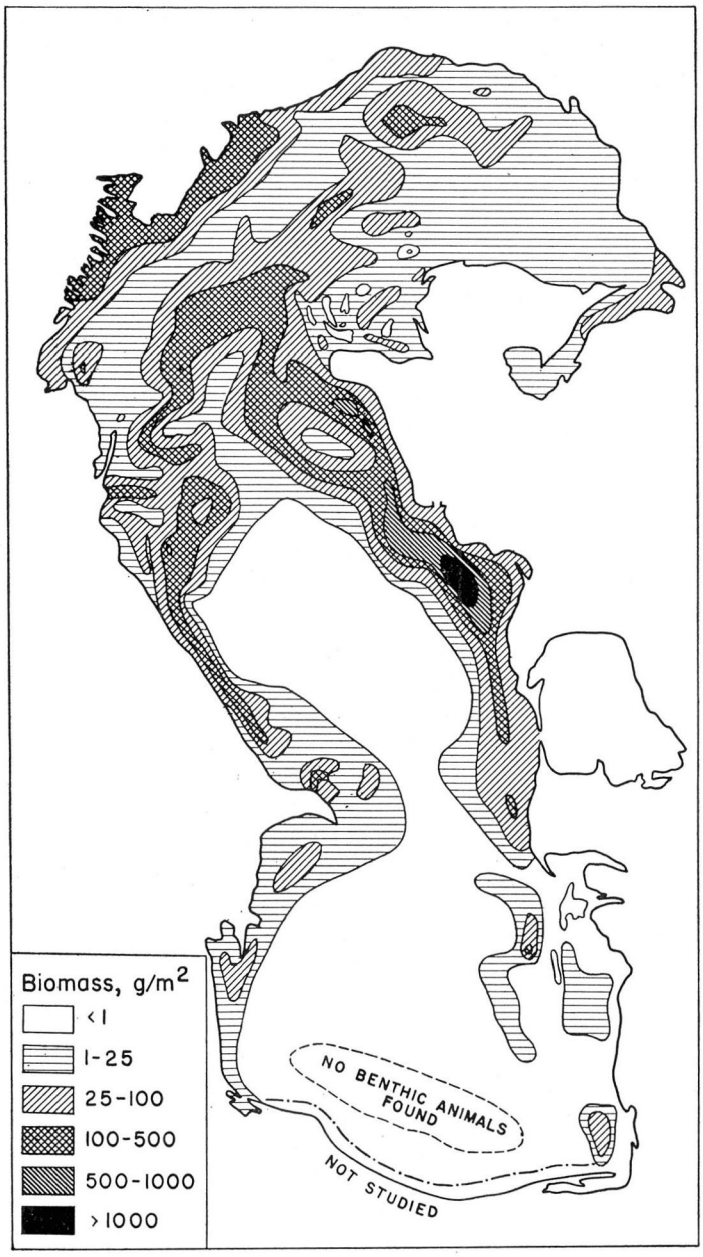

FIGURE 4.—*Distribution of the benthos biomass in the Caspian Sea in 1935*
Zenkevich (1951)

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of this plan is the reconstruction of river flow, which naturally should affect the regime of our southern seas and their fauna and flora.

Alongside all these investigations, of which we have spoken before, other remarkable facts have come to light.

Although the Caspian Sea at present is completely isolated from the Sea of Azov, some representatives of the flora and fauna of the Azov and Black seas have nevertheless penetrated into this basin by various means, either assisted by man or without his efforts. It is interesting to ascertain their fate in the new habitat. Several thousand years ago, *Zostera*, the marine plant, the bivalve mollusk *Cardium*; the little fishes, *Atherina*, the pipe fish [*Syngnathus nigrolineatus caspius*], and the goby *Pomatoschis*, and *Fabricia*, the polychaete, emigrated from the Sea of Azov through the Kumo-Manych depression. All these forms exist and thrive now in the Caspian Sea.

However, the process of immigration of the Mediterranean forms into the Caspian Sea has not yet ended. At the end of the past century and in the beginning of the twentieth century, the fisheries industrialists tried to introduce two species of flat fish, an oyster, the mussel *Mytilus*. Neither the oyster nor the mussel is now in the Caspian Sea. In prerevolutionary times and in the early Soviet time (1930, 1931) a flatfish (*Pleuronectes flesus*) was introduced. This species has not flourished in the Caspian Sea, but occasional specimens are still being caught. The other introduced species of flatfish (*Rhombus maximus*) has not been acclimatized here. The fate of other immigrants was a little different. Together with the small vessels transferred during the Civil War (1917–1920) from the Black Sea, a bivalve mollusk—*Mytilaster*—found its way into the Caspian Sea. This mollusk has multiplied immensely and at present is almost the most abundant species of the mass benthic organisms. In the early 1930's a mass planting of the two species of the commercially valuable mullets (*Mugil auratus* and *M. saliens*) from the Sea of Azov was carried out. Both species very successfully established themselves in the new environment, mainly in the southern part of the Caspian Sea, and at present they are objects of a substantial fishery. Two closely related species of shrimp (*Leander*) were released in the Caspian Sea with the mullets. These also thrive well in the Caspian Sea, but the "barabul'ka" (*Mullus barbatus*) and "hamsa" [*Engraulis encrasioholus*] from the Sea of Azov failed to develop. Also during the same period through unknown channels (possibly on the legs of migratory birds) a microscopic planktonic diatom (*Rhizosolenia calcar-avis*) found its way to the Caspian Sea. By 1934–1936 this species attained such a mass development that no one species of the native planktonic fauna could approach it.[6]

Thus, all these cases seem to prove that some Azov-Black Sea (Mediterranean in the broader sense) organisms can acclimatize well in the Caspian Sea and can reproduce there on a massive scale.

This knowledge should have been followed by the controlled introduction of the new forms and the application of planned system of measures leading toward a

[6] In 1955, *Syndosmya ovata*, transplanted in 1939 along with *Nereis* from the Sea of Azov, was first discovered in the eastern Caspian Sea, in rather large quantities. Up to this time we assumed that this species had not established itself in the Caspian. In 1956 *Balanus improvisus* was discovered in large numbers in the Caspian Sea, apparently introduced on vessels from the Sea of Azov through the Volga-Don Canal; it has multiplied like a "biological explosion." Most recently *Balanus eburneus* and the medusa *Blackfordia virginica* have been found in the Caspian. (Note by L. A. Zenkevich.)

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reconstruction of the Caspian fauna. As the above facts show, there is a great necessity for such reconstruction, and there are great possibilities in regard to utilization, first of all, of the rich fauna of Mediterranean origin of the neighboring Azov-Black Sea basin. Special attention should be paid to increasing the food supply for the commercial fishes of the Caspian Sea. When this idea was sufficiently studied, the basic details of the entire project were formulated as follows. It is necessary to introduce into this now-isolated basin of the marine character with its peculiar but qualitatively poor fauna new forms from the faunas of our other seas which could increase and improve the food base for the commercial fishes of the Caspian Sea, of which the sturgeons are the first to be taken care of. For solving this problem, it is necessary to select such forms (the acclimatization fund so to speak) which would satisfy the following requirements:

1. There must be a certainty that these forms could exist and reproduce massively under new conditions (in the new environment).

2. These forms should have high nutritive value, or at any rate not less than that of the native forms of the Caspian Sea.

3. There must be a certainty that these new forms will be readily used by the Caspian fishes as food in their diet.

4. Acute competition between the introduced forms and native forms should be avoided.

5. It is necessary to eliminate the possibility of introduction into a new habitat of some dangerous parasite along with the forms selected for acclimatization.

Beginning in 1936, extensive experimental investigations of the Azov- and Black-Sea faunas (and parallels for the comparison with that of the Caspian Sea) were undertaken. As a result of this study, a group of animal forms for planting in the Caspian Sea was selected; among these the sea worm (*Nereis succinea*) occupied the first place.

Biological and nutritive indicators of the selected worm gave assurance that this species satisfies all necessary requirements. It is the most valuable nutritive object of the diet of sturgeons, bream, and many other fishes of the Sea of Azov. This worm very easily stands sharp fluctuations in the environmental conditions; it is capable of abundant development both at low salinity and at a high concentration of salts, and it can exist for quite a long time in an environment lacking oxygen. It was established that *Nereis succinea* feeds mainly on detritus, of which there is an abundant accumulation in the northern part of the Caspian Sea. It is also important that this species has no parasites which could be considered dangerous.

In 1939–1941 about 65,000 *Nereis* were planted in the Caspian Sea.[7] The investigation of the stomachs of sturgeons caught in the western part of the northern Caspian Sea in 1944 revealed the presence of *Nereis* in masses. In 1948 this worm had already occupied an area of 30,000 square kilometers in the northern Caspian Sea (Fig. 5). In some parts of the western portion of the northern part of the Caspian Sea the density of population is very great (up to 1800 worms, weighing 86 grams, per square

[7 A detailed account of this experiment is to be found in the symposium volume edited by Nikitin (1952). Certain points about the habits of this worm, as reported therein, suggest the possibility that the *Nereis succinea* of this experiment and the *Nereis* (or *Neanthes*) *succinea* of western Europe and North America are different species. This is a question to be resolved by a specialist with adequate collections from various parts of the world.]

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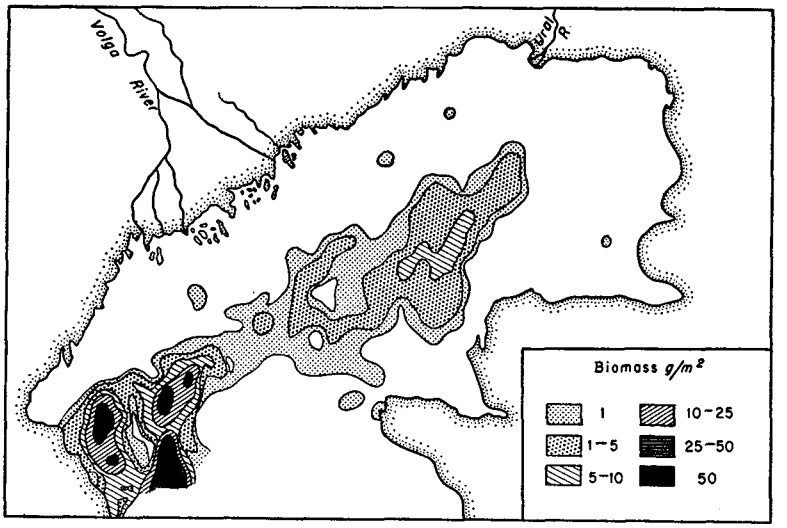

FIGURE 5.—*Concentration of* Nereis *in the northern Caspian, 1948*
Zenkevich (1951)

meter). The total quantity of this worm in the northern part of the Caspian Sea is estimated at 1½–2 million centners. The investigation of worms consumed by the fish indicates that all fishes in this part of the sea consume not less than 2 million centners annually. To understand the vastness of this quantity, let us assume that 2 million centners of worms were transported from the Caspian Sea by means of a railroad freight train. For this purpose we should need a train of 13,000 freight cars occupying 120 kilometers of railroad track!

At present *Nereis* occupies third place in the total mass of benthic fauna of the northern Caspian Sea (Table 15). As we mentioned before, when mature this worm easily adapts itself to the various salinity conditions of the basin. Its population remains unchanged when salinity is less than 2‰ or as high as 10–14‰. It is also known that this worm lives in the almost fresh water of Lake Paleostomi on the Caucasian shore. It is more sensitive to the type of the bottom: the soft silts are

TABLE 15.—*Quantitative composition of benthic fauna of the northern Caspian Sea*
g/m²

Animal Group	Average biomass in gr./m.²	In %
Mollusks	25.91	84.94
Crustaceans	1.96	6.42
Nereids	1.23	4.03
Oligochaetes	1.12	3.67
Others	0.29	0.94
Total	30.51	100.00

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rich in detritus and more favorable for mass development. As we shall see further, this is directly connected with its diet and the properties of its biology. The specific tendency of this worm to live in soft silts makes it an especially valuable component of the benthic fauna in the northern part of the Caspian Sea because these soft silts were much less populated by the native Caspian fauna. This is due to the unfavorable gas regime. With the insufficient circulation of oxygen, the silts rich in organic matter utilize it quickly, and the fauna perishes from oxygen deficiency. Here one more remarkable property of *Nereis* becomes evident: it can easily withstand short periods of absence of oxygen.

The study of the biology of this new inhabitant of the Caspian Sea has revealed a series of interesting particulars. The worms live in burrows up to 20 cm deep which they make in the sediment. The worm lives 1 year and dies after propagation. During propagation and immediately afterward, this worm is especially accessible to the fish because it abandons the burrow and swims about very intensively, reaching the sea surface. After propagation multitudes of dying worms are carried away by waves toward the shores. Here being favorable food, they attract vast numbers of birds, mainly gulls and crows. Searching for sea worms, they wade in shallow water and pick them up. An especially valuable quality of the species is its diet. It lives on silt rich in detritus and probably utilizes at the same time the innumerable bacteria inhabiting such silts. These silts are very little utilized by other animal forms, and the organic matter they contain is being lost from the food cycle and gradually transferred into greater depths of the Caspian Sea and deposited. The recycling of this unutilized and volumetrically colossal resource presents in itself one of the most valuable aspects of the entire business: masses of organic matter deposited in silts are transformed first into the body of the *Nereis* and then to the fish, and thus the potential resources of the basin are placed at the service of man. Feeding on silt, *Nereis* can also pick up the tiny animals inhabiting silts. All the benthos-eating fishes of the northern part of the Caspian Sea live on nereids. For some of them, and first of all, for the two sturgeons, *Nereis* has become a basic and sometimes almost sole food; it has also become an essentially important item in the diet of bream and "vobla" [*Rutilus r. caspicus*]. The two basic regions of concentration of *Nereis* in the northern part of the Caspian Sea correspond to the basic concentrations of the acipenserids fishes. Prior to the planting of *Nereis* in the Caspian Sea, the sturgeon and "sevriuga" lived on insect larvae (chironomids), crustaceans, fishes, and mollusks. Now they feed generally on nereids and consume almost no other food when this worm is available. With this change in diet, the sturgeonlike fishes have freed many million centners of food for other species (Table 16). Thus, the preference for *Nereis* to other food items by sturgeon and sevriuga and their active ability to select this worm is perfectly evident. Young generation of acipenserids and bream also feed on nereids. At present, sturgeonlike fishes are getting food of considerably higher caloric value and in not lesser quantities than before the planting of *Nereis* in the Caspian Sea. This, in turn, should reflect on the rate of growth, fertility, and fattening. In regions where the worm has not yet become established, the diet of the sturgeons in comparison with preceding years has not changed.

The bream also lives on *Nereis* everywhere it finds them, and they sometimes

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TABLE 16.—*Comparison of composition of benthic fauna with the stomach content of sturgeons in the region of Tulenii (Seal) island in northern part of the Caspian Sea*

Animal Group	Weight in per cent	
	In benthic fauna	In stomachs of sturgeons
Crustaceans	3.14	1.71
Insect larvae	1.58	6.27
Mollusks	94.65	0.00
Nereis	0.63	92.02
Total	100.00	100.00

compose more than a half of its stomach content. Many other fishes in the north part of the Caspian Sea also readily consume this worm.

The result of acclimatization of *Nereis* in the Caspian Sea is only the first successful experiment opening broad perspectives for reconstruction of the food base of the Caspian and Aral seas. The deepening and broadening of work on reconstruction of the faunas of our southern seas is a matter for the immediate future. Fisheries organizations possess a plan for further intensive action.

The Caspian Sea has one more remarkable biological feature. The richest concentrations of birds deeply connected in their biology with the marine flora and fauna are always present along the shore line. The delta reaches of such rivers as the Volga and Ural, and the bays such as Kirov's, Krasnovodskyi, and Hassan-Kuli, and many other places are richly abundant in birds. The birds gather here for wintering and for breeding from a vast territory, embracing the tropics, the Mediterranean region, Central Asia, and the Palaearctic Region. Files of black cormorants, lines of rosy flamingos, silvery clouds of gulls, dark swarms of geese and ducks, and multitudes of herons and pelicans are an inseparable characteristic of the Caspian shoreline landscape.

At a distance, the colossal flocks of resting birds in the sea look rather like large flat islands. At the approach of the boat or sound of a gun shot they fly up in the air with a deafening roar.

Among the birds gathering in the Caspian basin, there are two large groups, one of which migrates from the tropics, subtropics, and Mediterranean basin for breeding, while the other gathers from the vast stretches of the north for wintering. Among the first group of birds there are herons (and egrets), flamingos, sultan coots, ibis, curly and rosy pelicans, avocets, red ducks, and many others. As many of our birds undertake long migrations to breed in the far north, so do others fly to the Caspian basin to breed, very often from the far south. Innumerable masses of geese, ducks, swans, brants, gulls, grebes, and shore birds come here from the north.

It is difficult to estimate the total quantities of these birds, but one can state with confidence that the birds are counted in hundreds of thousands of tons, and the fish and various invertebrates they consume are counted in millions of tons annually. Some birds, such as cormorants, are excellent divers and fast swimmers. However,

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many of these birds, such as coot, gray goose, swans, sultan coot, and others feed on various shore plants.

II. ARAL SEA

The easternmost in the system of our southern salt-water bodies is the Aral Lake or Sea; in size it is the fourth largest land-locked basin in the world (Fig. 6). Its area is 64,490 square kilometers, and the greatest depth is 68 meters. The salinity of the Aral Sea is close to that of the Caspian and Azov seas; it is equal to 10‰, but the Aral Sea differs even more than the Caspian Sea from the open seas in regard to composition of salts (Table 17). The sulphate content exceeds 31 per cent of the sum of all salts, and sodium chloride makes up only 54 per cent.

The temperature of the surface water in summer time rises to 24–27°C. and in

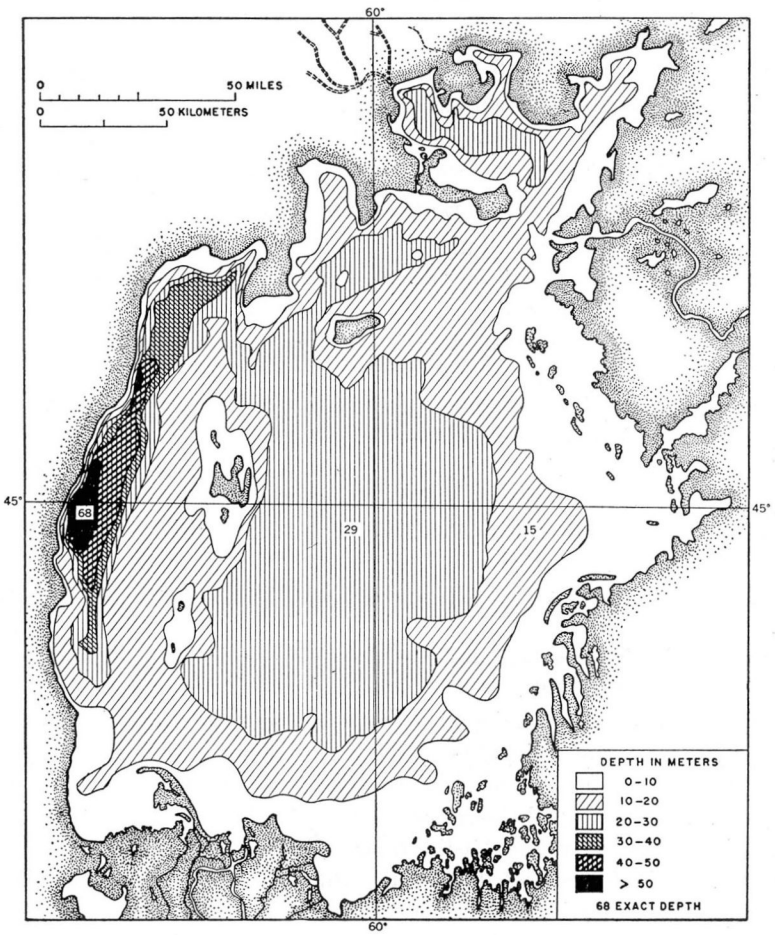

FIGURE 6.—*The Aral Sea*
Zenkevich (1951)

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TABLE 17.[8]—*Comparative composition by per cent of common ions in the Caspian and Aral seas* (Compiled principally from Clarke's Data of Geochemistry)

	Ave. ocean	Caspian Sea	Gulf of Kara-Bugaz		Aral Sea
			A	B	
CO_3	0.41	0.65	—	0.13	0.47
SO_4	7.68	23.89	17.39	15.57	31.12
Cl	55.04	41.91	53.32	50.26	35.51
Ca	1.15	2.44	—	0.57	4.25
Mg	3.69	5.87	15.83	7.07	5.45
Na	30.62	24.54	11.51	25.51	22.34
K	1.10	0.57	1.83	0.81	0.80
‰	35.00	12.80	285.0	163.9	10.75

the bays and harbors to 30°C. In winters, the temperature falls to zero, and for 4 months the Aral Sea is covered with solid ice fields along the shores and floating ice packs in the central part of the sea. The water temperature of the depths (over 25–28 meters) in the western part of the sea is uniformly low (1°–4°C.) all year round.

FLORA AND FAUNA OF THE ARAL SEA

Both flora and fauna are poor quantitatively and qualitatively (Table 18). However, in spite of the low salinity of this sea, the diatoms play the most important role in the phytoplankton in respect to mass development (mainly *Actinocyclus ehrenbergi*), and a much lesser rank is occupied by green algae (mainly *Botryococcus braunii*).

The zooplankton reflects to a greater measure its fresh-water character, and basically it consists of Rotifera and Cladocera. The most mass-developing form of zooplankton, *Diaptomus salinus*, a copepod, is also of fresh-water origin. It feeds on *Actinocyclus*, a diatom, and in turn it is consumed by fish larvae and sometimes by the adult fishes.

Among the bottom-dwelling plants the *Zostera*, which recently penetrated from the Mediterranean Sea through the Black, Azov, and Caspian seas, is of particular interest.

No group of animals in the benthos is represented by such a large number of species as the turbellarians (Table 19).

Most important in mass development of the benthos are some oligochaetes, the ostracod, *Cyprideis littoralis*, the same species as in the Sea of Azov; the only amphipod, *Pontogammarus aralensis*, which is very close to the Azov form; the bivalve mollusks *Adacna minima* and *Dreissena polymorpha*, both of Caspian origin; and finally *Cardium edule* from the Mediterranean basin, which probably immigrated simultaneously with *Zostera* and through the same channels. To these forms should be added the great quantities of larvae of caddis flies (Trichoptera) and chironomids.

The average biomass of the Aral benthos, consisting predominantly of bivalve mollusks, does not exceed 20 g/m²; in other words, it is not only less than that of the

[8] Added by editor.

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TABLE 18.—*Qualitative composition of the basic groups of population in the Aral Sea by number of species*

Group	Number of species	Group	Number of species
Phytoplankton	39	Phytobenthos	7
(diatoms)	18	Zoobenthos	48
Zooplankton	24	(of which—Mollusks	6
(Rotifera	8	Amphipods	1
Cladocera	7	Lower Crustaceans)	8
Copepods)	7	Fishes	20

TABLE 19.—*Composition of benthos in the Aral Sea by number of species*

Group	Number of species	Group	Number of species
Foraminifera	2	Amphipods	1
Nematodes	7	Gastropods	2
Turbellaria	12	Bivalves	4
Oligochaeta	3	Insect larvae	6
Bryozoa	1	Water mites	1

Sea of Azov but of the northern part of the Caspian Sea as well. In the Caspian Sea the biomass of *Dreissena* is not often 2–3 kg/m², in the Aral Sea it never exceeds a few tens of grams. The ostracod *Cyprideis littoralis* produces hundreds of thousands of specimens per square meter in the Sea of Azov, but in the Aral Sea hardly a thousand. The Aral plankton and benthos, although producing no high biomass indicators, serve as a good food base for the fishes.

The fishes of the Aral Sea are of fresh-water types—there is not a single representative of the clupeoids or gobies so abundantly represented in the Caspian Sea.

The ichthyofauna of the Aral Sea is represented mainly by the carplike species (Cyprinidae) (60%) and perchlike forms (Percidae) (15%). The basic objects of the Aral fisheries are carp, bream, and "vobla". The annual catch is about 400,000 centners (or 8–10 kg/ha).

From this brief analysis of the Aral flora and fauna one can conclude that besides the qualitative bareness of the basin, the most characteristic components of the relict Caspian fauna—crustaceans, mollusks, and fishes with the exception of a few forms—are absent.

This qualitative bareness can be explained only on the basis that this comparatively small sea has experienced such significant fluctuations of the hydrological regime, salinity in particular, that the greater part of the hardy Caspian fauna could not survive in this basin.

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The principal references to the Caspian and Aral seas, up to 1947, will be found in Zenkevich (1947). Most of the information appeared in the journals of the fisheries stations at Astrakhan and Baku, which are listed below. *See* also the journal listings for the preceeding chapter.

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(The listing follows the same scheme as in Chapter 25)

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Astrakhan. Volgo-Kaspiĭskai͡a nauchnai͡a rybokhozi͡aĭstvennai͡a stant͡sii͡a. Trudy.

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Geol. Soc. America
p.917–934, 2 figs.; 1 pl.

Memoir 67, Vol. 1, 1957
Made in U. S. A.

Chapter 27
Lunar Periodicity

P. KORRINGA

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In Nature many phenomena recur again and again in the same order. These are the cycles, which can be of very diverse duration. Geological cycles require millions of years and are a fascinating reality for only a small group of adepts. The daily cycle, on the other hand, the eternal alternation of day and night, is self evident to everybody, because man himself as well as many of the living creatures of his daily environment synchronize their periodic activities, feeding hours, and rest with this natural cycle. Few realize that many short-lived small organisms show a different pace of living, and that to them the 24-hour cycle is comparable to our annual cycle. Much has been written about this daily rhythm in nature, even in mathematical formulae. Many creatures exhibit a daily rhythm with such a great precision, and are so hard to disturb by experimental conditions, that the rhythm is considered as endogenous, as resident in the protoplasm (Park, 1941). It is hard to believe that. It would be very surprising indeed if careful and prolonged experimentation with artificial cycles, not differing too much from the natural 24-hour cycle, would not induce organisms of the so-called endogenous type to adopt eventually the new rhythm. The tenacity with which man, and still more so many other living beings, sticks to the usual 24-hour cycle under artificially changed conditions should sound a warning to the investigator who wishes to study natural cycles experimentally.

The annual cycle, the eternal sequence of the seasons, is a reality to everybody living in the temperate region. This is not so much because man himself follows an annual rhythm in his biology. Since time immemorial man has made himself practically independent of the seasons by storing food, by creating an equable microclimate inside his clothes, and by maintaining a climate to his own taste indoors. But most of the plants man has to cultivate for food and most of his cattle and fowl show a marked annual rhythm in their biology, and man, in his animal husbandry and agriculture, must consider these rhythms. The man in the street—perhaps we could better say "the man in the field" in this respect—is inclined to believe that it is primarily the rise in temperature which induces the plants to flower in spring and summer, the hardier the species the earlier in the year, and also that it is self evident that it is the approaching cold weather that drives the migratory birds southward in autumn. Scientific investigations revealed, however, that in many cases light is the factor which predominates in controlling these seasonal patterns of life. That some plants flower early in the year, others in midsummer, and still other species very late in the year appeared to be controlled in most cases by the length of the day, and not primarily by temperature. Experimental evidence could be adduced to demonstrate that some plants are so sensitive in this respect that they can "perceive" a difference in day length of half an hour! Though there is a rhythmical alterna-

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tion of light and dark (the daily cycle) and though the intensity of the sunlight varies considerably according to weather conditions and to the hour of the day, many plants can "measure," in a way not yet understood, the length of the days and regulate the time of their flowering accordingly. We should not assume, however, that all seasonal periodicity in plants is controlled by the length of the day. Tulips, for instance, can be forced to flower in an unusual season by subjecting the bulbs to a certain low-temperature treatment. This is what the bulb growers do before exporting bulbs to the Southern Hemisphere.

A system similar to that in plants holds good for the seasonal behavior of migratory birds. The cyclic increase and decrease in the length of the day (here also notwithstanding the daily alternation of light and darkness, and notwithstanding irregular changes in light intensity during the daylight hours) bring about cyclic events in the gonads of birds and in their migratory habits.

It is well to consider and study such phenomena before we turn to the organisms living in the sea, about which we still know so little. Some denizens of the sea exhibit a daily rhythm in their activities; many others do not. Most of the organisms living in temperate seas follow an annual rhythm—*e.g.*, by migrating to special feeding or breeding grounds in a given part of the year, and by limiting their reproductive activities to a shorter or longer period. Experiments have demonstrated that in the sea temperature is the factor that often controls to a high degree the initiation of the spawning season, in a lesser degree its termination. The factor of light should not be neglected, however. As the food chains in the sea invariably begin with CO_2 assimilation by small plankton organisms, periodic changes in duration and intensity of sunlight do exert their influence on the availability of the primary food. To what extent the length of the day is of influence on fish migrations is still unknown.

There is, however, ample evidence that cycles other than daily and annual rhythms exist among the organisms in the sea. Rhythmic fluctuations in the reproductive activities of marine organisms have been known for a long time. These cycles appeared to run so closely parallel to the lunar cycle that the term "lunar periodicity" was adopted. This does not necessarily mean that there is a direct causal relation between the moon's phases and the behavior of the marine organisms under consideration. Very precise information has been gathered on lunar periodicity in the spawning of two species which man collects as food while they perform their nuptial ritual—viz., the grunion and the Palolo-worm. The data collected over many years revealed so striking a parallelism between the lunar cycle and the periodicity in spawning that one feels oneself almost forced to admit that some kind of correlation must exist between the two phenomena, though it is hard to see how.

Here trouble starts, for many scientists are very skeptical when they hear about an influence of the moon on living beings. Since prehistoric times the moon has played an important part in popular belief and superstition. The moon is said to affect weather conditions, to influence the germination of the seed committed to the earth, to exert her influence on several marine animals, causing them to be "full" with the waxing and "empty" or "spent" with the waning of the moon, and so on. In modern times, science—going her way—is inclined to smile at these articles of popular belief, but anthroposophists, working in the borderland between mysticism

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FIGURE 1

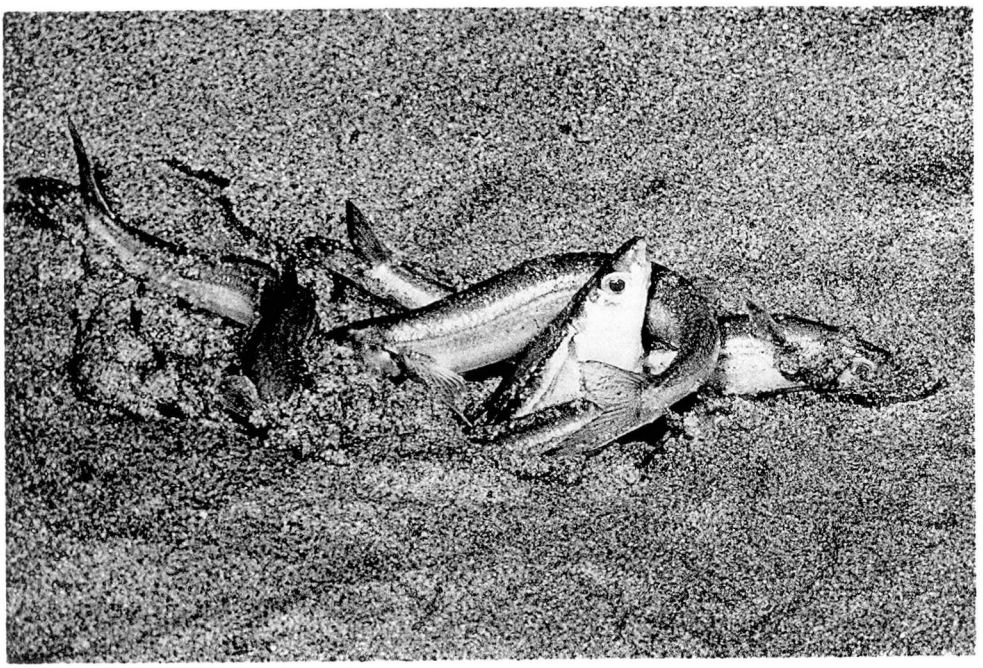

FIGURE 2

SPAWNING OF THE GRUNION ON A CALIFORNIA BEACH

The female digs a nest with her tail, while the male arches his body around her, releasing milt over the eggs.

Photographs by Joseph Brauner, courtesy Boyd W. Walker

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and superstition, try to give them a scientific tinge and do their utmost to stress the importance of the moon's influence on living beings. Unfortunately the authors who have studied lunar periodicity in the spawning of marine organisms broke down in their first efforts to investigate this matter experimentally. They therefore found it very difficult to offer a clear explanation for the facts observed and resorted to far-fetched hypotheses such as influence of the moon's gravitation, declination, or mysterious radiations, or of changes in electrical potentials and ionization of the air brought about by the moon. Though it is unwise to reject any hypothesis before irrefutable proof has been furnished on how Nature does work, it is easy to understand that many a naturalist shrugs his shoulders and turns to other problems.

Let us face the facts, however. There appear to be two entirely different types of lunar periodicity in the spawning of marine animals. One is operating on a fortnightly basis, the other once a month only.

A well-known example of a fortnightly rhythm is that of the spawning of the grunion (*Leuresthes tenuis*), a small atherinid fish which deposits its eggs in the sand of the beaches of Southern California (Pl. 1). To accomplish this, the grunions must leave the water for a short while. The eggs should remain buried in the sand for a fortnight and hatch when the tide washes them out again. If this does not happen after about 2 weeks, they still can hatch when washed out by the next series of high tides 14 days later. The spawning season of the grunion extends from late February or early March to August or early September. The actual spawning is restricted to a relatively few hours during this period. The grunion spawns only on 3 or 4 nights following each full or new moon, and then only for a 1 to 3 hour period immediately after high tide. During such a spawning run the beach may literally be covered with mating and egg-depositing grunions. None may be found an hour later. Clark (1925) adduced convincing evidence that the individual fishes participate in reproduction once every spring-tide—that is, at fortnightly intervals. Clark could track the development of the fortnightly batches of eggs; egg ripening appeared to require about 15 days. Detailed information is available to convince every skeptic of the vivid reality of lunar periodicity in the spawning of the grunion (Thompson, 1919; Clark, 1925; Walker, 1952), but the causal relations in this peculiar phenomenon are not yet clearly demonstrated.

Several authors have stated that only a few tides are suitable to bury eggs so that they remain covered by sand until they are washed out by wave erosion a fortnight later, and that it is just these tides the grunions utilize. Just how this timing is controlled is not known. One could think of the selective value of a correct spawning rhythm as, generation upon generation, only those fishes which do bury their eggs at the right moment will be successful in reproduction. But this does not explain just how the close association with the moon's phases is brought about. How can the grunion "know" early in each new spawning season—which may or may not be its first spawning season—that the correct tides have arrived, and how can it "know" when exactly the right hour is there, when the tide just starts receding? The moonlight need not be taken into account, for the runs come twice a month, after full moon and after new moon. The run does not start a certain time after sunset, for sunset takes place much earlier in March than in July, and high tides come

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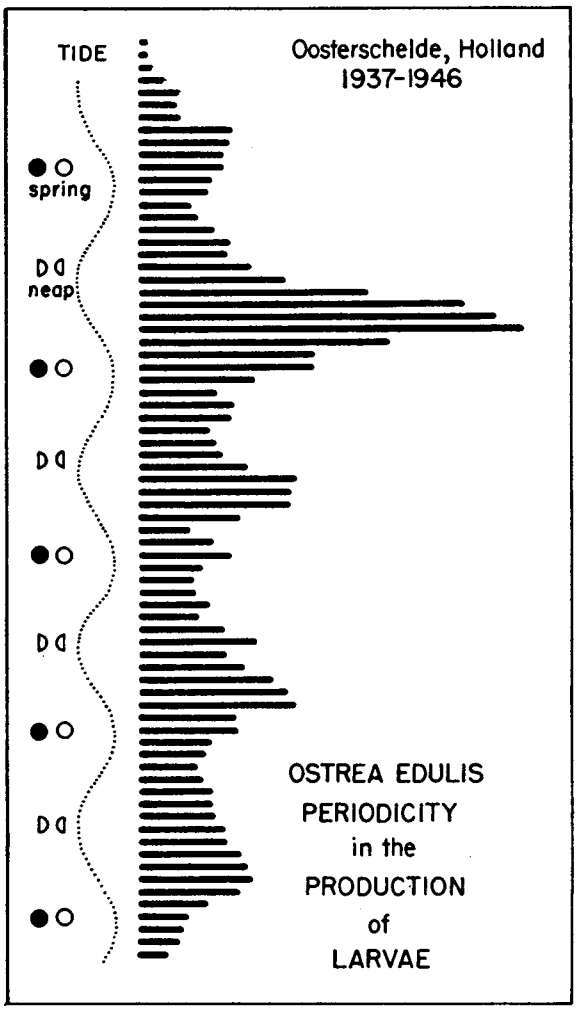

FIGURE 1.—*Periodicity of* Ostrea edulis
From Korringa (1940)

later in the night at new-moon springs than at full-moon springs. In the Gulf of California another atherinid, *Hubbsiella sarelina*, accomplishes its spawning runs in the late afternoons in February and April (Rechnitzer, 1952). This daylight run appears to be timed with the high spring tides (the tidal regime is incompletely known) and suggests that neither moonlight nor sunset have any influence on the timing of the grunion.

Unfortunately, the problem has not yet been approached experimentally, and it does not seem an easy task to do so. The writer feels convinced that the causal relations operate through the rhythm of the tidal cycle. The tides in the sea are probably just as important for many marine creatures as is the rhythm of day and night

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for man. We discussed above how plants, birds, and probably other denizens of the land react on the periodic lengthening of the days, notwithstanding the 24-hour rhythm of day and night and the fluctuations in light intensity. Is it too bold to suppose then that many marine creatures can perceive both the short tidal rhythm and the alternation of springs and neaps? If it could be demonstrated that such is the case it would no longer be so mysterious that grunions "know" when the right days for a run have arrived, and which is the correct hour to run! We are inclined to underestimate the vital importance of the tidal rhythm in marine biology, perhaps because the tides are not of biological importance to us. We do admit that the tidal cycle is of great importance for organisms living in the inter-tidal belt, but few biologists are aware that under fully marine conditions many creatures living below low-water level, including many that never adopted a sedentary style of living, exhibit periodic activities correlated with the tides. In this respect the investigations of Gompel (1938), who studied the oxygen consumption of a variety of organisms living in the coastal waters of northern Brittany (France), where the tidal range is considerable, are very interesting. Gompel found that organisms belonging to a variety of systematic groups, including fishes, show a rhythmical increase and decrease in oxygen consumption not correlated with the hours of the day but with the rhythm of the tidal cycle. Peculiarly enough, Gompel's animals carried on with the rhythm in his tideless aquaria. Some could even go on for weeks without losing pace with the tide in free nature! This remarkable experiment demonstrates a great tenacity to stick to the natural rhythm of the tides, just as has been demonstrated to be the case with the daily rhythm in many creatures living on the land. Anthroposophists would welcome these data as irrefutable proof of a mysterious influence of the moon, independent of the tides! Further experimentation in this fascinating field will be very welcome, especially efforts to make fishes and other marine creatures adopt a physiological rhythm correlated with an artificial man-made tidal cycle. Only in this manner can we find out whether both the shorter and the longer cycle is perceived, and utilized to synchronize breeding activities. As it seems logical to think in the very first place of rhythmical changes in water pressure as being perceived, and being the agent in synchronizing a tidal periodicity like that found by Gompel, special attention should be paid to this factor in the experiments. What we do know about rhythms in birds and plants does not make us hesitant to suppose that both the twice-daily and the fortnightly rhythm of the tides could be observed.

There are many other cases of lunar periodicity in the breeding of marine animals which resemble very closely the case of the grunion. Here also we can distinguish an *annual rhythm*, a breeding season of longer or shorter duration, which may be controlled by water temperature, a *lunar periodicity*, perhaps better called a tidal periodicity, which brings about maxima in spawning twice a month during the entire breeding season, and next a *daily rhythm*, which limits spawning activities to certain hours of the day, or of the tidal cycle. The biological advantage of such a system is clear. It tends to concentrate spawning in short periods, sometimes to a few hours a year. It is self evident that this greatly enhances possibilities of fertilization and cross-breeding. Knight-Jones (1952) advanced the interesting view that another biological advantage of lunar periodicity in breeding may be that the critical days of change

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from lecithotrophic to planktotrophic habits of the larvae may coincide with neap tides when turbidity and turbulence are at minimum in inshore waters. In studying the cases of a bimonthly rhythm it should be clearly understood that a definite tidal height is not the trigger mechanism which makes things run. Organisms brought into the laboratory some time before the natural spawning maximum is to be expected are not upset but perform just as well. In all cases it is a question of rhythmical ripening of eggs and sperm synchronized with the cycle of neaps and springs. The maxima are therefore not necessarily observed at full or new moon. Fage and Legendre (1927) observed, for instance, that *Platynereis dumerilii* performs its nuptial dances at first and last quarter only, in the waters of Concarneau (Brittany, France). The polychaete worm *Ceratocephale osawai*, on the other hand, shows clear maxima at new and full moon (Izuka, 1903). *Odontosyllis phosphorea* swarms in July and August 6 to 9 days after full and new moon, but in September about 15 days after full and new moon (Potts, 1913; Fraser, 1915). The writer explained this tentatively in terms of egg ripening requiring more days later in the season (Korringa, 1947).

Some animals incubate their larvae for some time, so that swarming of the larvae is to be observed a certain number of days after the eggs have been laid. Thus *Spirorbis* expels its larvae at first and last quarter, as a result of spawning at both full- and new-moon spring tides (Garbarini, 1933, 1936; Knight-Jones, 1951). The European flat oyster, *Ostrea edulis*, does not confine its spawning so very neatly to spring tides as *Spirorbis* does, but analysis of a great number of quantitative data collected in Holland revealed that this oyster shows marked maxima in spawning at both spring tides, leading to maxima in the emission of larvae about 8 days later (Korringa, 1947). As a rule, one of these maxima predominates. In the Oosterschelde (Holland) the most important maximum in the emission of oyster larvae is to be expected between June 26 and July 10, about 10 days after full or new moon (Fig. 1). This also held good for the period 1947 to 1956 inclusive.

It is surprising to learn (Caspers, 1948; 1949; 1950) that lunar periodicity in reproduction is found even among insects which have adopted the marine habitat. The larvae of the chironomid dipteron *Clunio marinus* Haliday live in tangles of algae in the intertidal zone, *e.g.*, near Helgoland and near Varna on the Bulgarian coast. The imagos, of which the females are wingless, are very short-lived. Within a few hours after leaving the pupa, copulation and egg deposition must be completed (Fig. 2). The egg strings are glued to some substratum and adhere very firmly. It is clear that all the ceremonies can be completed only in periods when the habitat is exposed for several hours in succession—*i.e.*, at spring tides near Helgoland and during the offshore winds in the morning hours near Varna in the Black Sea. It is therefore not so surprising that the swarming of *Clunio* is concentrated at both spring tides at Helgoland and at the early-morning hours of any day near Varna. Caspers tried to analyze the causal relations of this case of lunar periodicity. He transported *Clunio* larvae from Helgoland to Varna and kept them in the laboratory there. He exposed the algae lodging the larvae every day from 7–8 a.m. and from 5–8 p.m., which is an artificial tide not parallel to that in nature, and which eliminates the difference between spring and neap tides. Caspers found that the imagos appeared at the very

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same period they would have done in Helgoland (*i.e.*, in the days following the new and the full moon), and at the same time of the day (*i.e.*, 80 minutes earlier than they would have done at Helgoland, which corresponds with the 20-degree difference in longitude). Laboratory experiments demonstrated that even when *Clunio* pupae remained covered by water the imagos could escape, but could not possibly deposit their eggs on the immersed algae. From these observations Caspers concludes that it is not exposure to the air which provokes the emerging of the imagos, and that this case of lunar periodicity shows no causal relations with the tides.

If a man goes to sleep in a darkened room, he will nevertheless wake up the next morning, and a bat sleeping in a dark cave will fly out precisely at dusk. Would Caspers conclude from those observations that the rhythm of day and night has no causal relations to these phenomena? As *Clunio's* habitat is exposed at both spring tides and most of the neap tides, Caspers concludes that the spring tide cannot possibly control the periodicity in swarming. One should not forget, however, that both the number of hours of exposure and the column of water covering the habitat at high tide are considerably greater at spring tides than at neaps, and it certainly is not impossible that living beings "perceive" this in some way or other. As the swarms appear at both new-moon and full-moon spring tides at Helgoland, it is certainly not the moonlight which brings about the rhythm. Therefore Caspers himself feels compelled to adopt more far-fetched hypotheses, like influence of the moon's declination. The writer believes Caspers is too quick with his conclusion that the tides cannot possibly bring about the causal relation between the moon and the swarming of *Clunio*. In no other cases of lunar periodicity do moon-controlled conditions prevail at a certain instant or moment of time to call forth "running," swarming, nuptial dances, egg deposition, etc. It is always a case of rhythmical maturation, parallel to the rhythm of neaps and springs, and bringing about a concentration of reproductive activities, which is a biological advantage, as fertilization possibilities are thus greatly enhanced. This is more so when the nuptial ceremonies are moreover restricted to certain hours of the day or to a certain phase of the tide. Great tenacity to such rhythms of paramount biological importance is a common feature. That such rhythms are not easy to break by short-termed experimental conditions has been shown by Gompel. If one finds, like Caspers, that a periodicity in breeding is maintained for some time, notwithstanding the experimental conditions, this does not prove that the tidal rhythm has nothing to do with such a rhythm. It will require long-term

FIGURE 2.—*Clunio marinus*

A. A congregation of males. B. Copulation, showing attempt by a second male. Drawn from observations at Helgoland. (From Caspers, 1951.)

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experimentation with an artificial rhythm of neaps and springs to induce *Clunio* and the like to change their habits. As long as such experiments have not been carried through, the writer is reluctant to adopt hypotheses involving influences of the moon's declination, culmination, gravitation etc. The absence of a lunar rhythm in *Clunio marinus* in the Black Sea, where all influences of the moon, except the tides, are to be expected, speaks strongly in favor of springs and neaps as controlling factors in this case of lunar periodicity.

There are many other cases of a bimonthly rhythm in breeding of marine animals, but only rarely are the data at our disposal so complete as in the case of the grunion. One may expect that further investigation will reveal that a great number of marine animals tend to limit their reproductive activities to short periods synchronized with the bimonthly tidal rhythm. But, without doubt, many other, often closely related creatures will show no trace of such a rhythm.

A few cases of masked tidal rhythm in breeding were discussed earlier (Korringa, 1947). This may occur in regions where the two spring tides differ greatly in range. In such a case rhythmical breeding is synchronized with the predominating spring tide only. In species with a prolonged breeding season—*e.g.*, in the coral *Pocillopora bulbosa*—the synchronization with the predominating spring tide leads to shifting over in the course of the year from a full-moon rhythm to a new-moon rhythm.

A good and well-known example of the second type of lunar periodicity, operating once a month only, is the swarming of the Palolo worm, *Eunice viridis* (Gray). The natives of Samoa and the Fiji islands have known since time immemorial that the Palolo worm can be expected to swarm above certain old coral reefs, often in incredible numbers, at the last quarter of October and November (Samoa) or of November and December (Fiji). As baked Palolo worms are one of their favorite dishes, swarming of the Palolo always calls for a gaudy feast. Missionaries reported about it, but only in the last few years of the nineteenth century were attempts made to reveal the real nature of this phenomenon. The swarming worms puzzled the investigators, for one could not detect a head! After a careful study it was found that the swarming worms were nothing but the posterior part of a polychaete worm of the genus *Eunice*, tightly filled with eggs (which give the worm a bluish-green color) or sperm (giving the worm a red or brown color), while the anterior and thicker part of the animal, including its head, remained in its shelter in the old honey-combed coral rocks. The posterior or epitokous part of the body is far thinner and longer than the anterior part and carries eye spots on the ventral surface of each of the numerous segments. The worms were detected in the old decaying coral rocks almost simultaneously by several investigators. Friedländer (1898 to 1904) procured the first worm that clearly displayed the transition from thicker anterior part to the thin epitokous part of the body, but the way he defended his priority in his papers (1904) is far from sympathetic: "dass der zoologische Hauptteil der Palolo-Frage von mir, und zwar von mir zuerst, und von mir allein, definitiv entschieden worden ist."

It is, however, the peculiar rhythm in swarming which attracts our attention here. So many data have been collected on the occurrence of the swarms of the Palolo-worm that not the slightest doubt remains that they indeed appear at last quarter

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of the months mentioned. Corney (1922) gives a list of dates covering 25 years of observation at Levuka (Fiji), and as his paper is quite rare in libraries his tabulation is given here in full, to show with how great a regularity the swarms appeared:

1897	17 November	F.M. +8	1910	25 November	F.M. +8
1898	7 November	F.M. +9	1911	13 November	F.M. +7
1899	25 November	F.M. +8	1912	2–3 December	F.M. +8/9
1900	14 November	F.M. +8	1913	21 December	F.M. +8
1901	5 December	F.M. +9	1914	11 December	F.M. +9
1902	22 December	F.M. +7	1915	29–30 November	F.M. +8/9
1903	11 December	F.M. +7	1916	17 November	F.M. +8
1904	1 December	F.M. +9	1917	7 November	F.M. +8
1905	19 December	F.M. +8	1918	26 November	F.M. +8
1906	9 December	F.M. +9	1919	16 November	F.M. +8
1907	28 November	F.M. +9	1920	4 December	F.M. +9
1908	17 November	F.M. +9	1921	23 November	F.M. +8
1909	5 December	F.M. +8			

There are many efforts to give a plausible explanation of the sudden and regular appearance of the dense swarms of the Palolo worm. The tidal rhythm is not very impressive in these Pacific waters, and, though slight differences between full-moon and new-moon spring tides may be observed, predominance of full-moon spring tides alternates with a preponderance of new-moon spring tides a couple of years later. As *Eunice* appears only at the last quarter and stays away at the first quarter, we can agree with Friedländer that the tides cannot be held responsible ("zufolge den Gezeiten ist das Paloloproblem nicht zu erklären"). Brunelli and Schoener (1905) considered that the case of the Palolo represented the highest degree of emancipation from external factors, as the rhythm in *Eunice's* reproduction seems to be completely endogenous. They do, however, believe that the tides may have something to do with it, but do not explain why it is only after full moon and not after new moon that the swarms appear. Woodworth's statement "the Palolo makes its appearance in Samoa in the months of October and November during the last quarter of the moon. This is the time of lowest spring tides when the reef flats in shallow places are uncovered or only awash, and at this season the sun is nearest to the zenith" is not quite correct, as the last quarter coincides with neap tides, and as spring tides occur twice during the lunar cycle. Perhaps Woodworth wanted to give an explanation of the somewhat higher water temperatures at this time of the year, but this can only help us in finding an explanation for the occurrence of the breeding season in the months mentioned, and not for the peculiar rhythm.

Krämer placed blocks of coral containing the worms in a pail filled with sea water the day preceding last quarter and saw that the worms swarmed in the pail (without tidal influence) as they did outside in the sea. Though the possibility remains that lack of oxygen in the pail of water forced the worms out of the stone (but then the whole worms, not the epitokous parts only), we should not be surprised to find the worm swarming under controlled oxygen conditions as well, as the worm starts swarming after termination of the maturation process.

Friedländer (1899a) tried to correlate the phenomenon with differences in illumination, but, as he found that swarming took place in the early morning before dawn, and

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that an overcast sky intercepting the moonlight did not prevent the appearance of the worms, he did not succeed in finding a plausible explanation. In his despair he caught at Arrhenius' quaint, never-corroborated theory, that the phases of the moon could exercise an influence on living beings, by causing differences in atmospheric electricity, but after a careful study Friedländer admitted that he found himself forced to reject this possibility, and that the periodicity remained "vollkommen rätselhaft."

Friedländer could have devised a plausible explanation but for his lack of biological imagination. He suggests once the possibility that maturation could initiate at the full-moon spring tide but did not mention it again. He cannot see how on earth the moon can exercise an influence on the adult worm living coiled up in its burrow in the coral rocks.

Krämer (1899) had a better idea of the animal's way of living: "Nun liebt aber der Palolo das Licht nicht; sein Freund ist die dunkele Nacht, wenn er auf Abenteur ausgeht." The writer explained earlier (Korringa, 1947) why he believes this is the key to the problem. The Palolo worm living in shallow water (but not in the tidal flats) is found coiled up in a burrow in the old honey-combed coral rocks during the daylight hours. It cannot stay there forever, for it has to collect its food. Since it is no plankton strainer or rock eater, it must leave its burrow, at least with its anterior part, which it does during the hours of the night. Krämer is certainly right in stating that the Palolo has a nocturnal style of living. As the tides are of little importance and temperature is quite equable throughout the year, at most showing a slight increase during spring and summer (October, November, December), the rhythmical sequence of periods with dark and moonlit nights must be of paramount importance in this animal's biology. During the breeding season, which is quite short in this worm, the moonlit nights evoke a simultaneous ripening of the gonads. It is not the intensity of moonlight that counts most—this being somewhat different at various depths—but the number of hours of nocturnal illumination, analogous to maturation in birds and plants. At full moon the maturation process is in full swing, and at last quarter all the worms reach maturity about the same day. Then they proceed, at a particular phase of the tide, to cast off the posterior epitokous part, which immediately starts to swim toward the surface. At one particular night swarming reaches its height; the nights before and after show the predecessors and late comers. Swarming is executed at low tide, in the dark of the night, irrespective of lunar illumination conditions.

The writer believes this is the whole secret, an explanation far simpler than the invocation of aid from atmospheric electricity or polarized moonrays, and moreover it is in accordance with the events in many other noctural, but light-sensitive animals.

We can characterize the behavior of *Eunice viridis* concisely as follows: Breeding season at Samoa (13°41′ S.) October, November, seldom December; at Fiji (17°41′ S. and getting its spring about a fortnight later than Samoa) November, December, seldom January; New Hebrides (Gravier, 1924), October. Clear-cut swarming maxima about at the last quarter, most probably brought about by rhythmical maturation closely correlated with the sequence of periods of dark and moonlit nights. Nocturnal habits. Epitokes very sensitive to light, swarming in tight masses in the surface layers of the sea. Swarming at Upolu (Samoa) shortly before sunrise at low water, at Tu-

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tuila island (Samoa) about at midnight, at the New Hebrides from 9 until 11 p.m.: "le soir du dernier quartier de la lune qui commence en Octobre. Les vers se montrent vers 9 heures du soir et vers 11 heures ils disparurent pour ne plus revenir que l'année suivante à la même époque."

Another interesting case of lunar periodicity showing its maxima only once a month is that of the reproduction of *Platynereis dumerilii* near Naples, observed by Ranzi (1931a; 1931b). Intrigued by the discrepancy in the results of several investigations on periodicity in reproduction, Ranzi plotted a set of observations to check periodicity in swarming of polychaete worms in the Mediterranean. His observations are of particular value, for he combined a high frequency of sampling, carried through with great assiduity during an entire year, with the utmost caution in checking the reliability of his data.

Ranzi chose the little harbor of Mergellina as his field of operations. In this harbor, which has a depth of 2–3 meters, Ranzi established four stations and at each he sampled during a fixed number of minutes, starting 1 hour after sunset, daily during the first 3 months, thereafter thrice a week. His samples cover the period from June 1929 to June 1930. Ranzi caught several species of polychaetes, but *Platynereis dumerilii* predominated in his samples. Ranzi used a lamp to lure the worms and tried to catch them quantitatively during the fixed periods he placed his lamp in the water. If the numbers of animals appearing in the lamp's radiation were not too large, Ranzi quite probably caught them all, but if they came in enormous numbers his figures may be too low, as some may have been missed. His figures are certainly not exaggerated.

Ranzi found that the mature form of *Platynereis*, the so-called heteronereis, performing its nuptial dances at night in the surface layers of the water, is quite sensitive to differences in illumination. Therefore it was necessary, in order to collect comparable data, to use the same type of lamp, as a lamp of 150 candle power appeared to lure far fewer individuals than a lamp of 200 candle power. To investigate whether the number of worms swimming in the surface layers remained the same during the entire night, Ranzi sampled nine times during an entire night in the months June, July, and August. The figures for the periods 21–22 h., 24–1 h., and 3–4 h. resemble each other very much, so that Ranzi is correct in stating: "Da questi dati sono autorizzato a concludere che la quantità di Heteronereis dumerilii attratta dalla lampada resta constante durante tutta la notte." Moreover, his laboratory experiments showed that no variation in the intensity of phototactical attraction can be observed in the course of the night. Thus Ranzi could collect quantitative samples by placing his lamp in the water for periods of only 15 minutes in each of his four stations, starting 1 hour after sunset.

External conditions appeared to have had little influence on the number of worms Ranzi collected. Rain prevented the worms from reaching the upper layers of the water, and this fact could easily be corroborated by laboratory experiments, but fortunately rain seldom disturbed Ranzi's observations. Currents and tides are practically absent in this part of the Mediterranean and thus had no perceptible influence on the number of heteronereids Ranzi collected. Moreover he soon found out that the same number of worms could be caught before and after moonrise, and that an overcast sky did not prevent the worms from coming.

Ranzi's extensive data show that swarming of *Platynereis dumerilii* is of little or no importance in mid-winter, but from March to October inclusive Ranzi caught considerable numbers; swarming reached its height in July and August. Their breeding season, therefore, appeared to be quite long. In that breeding season *Platynereis* showed a marked periodicity. High numbers were collected at about full moon; the maximum showed its peak exactly on the third day of July, 1929, and on an average the third day after full moon (August, October 1929; February, March, May, June 1930), and minima, though seldom as low as zero, were demonstrated to occur at new moon and first quarter.

Ranzi did his best to explain this remarkable rhythm in the reproduction of *Platynereis dumerilii*. As the phenomenon has virtually the same character from March to October inclusive, it is useless

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to try to correlate it with temperature conditions. Temperature may be the cause of the slowing down of reproductive activity in winter and of the occurrence of very high figures in July and August, but it cannot be responsible for the curious periodicity. Currents and tidal differences are of little importance here and show about the same values twice in the lunar cycle and thus cannot be held responsible either. Of course, Ranzi tried to correlate the phenomenon directly with the moonlight, but, as he could find no difference in swarming before and after moonrise, and as overcast skies gave the same results as bright weather, he found it quite a difficult task. Since moonlight is nothing but a little reflected sunlight Ranzi could not imagine what kind of influence moonlight could exercise on these worms, and at last, in his despair, he inclined to believe in some kind of mysterious radiation, not noticed by us, so far: "pensare a qualche azione di nature ignota, tale da non essere percepita dai nostri mezzi di indagine, ma da essere percepita dagli organismi."

We need not take this desperate step, however, to arrive at a plausible explanation. The writer believes that Ranzi was very close to the truth when he remarked: "supposto che la luna agisca in una maniera qualunque nel determinare il differenziamento sessuale delle Platynereis," and: "dopo un certo numero di giorni dall' azione ambientale subordinata al ciclo lunare, cominciano le Platynereis a devenire Heteronereis e raggiungono questo stadio in forte quantità nei giorni che seguono la luna piena, mentre altre divengono Heterenereis solo nei giorni successive."

The writer believes this is certainly the case. A maximum in swarming during a period of a few days, reaching its height the third day after full moon and independent of lesser variations in temperature, tides, or light on these particular days, should be understood as the result of a rhythmical maturation of the animals, and not as their responding to certain environmental conditions on the day of swarming! Since tidal differences are nearly negligible here and the phenomenon occurs only once in the lunar cycle, we wonder what factor governs a rhythmical ripening of the gonads.

When we consider that *Platynereis* is found sheltered under seaweed or stones during the day and leaves its burrows only at night in search of food, and that this animal possesses four well-developed eyes, we come to the conclusion that it must be of concern to these creatures whether the night is dark or moonlit. To this and kindred marine animals which hide in their dark shelters during the daylight hours, the rhythm of the moon must be of utmost importance. We know that birds react sharply to rhythmical differences in illumination (the lengthening and shortening of days) in their sexual and migratory activities, and that many plants are highly sensitive to the length of the day (more so to the number of hours of illumination than to the intensity of light) in their breeding activities. Could it surprise us if the rhythmical alternation of dark nights and moonlit nights exercised some influence on sexual maturation in nocturnal animals living in shallow water?

The animals are active only during the night, and in the breeding season the period of moonlit nights (the waxing of the moon) initiates sexual ripening, resulting in swarming during a short, well-defined period of the lunar cycle. This seems the only plausible explanation for the phenomenon observed by Ranzi.

Observations on other species of animals with nocturnal habits fit in remarkably well with this hypothesis. As examples we can mention the case of *Platynereis megalops* (Just, 1914), of *Odontosyllis enopla* (Galloway and Welch, 1911), of *Platynereis* sp. (Aiyar and Panikkar, 1937) of *Odontosyllis hyalina* (Van Lummel, 1932), of *Odontosyllis* sp. (Crawshay, 1935), of *Chaetoplaeura apiculata* (Grave, 1922), and of *Acanthozostera gemmata* (Stephenson, 1934).

The animals in this list, and discussed in greater detail elsewhere (1947), all show a marked periodicity in reproduction, directly associated with the phases of the moon.

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The breeding season may vary from one month to all the year round, and maxima in spawning and swarming may vary in duration from one single night or day to about a fortnight, but in all the species concerned a simultaneous maturation occurs, correlated with the periods of moonlit nights. Though the number of days required for egg ripening may vary from place to place and from species to species, as a rule maturation is completed between full moon and last quarter, and at these phases of the moon spawning and swarming occur.

There is ample evidence that it is not the duration or the intensity of nocturnal illumination on the day of swarming itself which counts, but that swarming starts as soon as maturation is completed, although several species select a special hour of the day or a special stage of the tide for performing their nuptial ceremonies.

The influence of nocturnal illumination on maturation can be understood by taking into consideration that the animals concerned live in shallow water in an area with a very modest tidal range (considerably above 1 meter only in the case of *Acanthozostera gemmata*); as they are highly sensitive to light they display nocturnal habits and live in a shelter during the day. In cases where the breeding season is short and the maxima are clear-cut, reproductive activities are often concentrated into a very few hours a year, thus highly enhancing the possibility of fertilization.

Classification is always a very difficult matter in biology. There are always cases which do not fit readily into our systems. Lunar periodicity of breeding phenomena is no exception to this rule. Not every well-documented case encountered is either of the fortnightly type, in which the fortnightly rhythm of the tides is presumably the factor of causal relation, or of the monthly type, controlled by the moonlight itself. The attentive reader will already have noticed the peculiar fact that the polychaete worm *Platynereis dumerilii* performs a fortnightly rhythm in Brittany, where the tidal range is great, and a monthly rhythm near Naples, where the tides are insignificant. We could think of different biological races or imperfections in the classification of this difficult species (Hauenschild, 1951), but it does not seem entirely impossible that some creatures are sensitive to both the tidal cycle and the moonlight rhythm, and that local conditions determine which factor will dominate. Similar cases of rhythms exist in birds and plants, where sometimes both light and temperature should be taken into consideration, indicating that Nature does not always follow the same paths, and that there certainly are complicated cases, difficult to analyze.

In the field of lunar periodicity, the Atlantic Palolo, *Eunice fucata* from the Tortugas Islands, Florida, is an instance of such a complicated case.

Remarkably similar to the Palolo worm's habits is the swarming behavior of its near relative *Eunice fucata*, discovered by Mayer (1900). This worm, with good reason called the Atlantic Palolo, appeared to swarm at sunrise in dense masses above the old decayed coral reefs near Tortugas Islands on July 9, 1898 (last quarter −1), and on July 1, 1899 (last quarter +2). Mayer looked for swarming at other dates, but though he sailed early every morning from June 25, 1898, to August 19, 1898, and from May 17, 1899, to July 4, 1899, he witnessed dense swarming only at the days mentioned and slight swarming on the days immediately preceding or succeeding these maxima.

Mayer had the opportunity to carry out further investigations, and he soon found that conditions

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resembled very much those described for *Eunice viridis*. Here too the worms appeared to live in great number in shallow parts of the sea, below the low-water level, within "crevices in dead corroded coral or in limestone beach rock, which have been honeycombed by the burrows of marine animals" (Mayer, 1908). During the daytime he found that "the animal lies coiled upon itself within this burrow" (Mayer, 1902). In the breeding period (June, July) metamorphosis takes place in the adult worms, during which the posterior, epitokous part of the body, tightly filled with eggs or sperm, is developed. Swarming appeared to take place "within 3 days of the day of last quarter of the moon between June 29 and July 28" (Mayer, 1908). "Before sunrise on the morning of the day of the annual breeding swarm the worm crawls out backwards from its burrow, until all of the sexual segments and a portion of the slender middle part of the body have been protruded. A vigorous helical, corkscrew like twisting movement then comes over the sexual segments." (Mayer, 1908). Finally the epitokous part snaps off at the junction between the two parts of the body and darts to the surface, swimming tail-end first. Mayer witnessed the breaking away of the epitokous part, as mature worms disturbed by a breaking open of their burrows are inclined to perform this behavior at any time of the day, which could be called "abortive swarming."

Natural swarming "commenced very early in the morning, before sunrise, and soon vast numbers of the worm were to be seen swimming upon the surface of the ocean" (Mayer, 1900). They had "no tendency to congregate in masses, each worm pursuing its own course." Mayer (1908) added: "I have seen these in such abundance over the surface above the coral reefs at Tortugas, that hardly a square foot of the surface was free of a worm." At sunrise the swimming worm "begins to contract violently so that the sexual products are cast out through rents and tears in the dermo-vascular wall." Mayer is certainly right in supposing that the swarming behavior greatly enhances fertilization possibilities.

Gradually more details were discovered. The writer believes the most important one was Mayer's discovery (1902) that "none of the eggs become mature until the time of the normal swarm, when all the eggs mature simultaneously." Artificial fertilization with living sperm added to eggs taken from animals collected in their burrow proved to be impossible until 12 hours before the moment of natural spawning! So here, too, it is simultaneous maturation which is closely correlated with the swarming phenomenon. Later Treadwell (1914) could corroborate that egg maturation proceeded as the swarming date approached by demonstrating that the CO_2 output of eggs taken from the mother animal rapidly increased as ripening proceeded, which led him to the conclusion that "a definite increase in metabolism goes on in the egg as it approaches maturity," and that at least "some part of the stimulus leading to egg-laying comes from the activity of the egg itself."

Mayer carried out a series of experiments to establish which factor is responsible for the swarming phenomenon, and later Treadwell and Clark followed in his steps. Mayer placed pieces of rock containing living worms in spacious floating life cars in which ample circulation was secured, while overheating during the warmer part of the day was efficiently counteracted. Moonlight was freely admitted, and it appeared that in all three experiments, during which the worms stayed, 30, 4, and 30 days respectively, preceding natural swarming in the boxes, some of the worms swarmed normally within 3 days of the last quarter of the July moon. Mayer does not mention whether or not the worms were fed appropriately. "On the other hand, the worms never swarmed when the moonlight was prevented from falling upon the rocks within which they lived." This led Mayer to assume that moonlight had an influence on his worms. He failed, however, to distinguish between an influence on the maturation process and conditions required for the performance of the swarming phenomenon itself. This finally led him astray. Thus he tells us that in nature the worms will swarm even in overcast or cloudy weather, so that "even diffuse moonlight appears to be capable of calling forth the breeding swarm." At the time of Treadwell's demonstration (1909) that the worm swarms even if the rocks containing them are placed in a dark chamber upon the day preceding the night of the swarming, Mayer thought that his supposition that the presence of moonlight is necessary for the swarming reaction was severely shaken.

After the above discussions of similar cases, we conclude that maturation in *Eunice fucata* is influenced by the occurrence of a series of moonlit nights in its breeding season. Simultaneous maturation continues, and swarming takes place the very day

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the eggs are ripe and at a special hour of the day (sunrise). Some worms attain maturity 1 or 2 days before, others somewhat later than the large majority, thus calling forth swarming of little importance on the days preceding or succeeding the big swarming maximum. This corresponds with Clark's (1941) conclusions from his experiments: "if the average duration of light is increased, reproduction occurs before the controls, and if the average duration of moonlight is decreased, the time of swarming occurs after the controls or not at all."

Moonlight is of no importance during swarming itself, and we can easily understand why the worms swarmed in overcast weather and in Treadwell's dark chamber.

Mayer supposes that *Eunice fucata* stays in its burrow, coiled upon itself, but we feel sure that this animal too has nocturnal habits. Clark's observations (1937) give strong indication that our supposition is right, for he demonstrated that the immature worms are positive to light from 0.001 to 0.01 foot candles and negative to higher illumination. The epitokous parts, swarming at sunrise, showed other figures: "swimming sexual ends are positive to intensities from 0.00005 foot candles (the threshold) to at least 50 foot-candles and negative to gravity."

Still, we cannot consider *Eunice fucata* a satisfactory species for carrying out experiments to lay bare the roots of lunar periodicity, as its case is quite complicated. Mayer (1908) saw that the worms in the life cars did not swarm 100 per cent as in nature, even if moonlight was freely admitted, as some worms "did not cast off their posterior ends, but remained passive in their burrows." Though the number of worms used in his experiments is not overwhelmingly great, Mayer is probably right in assuming that "changing pressure due to rise and fall of the tide over the reefs is a contributory factor, but not a necessary component of the stimulus which calls forth the breeding swarm."

Observations on the occurrence of swarming in nature support this view, and, although Clark (1938) showed that some of the eggs may be found floating in the water during many days of the breeding season and that swarming on a very small scale is easily overlooked, yet the occurrence of sharp maxima in swarming cannot be denied. Treadwell (1914) gives a list of swarming dates, in which the dates of principal swarming are printed in italics:

Year	Date	Phase of the moon
1898	July *9*, 10	L.Q. −1
1899	July *1*, 2	L.Q. +2
1900	July 19	L.Q. +1
1902	July *24*, *25*, 28	L.Q. −2, 3
1903	July 17	L.Q.
1905	July 9,10,21,*22*,23,24	L.Q. −2
1906	July *11*, *12*, *13*	L.Q. −1, 2
1907	July *2*, *3*	L.Q. +0, 1
1908	July *10*, 19	F.Q. +4, L.Q.
1909	July 6, 7	L.Q. −3, 4
1910	June *29*, 30	L.Q.
1911	July *16*, 17	L.Q. −1, 2
1912	July 6, 7	L.Q.
1914	July *11*	L.Q. −3

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The years 1905 and 1908 showed swarming both at the first *and* at the last quarter. Apparently the moon is not all powerful in this species, so Mayer is right in assuming that tidal influence is a component in calling forth swarming. Mayer said: "when the last quarter falls late in July, there may be a response to the first quarter as well as to the last quarter." Treadwell's table suggests, however, that the word "July" should be replaced by "breeding season," which does not necessarily conform very closely to our calendar. Without a doubt the influence of moonlight nights preponderates in this species, which lives in water with quite a modest tidal range. Clark (1941) tries to explain the anomalous character of *Eunice fucata's* breeding periodicity in terms of a correlation of swarming and the reciprocal of the difference in the daily rate of change in moonlight, either in the positive or in the negative direction. The writer is not inclined to adopt this rather far-fetched hypothesis before convincing experimental evidence is adduced that such a factor could control the worm's maturation.

Thus there is as yet no need to resort to mysterious factors like periodic changes in the moon's declination, gravitational influence, air ionization, etc., to explain the causal relations between the lunar cycle and periodicity in the breeding of many marine animals. The tides and the moonlight itself are probably of a much greater biological significance than we, human beings, are inclined to admit. Field observations may establish many more cases of monthly and fortnightly rhythms in the reproduction of a variety of marine animals and will adduce new data to the cases of others. Carefully devised experiments should prove whether or not the theories and hypotheses discussed here hold good. To analyze cases of periodicity in reproduction, the *annual rhythm* (the length of the breeding season), the *monthly rhythm* (periodicity correlated with tidal sequence or moonlight cycle), and the *daily rhythm* (concentrating spawning or swarming to a certain well-defined hour of the day, or to certain phases of the tidal cycle) must be clearly differentiated. In extreme cases these three rhythms in combination may result in a complete concentration of reproductive activities in the species concerned, so that an entire population may spawn simultaneously during one single hour a year.

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Chapter 28
Fluctuations in Littoral Populations*

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Every person familiar with the life along the nearshore must have observed some of the variations that occur from year to year in the size of the populations of the invertebrates as reported by Dexter (1944) for mollusks. During the past half century many of the species have changed repeatedly from scarce to abundant and then to scarce again, usually at irregular intervals and in different localities. Various species of invertebrates previously unknown to a particular region have been added to the local fauna by migration from other localities, while others have been either intentionally or accidentally introduced. Some species formerly abundant have become scarce or can no longer be found. In other cases species formerly so scarce that they have been overlooked have increased gradually or suddenly to large populations. Some of these resurgent populations have disappeared again after flourishing for a brief period.

Because of their enormous fecundity, some of the species in the local population may be increased a hundred fold in a single year, or, because of a high rate of mortality, may be similarly decreased. Most of the fluctuations, however, are relatively small.

CATASTROPHIC CHANGES IN POPULATIONS

Changes that are catastrophic in nature occur occasionally. They result from such radical causes as changes in substrate, floods, abnormally high temperature during periods of low tide, freezing, pollution by oil or other deleterious substances, parasitic organisms, including those that cause diseases, or other enemies (Blegvad, 1929; MacGinitie, 1939; Gunter, 1947). Any of these may decimate or annihilate the susceptible species over a considerable extent of coast line. Repopulation later occurs by the arrival of larvae or migrants from unaffected areas. Some of the most extensive catastrophes have resulted from the arrival of such vast populations of dinoflagellates as to give the water a reddish tinge. Such "red water" or "red tide" was recorded on the coast of southern California, either locally or over an extent of 100–200 miles, in 1894, 1901, 1907, 1917, 1924, 1933, 1939, 1945, and 1952. Several of these visitations have caused great destruction to both vertebrates and invertebrates, while others have resulted in little or no apparent injury. The dates here mentioned give no indication of a regular periodicity, although Hutchinson (1950) has concluded that the guano deposits on the Peruvian coast indicate a regular 7-year cycle from 1864 to 1939 but not in the years prior to that period nor at any period on one of the islands. He decided that this periodicity is not persistent. On some sea coasts the advent of "red water" is of annual occurrence.

* Contribution, University of California, Scripps Institution of Oceanography, New Series No. 91672.

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FLUCTUATIONS

In contrast to these catastrophic changes in populations are the much more frequent relatively minor fluctuations also dependent on the environmental conditions. Since these are constantly changing, the size of local populations in two successive years is seldom identical. Nevertheless, the colonies of some species, as mussel beds, for example, may maintain themselves for many years; new members arrive to replace those that die, but always there are fluctuations in numbers.

The greatest ranges of fluctuations occur in restricted bodies of water, such as tide pools, lagoons, bays, and estuaries, for there are the greatest variations in environmental conditions, including enemies, temperature, salinity, organic matter, and oxygen supply.

FLUCTUATION AMONG YOUNG INDIVIDUALS AS COMPARED WITH THOSE OF ADULTS

In species whose members live for only 1–2 years, maximum and minimum populations often follow each other directly, but in other species one or more populations of medium size usually intervene between each extreme. Since the greatest fluctuations occur in each first year class, it is obvious that the survival of successive year classes tends to decrease the effect of any one year class on the total population.

The older, but not the oldest, year classes consequently have more uniform populations than the younger. This is shown in Figure 1, where the classes four or more

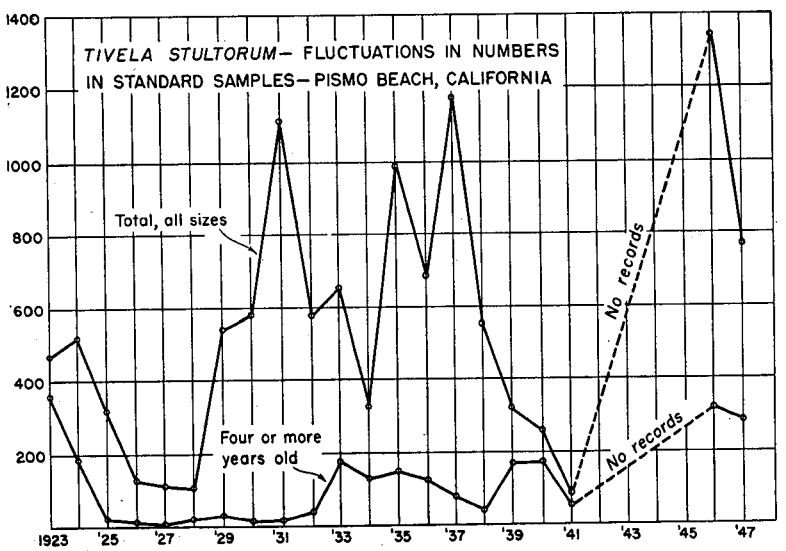

FIGURE 1.—*Fluctuations in the populations of the Pismo clams found each year in three trenches, each 16 cm. wide, in separate locations on Pismo Beach, California, at corresponding dates, 1923–1941 and 1946–47*

Between 1930 and 1938 the total population showed a biennial periodicity because of an increased set of young clams in each alternate year. The relatively small number of clams reaching the age of 4 or more years indicates the high rate of mortality both because of natural causes and human agency. (Data from Aplin, 1947, and from California State Fisheries Laboratory; from Coe and Fitch, 1950).

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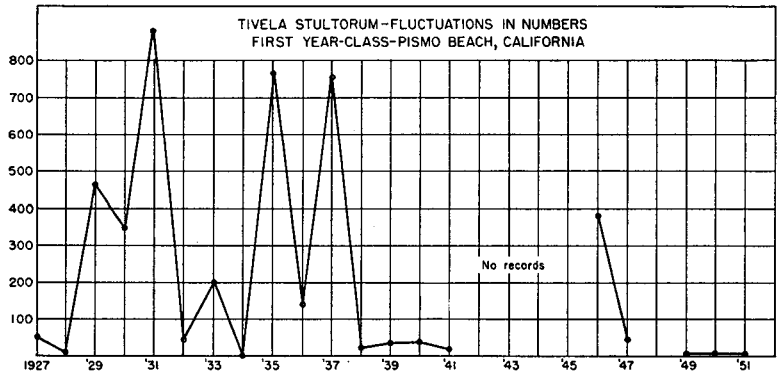

FIGURE 2.—*Fluctuations in number of Pismo clams in the first year class in the same population as shown in Figure 1*

A distinctly biennial periodicity occurred during most of the period indicated. The apparent absence of this year class in 1949 to 1951 was another notable feature of this population. (Data from California State Fisheries Laboratory).

years old show much more uniformity in different years than does the entire population. Even larger fluctuations characterize the first year class of the same population, as indicated in Figure 2, which shows also a biennial periodicity for a number of years.

Similar fluctuations have been found in the populations of other invertebrates investigated. The records for the oysters extend over a period of 80 years, but in none of these is there satisfactory evidence of a predictable cyclical periodicity. All the observed fluctuations seem to have occurred at irregular intervals because of a corresponding irregularity in the environmental conditions. Mention should be made, however, of the fluctuations reported by Burkenroad (1946) for the populations of starfish in Long Island Sound. From newspaper items, the statements of oyster growers, and other sources, he concluded that the starfish, which is the chief enemy of adult oysters in that region, has shown a 14-year periodicity for the past 90 years.

RESURGENT POPULATIONS

Some local populations experience the usual minor fluctuation for a number of years and then suddenly increase to a hundred, or even a thousand, fold over their former numbers. After one or several generations, the population may return to its usual size or disappear. Such resurgent populations of "bean clams" of the genus *Donax* have been noticed in Europe and on both coasts of the United States. On the coast of California they have occurred at La Jolla in 1894–1895, 1909–1910, 1913–1915, 1931–1932, 1934, 1937–1938, and 1950–1952.

In the latest period, the population exceeded 20,000 individuals per square meter in a zone 2–5 meters wide and extended in favorable situations for more than 5 miles along the coast. In the preceding year, the population averaged less than one clam per square meter. Within 2–3 years, which is the usual maximum life span of individuals in this locality, the entire population had died. Extensive search revealed not a single individual in an area that had been occupied by millions a few months previously; but in the meantime a younger year class had settled on a beach about 2 miles away.

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INTRODUCTION TO NEW LOCALITIES

Local populations may be augmented by the arrival of migration, the transportation of larvae, or by the accidental or intentional introduction of individuals from other territories. Such introduction may result temporarily in an astonishingly rapid rate of multiplication, often followed by a rapid decline in numbers. More frequently the introduced species finds the new locality unsuitable for reproduction and is thereby eliminated. Attempts to cultivate breeding populations of the oyster *Crassostrea virginica* from the American Atlantic coast to the Pacific coast and to Europe have thus far resulted in failure, although some of the oyster's enemies and associated invertebrates carried inadvertently with the stock of oysters have survived and have now become pests on the native species.

The Pacific oyster (*Crassostrea gigas*) from Japan and the soft-shell clam (*Mya arenaria*) from the Atlantic coast, on the contrary, have become important additions to the sea-food supply of the Pacific coast. This supply has been further augmented by the Japanese little-neck clam (*Paphia philippinarum*) which came as a stowaway with the oysters.

In 1943 a few representatives of the bay mussel (*Mytilus edulis diegensis*) arrived in San Diego, California. Within 3 years the mussel population had become so large it covered the rocks and piers with a hundred times as many young as could have survived because of lack of space for growth and became a nuisance by clogging the intake pipes of salt-water cooling systems. Five years later only a relatively sparse population remained (Coe, 1946). The little sea anemone *Diadumene luciae* has had a similar history in its journeys around the world; it is transported on the hulls of ships. Since it was first noticed on the American Atlantic coast in 1887, it has undergone alternate periods of vast abundance and scarcity, although in none of its later resurgences has its population equalled those of the years immediately following its introduction. Other examples of such exuberant populations are known to everyone who has had a wide acquaintance with the life on the seashore.

PRODUCTION RECORDS

The records of the annual changes in the production of the commercial fisheries, including those of shrimps, crabs, lobsters, clams, oysters, scallops, and cockles, as compiled by Tressler *et al.* (1951), do not furnish reliable evidence of the fluctuation of their populations, since the extent of the fisheries depends so largely on economic conditions, the price, and the demand. For a limited time the production may be increasing while the population is decreasing. There can be little doubt, however, that for all the invertebrates mentioned, with the exception of shrimps and crabs, both the production and the populations have declined more rapidly in most localities during the past decade than in any earlier period of equal length. But this is not considered satisfactory evidence that the decline will necessarily continue. In many of the species of oysters, clams, scallops, and cockles, each large female may be expected to produce millions of eggs annually. The eggs develop into pelagic larvae which under favorable conditions may be carried by currents to suitable, relatively barren areas and there produce resurgent populations, as described on the foregoing

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pages for the bean clams and mussels. A maximum population may be produced in a single generation.

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Chapter 29

Mass Mortality in the Sea

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INTRODUCTION

This chapter surveys mass mortality in the sea, its causes, and its significance to paleontology.

Section I discusses mass mortality in sea and a few examples of mortality in inland waters (rivers entering into salt lakes, etc.). Various causes of these phenomena are discussed. Surveys of the literature concerning one of these causes (noxiousness of waterbloom) were published by Brongersma (1948) and Galtsoff (1948; 1949); the paleontological significance of mass mortality by red water has been discussed by Brongersma (1944; 1947; 1948), Falke (1950, p. 64), Gunter (1947b), Pratje (1949), and Richter (1950). The present survey is certainly not exhaustive. Furthermore, the cause of some mortalities is still uncertain. In paleontological literature, there are so many erroneous explanations of recent mass mortalities that a critical review is desirable. It is obvious that an incorrect explanation of the cause of recent mortalities leads to a completely erroneous interpretation of mass mortalities in the geological past.

Section II deals with the problems with which mass mortality has been connected in geological literature. While it is impossible to treat these problems in detail, the discussion may suffice to show that recent mass mortality occurs in regions where future deposits of geological importance (phosphorite, highly bituminous rocks) are developing.

The numbers in this chapter refer to the detailed accounts of mass mortalities in the appendix.

CATASTROPHE AND "ANASTROPHE"

In the first half of the nineteenth century scientists searched for records of mass mortality in recent times to confirm Cuvier's theory of catastrophes. By a mortality extending over a very large area whole species or even higher systematic units (genera, families, etc.) may be exterminated, even if such catastrophes occur only once. A marine transgression may be the cause of such a catastrophe. A recent example of mass mortality by a marine invasion is the 1825 mortality in the Limfjord (no. 23). As this mortality did not occur over a very great area, whole species or higher systematic units were probably not exterminated. For these mortalities in limited areas, Walther (1927) and Weigelt (1927, p. 85) use the name anastrophe. Nearly all records of recent mass mortalities refer to "anastrophes"; it is possible that some species with a very limited distribution are exterminated by them, but only rarely. Hence, "anastrophes" cannot be used to explain the extermination of a number of species (genera, families); they can be used only to explain the abundance of fossils in certain deposits and similar peculiarities. As the word anastrophe has another meaning in the English language (inverse word order), it is not used here.

ANALOGOUS RECENT MASS MORTALITY

There has been much debate whether or not the fossils of certain deposits perished by catastrophic events. Assuming they did, it is of primary importance to find an analogous occurrence in Recent time. This has not always been attempted. Relying on the peculiarities of a particular deposit, some paleontologists have invented

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catastrophes to explain the death of the animals in such deposits. Thus, the high copper and silver content of the Permian Kupferschiefer led Abel (1912, p. 39; *see also* Moret, 1940, p. 8) to suppose that the fish found in these shales were repeatedly poisoned by springs containing these minerals. However ingenious such hypotheses may be, they are useful only if one finds similar mortalities in recent time. Recent destructions of marine fish by mineral springs are unknown.

IMPORTANCE OF RECURRING MASS MORTALITY IN THE SAME PLACE

Fossils generally do not occur in a single stratum of a deposit, but in several strata one above the other. If catastrophes killed the organisms represented in such a deposit, these events must have occurred again and again in the same area. Hence, those cases of mass mortality that occur repeatedly in the same place are particularly important. It will be shown that mass mortality by low temperatures, by supersalinity, or by noxiousness of waterbloom occurs with very short intervals (once every few years) in some areas; the intervals between destructions in the same locality caused by vulcanism usually are much greater.

ANALOGOUS RECENT SEDIMENT

In some regions where mass mortality occurs, the sediment shows characteristic features. If the same combination of characteristics occurs in a fossil sediment, catastrophic killing or mass mortality probably occurred there in the past. By following this method, we may assume that certain mass mortalities have played a part in geology.

RECENT MASS MORTALITIES OF THE SAME OR RELATED SPECIES

The victims of some recent mass mortalities consist to a high percentage of one species (no. 42 *Pleurogramma antarcticum* Blgr.; no. 90 *Mallotus villosus* (Müll.); no. 101 *Entelurus aequoreus* (L.); no. 104 *Centriscus scutatus* L.). In some instances the same species or a closely related species is characteristic of certain fossil deposits; the fish *Mallotus villosus* occurs very frequently in postglacial Marlekor concretions; *Centriscus heinrichi* (Heckel) (= *Amphisile heinrichi* Heckel) and other *Centriscus* species frequently occur in Tertiary deposits. *Centriscus heinrichi* is known from the Caucasus to the "Mainzer Becken" (Fröhlicher and Weiler, 1952, p. 30). In these cases it is tempting to connect the recent mortalities to the phenomena of the geological past, but there is no certain proof that they came about in the same way.

ERRORS IN PALEONTOLOGICAL LITERATURE

It is to Weigelt's credit that he defended the paleontological importance of mass mortality at a time when its importance was denied by nearly everybody. In 1927 and 1930 Weigelt gave an interesting survey of all records of mass mortality in recent time known to him from literature or by personal communication. Concerning the records of mortality in the sea, it must be remarked that the majority of the supposed causes are not correct. The chief reason for these errors is that most mortalities were not observed by oceanographers, but by travellers who by chance saw or heard of a mortality. Moreover, the stories were copied by one paleontologist from the other without consulting the original papers; in this way errors accumulate.

The data concerning the mortality near San Ferdinandea in the Mediterranean have been confused with those of a mortality near the Azores (no. 6 and no. 101). This confusion occurs in Walther (1927, p. 325) and is copied by Weigelt (1927, p. 37). Lodden is noted as one of the localities where

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mass mortality of *Mallotus villosus* occurs (Weigelt, 1927, p. 205; geographical index, p. 220); Lodden is, however, not a place where mortality of this fish occurs, but the German name for *Mallotus* (no. 90). Further, various records cited by Weigelt under different headings refer to the same place, and these records represent different conceptions of travellers who observed a periodical mortality in different years—*e.g.*, the Walvis Bay mortality (no. 68), which is mentioned under three different headings: H_2S (1927, p. 39), vulcanism (1930, p. 309), and a red mite (1927, p. 203). More errors are mentioned in the discussion of the various causes of mortality and in the appendix; see especially under Mass Mortality by Waterbloom.

RECENT OCEANOGRAPHICAL WORKS

In recent years valuable researches on catastrophic killing and on red water have been made by oceanographers. Among these are researches in the Gulf of Mexico, in the coastal waters of British Columbia and California, New Zealand, Greenland, Norway, Denmark, Southwest Africa, Brazil, Antarctic Ocean, India, etc. Much remains to be done; even the cause of some mortalities occurring episodically in the same place (Azores mortality, no. 101) is still doubtful. It is hoped that this compilation of occurrences will stimulate new observations, and that the real cause of these occurrences will be determined.

SECTION I. RECENT MASS MORTALITIES

MASS MORTALITY CAUSED BY VULCANISM (FIG. 1)

The injurious effect of vulcanism on marine organisms may be attributed to

(1) A strong increase in temperature (no. 2, 5, and 7 (years 1631 and 1794); also one of the causes in no. 6).

(2) Covering with a thick layer of ash (no. 1, 7 (year 1906), 8). This causes most destruction in inland waters and in shallow bays where affected by streams; the ash deposited over a great land area is carried by runoff to the rivers, and part of it finally is washed to the bays. As the rivers become almost liquid mud many animals die (no. 1). In the sea, that means in waters of considerable depth and extent, there is less upsetting of natural conditions by falling ash. To kill corals it is not necessary to cover them with ash; even the turbidity of the water caused by falling ash may exterminate them for many years (Gislén, 1931, p. 415).

(3) Flood waves (no. 3 in part, 8).

(4) Poisonous gases escaping from submarine volcanoes (probably part of the cause of death in no. 4 and 6).

(5) Strongly acid rivers flowing into the sea. Strongly acid streams flowing into fresh-water rivers occasionally cause mortality; when such water is carried to the sea, it will have no great influence on the fauna as sea water is a buffer solution. An uncertain record of marine mortality by this factor is given under no. 9. Catastrophes probably occur in the sea when the whole content of acid crater lakes is thrown out during eruptions.

The records given here are certainly not exhaustive; widespread mortality in the sea will often occur without being observed. On the other hand, the frequency of the phenomenon has been exaggerated in paleontological literature. Several paleontologists consider vulcanism the most important cause of mass death. This is due to underestimation of other causes and to the fact that several catastrophes erroneously were ascribed to vulcanism. One reason leading to these errors is that discoloration of the sea has often been considered the result of vulcanism instead of some other agent such as accumulations of plankton (no. 47, 48, 68, 72, 77 literature in appendix under Mass Mortality by Waterbloom).

Rudolph (1887, p. 166) was aware of this error, for he states that discolored water is no certain proof of submarine volcanic phenomena. Moreover, mortality due to tectonic seaquakes has been mentioned under vulcanism (no. 12).

Weigelt (1927, p. 37) states that the literature contains many records of marine mass mortality caused by vulcanism. Of the five records given by this author (1927, p. 37; 1930, p. 309), two are

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caused by red water (Somaliland, no. 77; Walvis Bay, no. 68); in the third (mentioned as mass mortality of *Syngnathus anguineus* near San Ferdinandea) two cases of mass mortality have been confused (no. 6 and 101)—only one of these was caused by vulcanism. As I could not find the original literature on the fourth (mass mortality of "Haifische, Seezungen, Stockfische" in Wales Bay near Cape Down), and supposing that it is a record of mass mortality by red water near the coast of Southwest Africa (the mortalities occurring repeatedly at various localities along this coast are mentioned in the newspapers again and again under vulcanism) I asked Professor Weigelt if this might be a misprint for "Prince of Wales Bay" north of Cape Town; he kindly answered that he had no information whether or not this is correct.

MASS MORTALITY CAUSED BY EARTH- AND SEAQUAKES (FIG. 1)

Earthquakes may be tectonic or volcanic. Most volcanic earthquakes are perceptible close to the epicenter only; usually the damage done by this type of earthquake is not great. All great, disastrous earthquakes are tectonic. If the epicenter lies in the sea, they are called seaquakes. They may cause great flood waves (Escher, 1948).

Rudolph (1887, p. 212) states that mass mortality of fish by seaquakes is rare. In more than 550 records of seaquakes (part of these will be of volcanic origin, Sapper, 1917, p. 74) given by Rudolph (1887; 1895; 1898), fish mortality is mentioned four times only. Von Sieberg (1923, p. 82, 87; 1927, p. 320) on the contrary states that there are many observations of fish mortality by seaquakes; dead or nearly dead fish with ruptured air bladders float on the surface of the water. Unfortunately, Von Sieberg (l.c.) does not record individual cases of mortality in the sea, but he gives an interesting example of mortality in fresh water (no. 10).

Whether seaquakes of low intensity cause mortality is doubtful, but certainly great tectonic earth- and seaquakes may cause mortality in the sea. The injurious effect is produced by various factors:

(1) By the shock (no. 10, 11, 14, 17, 18, 20, 21, 22); it is noteworthy that the victims often are deep-sea fish (no. 10, 17, 20).

(2) By an uplift of the bottom by which the former bed of the sea is laid bare and dry (no. 11, 14, 15, 17).

(3) By flood waves throwing marine animals on the beach (mortality of terrestrial animals is not considered here) (no. 12, 16, 17, 19).

(4) By release of H_2S or other poisonous gases when an earthquake occurs in a place where the sediment contains a great quantity of this gas (no. 13, 17, and perhaps no. 85).

(5) By land slides (no. 17).

This enumeration is in no way exhaustive, but the examples may suffice to show what damage is done. The effect of the Kwanto earthquake (no. 17) has been studied in particular detail by Japanese investigators. The injury to marine fauna in other instances probably is much greater than has been mentioned here.

MASS MORTALITY IN SEA AND IN SALT LAKES CAUSED BY A SUDDEN CHANGE IN SALINITY (FIG. 2)

In the oceans the salinity is generally from 33 ‰ to 37 ‰; where there is high rainfall, dilution by rivers, etc., it may be considerably less. In semiseparated parts of the sea the range in salinity is much greater, from fresh water to oversalinity, and a change in salinity—*e.g.*, a decrease by a great influx of fresh water—continues much longer than in the open sea. Nearly all mortalities mentioned here occur in bays and lagoons, and some in salt lakes. The salt tolerance of fishes and other animals varies within wide limits (for salt tolerance of fresh-water fish *see* Myers, 1949; for penetration of the sea by fresh-water fish and of fresh water by marine forms *see* Gunter, 1942a); some of them occur within a wide range of salinity, for others a slight change is fatal. The latter often can stand a change for a short time but are killed if it continues.

In areas where changes in salinity are regular, most animals are adapted, but, if in certain years the change is greater or continues much longer than usual, widespread mortality occurs. Killing may also occur if animals are carried by currents into water of high salinity, or if the high salinity is brought by convection currents to the organisms living in the surface layers.

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Mortality by a decrease in salinity.—When great quantities of fresh water are suddenly poured into estuaries, widespread mortality of marine animals occurs. In the Cape Province (Union of South Africa) sudden and heavy rainfalls after a period of severe drought greatly reduce the surface salinity in the estuary of the Zwartkops River (*i.e.*, over a distance of about 6 miles). This also occurs in the case of great floods in other rivers of this coast—*e.g.*, the Knysna River. This decrease in salinity in these estuaries causes mortality among fish, octopus (*Octopus vulgaris* Lam.), red bait (*Pyura stolonifera* (Heller)), and other invertebrates (Gilchrist, 1914, p. 15; Dr. P. Korringa, in litt.).

On the South African coast bordering the Agulhas Bank there are probably three conditions which bring about widespread mortality among the marine fauna. Besides a sudden influx of fresh water these are cold (no. 41) and phytoplankton blooms (no. 69). Destruction by the sudden appearance of cold water occurs along a great part of this coast and is probably the most important cause. Killing by red water is restricted chiefly to the Cape Peninsula.

Special attention has been paid to mortality of oysters by a decrease in salinity. In Chesapeake Bay heavy mortality among oysters—*Gryphaea virginica* (Gmelin) = *Crassostrea virginica* (Gmelin)—occurs in some years when the Susquehanna River discharges exceptionally large volumes of fresh water (Beaven, 1946; Engle, 1946). Around the mouth of the Mississippi, crevasses and spillway openings have occasionally obliterated marine life over some hundreds of square miles. In Mississippi Sound long-continued low salinities occur in some years when several factors coincide: local rainfall, drainage from the Pearl River basin, and overflow from the Mississippi River through the Bonnet Carré Spillway. These long-continued low salinities cause serious mortalities among oysters and other organisms (Butler, 1949; 1952; Butler and Engle, 1950; Gunter, 1950; 1953). In Texas such mortality was observed in Nueces Bay in 1935, following the greatest flood on record of the Nueces River (Hedgpeth, 1953, p. 151).

On the Gulf Coast of the United States four conditions bringing about widespread mortality to marine life: a great influx of fresh water, cold waves, phytoplankton blooms, and oversalinity. Cold waves and plankton blooms occur all over the Gulf Coast, although mortality caused by the latter occurs most often along the lower west coast of Florida; the oversalinity is restricted to the Laguna Madre (Gunter, 1947b).

Two periodic or episodic catastrophes are often attributed to a sudden influx of fresh water, but this interpretation is erroneous. The mortality along the Malabar coast (no. 80) is ascribed to a decrease in salinity caused by a sudden influx of river water after the monsoon rains by Denison (1862, p. 453), Anonymous 2 (1862, p. 320), Jones (1882), Geikie (1893, p. 648), and Stutzer (1931, p. 309). Undoubtedly this mortality is caused by red water. The mortality near Florida mentioned under no. 72 is attributed by several paleontologists (Agassiz *in* Shaler, 1890; Abel, 1912, p. 37; Weigelt, 1927, p. 63, 204; Stutzer, 1931, p. 309) to a change in salinity owing to sudden discharges of fresh water from great swamps, the Everglades. This mortality is also caused by red water. Data given by Slobodkin (1953) show that often high rainfall precedes the Florida red tides (the cause of this relation is not yet settled); hence there may be an indirect correlation between overflow from the Everglades and mass mortality. In the Lagoa dos Patos mass mortality of fish occurs in summer time. Von Ihering (1885, p. 176, 182) supposes that these fish are killed by an increase in salinity when sea water enters the lagoon (no. 25). New researches are very much needed to confirm Von Ihering's view. This mortality has attracted the attention of paleontologists (Von Freyberg, 1930, p. 73).

Mortality by an increase in salinity.—When a body of fresh water is separated by a narrow bar from the open sea, a change in salinity occurs when the bar is suddenly destroyed.

A catastrophe due to the destruction of such a bar occurred in the Limfjord (no. 23). The paleontological importance of this catastrophe has often been suggested (Forchhammer, 1841, p. 11; Abel, 1912, p. 38; Wiman, 1914; Stutzer, 1931, p. 308). It must be admitted that such an occurrence will bring about a drastic change in the fauna, but it cannot be considered important geologically, as it occurred only once in the same area. The mortalities from oversalinity which occur repeatedly in the same area (annually or once every few years) are much more important from the viewpoint of paleontologists.

Great amounts of fresh-water plankton are killed when carried into the sea. If the currents are very strong fresh-water fish may also be transported. The Lagoa dos Patos receives a great quantity of river water during the fall. This water is carried off through the narrow Canal do Norte; as the

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current is strong, fresh-water fish are sometimes carried into water of lethal salinity and are thrown dead on the beach (Von Ihering, 1885, p. 182; 1897, p. 28).

Oversalinity occurs in special parts of the sea: semiseparated parts in semiarid or arid regions. The oversalinity may be episodic (Laguna Madre, no. 24) or permanent. In the Laguna Madre fish die in large numbers in very dry and hot summers when the water becomes oversaline. In permanently oversaline lagoons, the salt content is too high for fish and most other organisms all the year round. At first sight it seems unlikely that fish mortalities should occur in such waters; most fishes are good swimmers and might turn back if they enter a highly saline lagoon from rivers or from the sea. Nevertheless, destructions happen in these places. A well-known example is the Gulf of Kara Bugaz at the eastern border of the Caspian Sea (no. 27), where water of medium salinity flows through the 5-km long channel into this highly saline gulf. In the gulf itself life is impossible for fish and most other organisms. A great fish mortality occurs near the entrance of the channel. The writer, not certain whether a change in salinity is the direct cause of this mortality (recent literature concerning this region is not available), searched for an analogy. The outflowing water of medium salinity through the 5-km long channel into the Kara Bugaz may be compared with a river flowing into a salt lake. Hence, the question arises whether mass mortality of fish also occurs in salt lakes near the entrance of rivers. Such mortalities occur indeed (no. 26–31). Although this chapter is concerned primarily with mass mortality in the sea, it is worthwhile to mention these records, as similar occurrences possibly played a part in geology. The fish enter the lakes in a layer of fresh water floating on the highly saline lake water, and they perish when this layer evaporates or is mixed with underlying water.

MASS MORTALITY IN SEA CAUSED BY A CHANGE IN TEMPERATURE (FIG. 2)

In the oceans the temperature ranges from about −2° to 30° C.; in land-locked areas the surface temperature may be much higher, but in the open ocean it rarely exceeds 30° C. (Sverdrup *et al.*, 1946, p. 55). Many groups of marine animals occur within a wide range of temperature; fish occur from about −2° C. to at least 37° C. (Doudoroff, 1942, p. 219). The range of tolerance of most species, however, does not include both extremes. According to J. L. B. Smith (1949, p. 8), the average fish lives comfortably within a range of only about 17°C., while any greater change results in discomfort, paralysis, and, if maintained, even in death. This statement obviously refers to tropical, stenothermic fishes, since fish in temperate waters and on the high seas undergo a much greater temperature range from day to day or if they pass regularly through a thermocline.

Cold winters and northers.—A sharp decrease in temperature occurs in severe winters, and the shallow-water fauna may be greatly affected. In arctic seas severe winters are normal, and the littoral fauna is adapted to the prevailing conditions (Guryanova *et al.*, 1930; Madsen, 1936). The perennial species of the littoral fauna spend the cold time of the year in deeper water, unless they are very resistant to cold; other species live one summer only and are annually recruited from deeper water. In boreal areas the winters are normally mild and permit the existence of an abundant and perennial littoral fauna. In such regions widespread mortality occurs during an abnormally severe and prolonged winter (Smidt, 1944, p. 33). Mortalities occur particularly when shallow water is covered with ice for a long period; some of the animals are killed by lack of oxygen, others directly by the low temperature. The effect of such abnormally severe winters has been studied in Danish waters by Blegvad (1929), Johansen (1929), Smidt (1944); in the Baltic by Schnoor (1929); in the Skagerrak by Dannevig (1930; 1943); in the Kattegat (Swedish coast) by Gustavson (1942); in the North Sea by Lumby and Atkinson (1929) and Lumby (1931); in France (Channel coast, Boulogne) by Caullery (1929); in the Black Sea (Romanian coast) by Borcea (1931). The mortalities in Danish waters (particularly in the spring of 1929) and the 1929 mortality in the North Sea are discussed in some detail (no. 32, 33). The seasonal variations are very sharp in the Sivash, a body of very shallow water accessory to the Sea of Azov. The average depth ranges from 0.63 m in the northern portion to 0.86 m in the southern part. Partial freezing to the bottom in winter causes a mass killing off or movement of animals to the deeper parts of the bay (Zenkevich, 1947, p. 393; 1951, p. 313).

In low latitudes the winters are seldom severe enough to cause negative temperatures and the formation of ice. The minimum temperature tolerance of several species living in these waters is, however, high, and widespread mortality occurs when the temperature drops below that minimum during some days (no. 34–38). The cold winter of 1929 caused serious mortality in the northern

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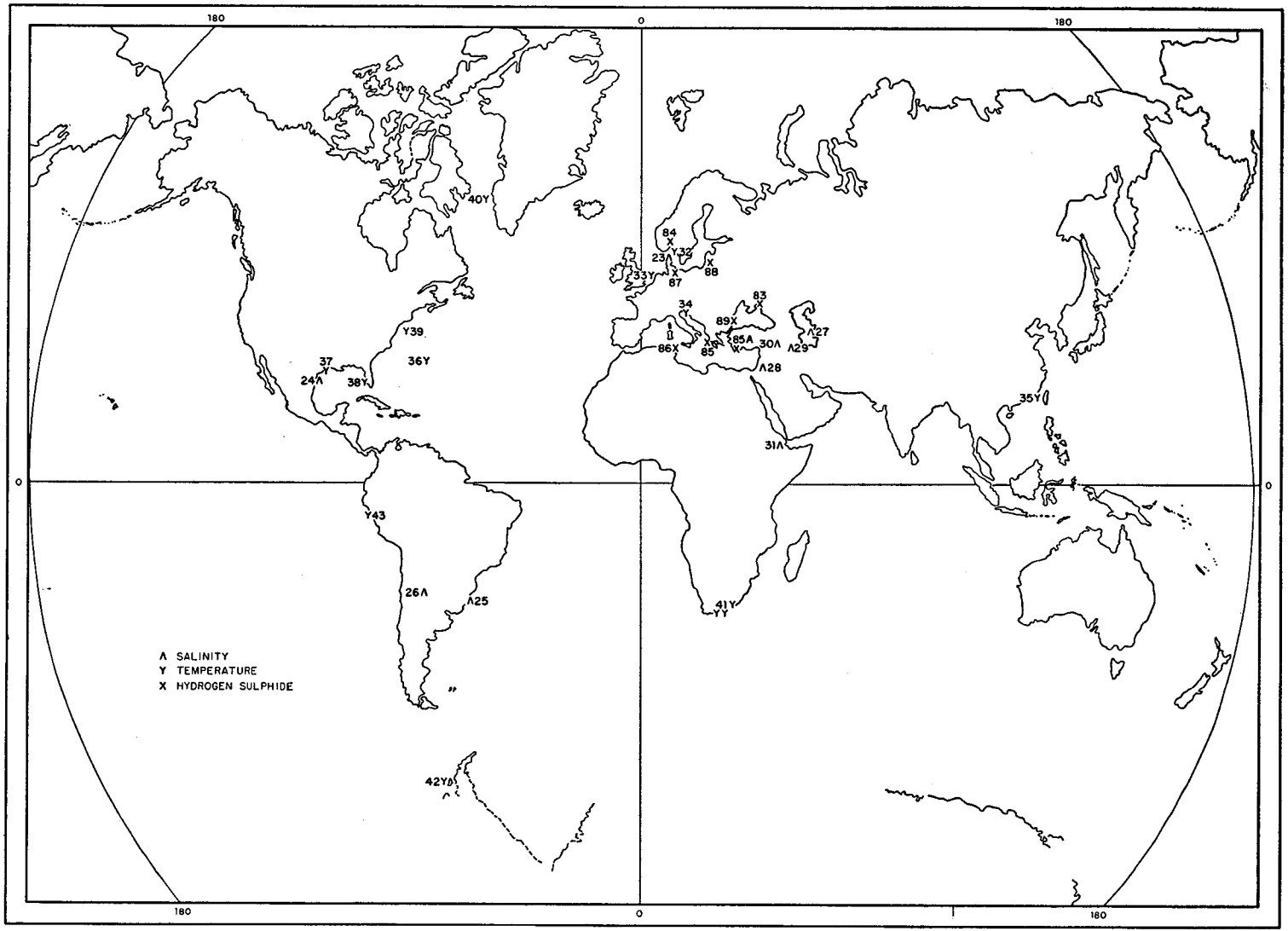

Adriatic (no. 34); here the temperature of the surface water dropped to +5.9° C. These temperatures caused a mass mortality of squids (*Sepia officinalis*) and of certain fishes (especially of *Dentex vulgaris*) which cannot stand a temperature below 7° C. (Vatova, 1934, p. 25). Fish and great numbers of *Sepia* are also killed in cold winters near the Pescadores Islands (no. 35).

A sharp drop in temperature often occurs in various parts of the Gulf of Mexico during heavy northers, in some years causing catastrophic killing. The shallow-water fauna of the Texas coast and of the west coast of Florida seems to be particularly subject to destruction by hard cold spells; in the very severe winter of 1894–1985 not only were vast quantities of shallow-water fishes killed but even many deeper-water species (Storey and Gudger, 1936, p. 641) (no. 37, 38).

"The south Texas coast in the general region of Corpus Christi is at the same latitude as Tampa, Florida. Cold polar fronts push as far south here as at any place of the world" (Gunter and Hildebrand, 1951, p. 731). The destructiveness of the cold waves depends more upon the rapidity of the temperature drop than upon the minimum attained (Storey and Gudger, 1936; Gunter, 1945a; Gunter and Hildebrand, 1951). In shallow waters the temperature drops more rapidly than in the deeper parts of the Gulf. The extremely rapid onset of the northers combined with the great extent of shallow bay waters along the coasts of Texas and of Florida favor the frequent occurrence of catastrophes in these areas. In shallow bays along the Texas coast surface temperatures may drop from 20° to 4° C. within a few days. At such times, when water temperatures fall to about 4° C., large numbers of fish and some invertebrates are killed (Collier and Hedgpeth, 1950, p. 147). The number of fish killed in years of "freezes" is considerable. The word "freeze" connotes not necessarily freezing temperatures but frost or unusually disagreeable cold weather (Storey and Gudger, 1936, p. 640).

In some years destruction attains catastrophic proportions. In the winter of 1845–1846 an army camping near Corpus Christi was fed by the fish and turtles thrown up on the beach after a rather heavy frost (Collins, 1884, p. 276). The weight of fish killed along the Texas coast in January 1951 was estimated at several million pounds (Gunter and Hildebrand, 1951), and during the catastrophe in 1947 at 16 million pounds (Baughman, 1947a). Not all cold spells are fatal to fish. During the very cold weather of January–February 1949 a few dead fish were observed along the Texas coast, but there was no major catastrophe; a combination of several factors—low-tide levels, several days of low temperature, etc.—controls the amount of damage (Collier and Hedgpeth, 1950, p. 147). Mass mortalities occur every few years; according to the records by Storey and Gudger (1936) fishes were killed in large numbers on an average in one of every six years at Sanibel Island, Florida, from 1886 to 1934.

Change in currents.—Changes in currents may also have an important bearing on the distribution of the temperature in the sea. They may bring about mortalities by a decrease and also by an increase in temperature. Big changes occur on the boundaries of cold and warm currents, in a vertical as well as in a horizontal direction. Here the mortalities are not confined to shallow-water fish, but many deeper-water species are killed in great quantities. Since Murray's hypothesis of the origin of phosphate concretions was formulated, many authors emphasize the paleontological importance of the tilefish disaster (no. 39). It is not improbable that these fish were killed by a decrease in the temperature of the sea water, but data concerning the temperature are not available, and later records of catastrophe of this fish by which the hypothesis could be confirmed are not known. A better example of mortality caused by a change in currents is the episodic mortality near Sukkertoppen (no. 40). This mortality happens near the border line of the Polar and the Irminger currents. The temperature of the water near Sukkertoppen is chiefly dependent on the proportional strength of these two currents. Mass mortality occurs rather exceptionally, in years in which unusually low temperatures prevail, as shown by Hansen (1939; 1949, p. 9; Jensen, 1939, p. 73).

A sudden drop in temperature repeatedly occurs in the Agulhas Current close to the southern coast of Africa. Along these coasts with a summer temperature of about 18° C. a large body of water of 10° C. may suddenly appear. This may occur anywhere from Mossel Bay to just south of Port St. Johns and is fairly common at Knysna. When it lasts for more than 62 hours the shore may be littered with dead and dying fishes, sometimes countless millions, and many rock pools are an almost solid mass of fishes of many species either dead or, if alive, in only partial control of their movements

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(J. L. B. Smith, 1949, p. 8) (no. 41). Recent records on these sudden decreases in temperature are given by Gilchrist (1914, p. 27) and by Korringa (in litt.).

The Agulhas Current is a strong density current. As heavy, cold water occurs on the right-hand side of an observer looking in the direction of flow in the southern hemisphere, the isopycnals slope upward toward the coast. This phenomenon is not usually perceptible at the surface, but in certain times of the year cold water may appear near the coast, the so-called "dynamically caused upwelling" (Dietrich, 1935a, p. 17). Korringa (in litt.) gives another explanation of the occurrence of cold water. He investigated the plankton occurring in the cold water near the coast of Knysna; the plankton pointed to pelagic surface conditions. Considering that (1) the temperature was several degrees lower than that of the Agulhas surface water, (2) the plankton points to pelagic surface conditions, (3) the appearance of cold water coincides with strong easterly winds, Korringa assumes that during gales cold surface water derived from south of the subtropical convergence is driven to the coast. Strong southeasterly winds indeed preceded the mortalities mentioned under no. 41. If Korringa's hypothesis is correct, cold surface water appears not only near the coast but occasionally is swept all over the Agulhas Bank; the indirect cause of the mortalities is not the sloping of a strong density current but the vicinity of a strong convergence. Observations on the temperature of the offshore surface water during storms are needed.

A most interesting mortality was recently reported by Nani (Popovici and Nani, 1953) from the Antarctic Ocean (no. 42). A great number of dead fish, all belonging to the species *Pleurogramma antarcticum* Blgr., floated in the Bellinghausen Sea. The cause of this mortality probably was a sudden drop in temperature caused by vertical currents. Below the very cold antarctic surface water lies the warmer and more saline antarctic circumpolar water (Sverdrup *et al.*, 1946, p. 610). *Pleurogramma* lives in the circumpolar water. When surface water with a negative temperature sinks through the warm circumpolar water in some places these fish are in a perilous situation. Nani states that dead specimens of this species also have been found in other parts of the Antarctic Ocean.

An example of killing by a great rise in temperature is given under no. 43.

MASS MORTALITY IN SEA CAUSED BY NOXIOUSNESS OF WATERBLOOM (FIG. 3)

Plankton is usually of great benefit to invertebrates and to fish, for all of them feed directly or indirectly on these tiny organisms. Under certain circumstances one or a few species of plankton organisms multiply with great rapidity, the number of individuals becomes extremely high, and they predominate over all other organisms. A discoloration of the water caused by such rapid multiplication or by swarming of microscopic organisms is called waterbloom. The color may be red, yellow, green, blue, etc. Waterbloom of certain groups of the phytoplankton as well as of the zooplankton may bring about enormous destruction among invertebrates and fish. In some years these mortalities attain catastrophic porportions; 1880 was a year of great catastrophes in Southwest African and in Florida waters (no. 68, 72). "The whole sea seems to die" (Clark, 1929). It is a peculiar fact that noxious marine waterbloom nearly always has a red, pink, or brown color, the so-called "red water".

A survey of the literature on red water and destruction of marine life was given by Brongersma in 1948 (*see also* Galtsoff, 1948; 1949; and Fage, 1951). Records that escaped the writer's notice or were published afterward are given below. An interesting map showing the distribution of discoloration in the sea was published by Hayes and Austin in 1951; although the cause of the discolorations is not indicated, plankton blooms are at least partly responsible (Fig. 4).

There has been much discussion about the noxious effect of red water. Several authors (Nishikawa, 1901; Kofoid, 1911; Lindemann, 1924; Marchand, 1928; Chidambaram and Unny, 1944) attribute the mortalities in red water to putrefaction and pollution caused by the dead plankton. If this is correct, waterbloom should be only indirectly noxious. In some of the regions where red water occurs there is certainly shortage of oxygen and development of H_2S, but the direct cause of the mortalities during waterbloom in lakes and in the sea probably is a strong poison produced in the living plankton of dinoflagellates or blue-green algae. Waterbloom may be very noxious not only to fish and invertebrates but also to air-breathing animals for which lack of oxygen in the water is of no importance. Cattle and chickens may be killed by drinking water with waterbloom (Fitch *et al.*, 1934; Steyn, 1945a; 1945b; Prescott, 1948; Stephens, 1948; 1949). During a mortality in waterbloom of blue-green algae in the former Zuiderzee newts and frogs near the shore were killed, as well as fish in the water

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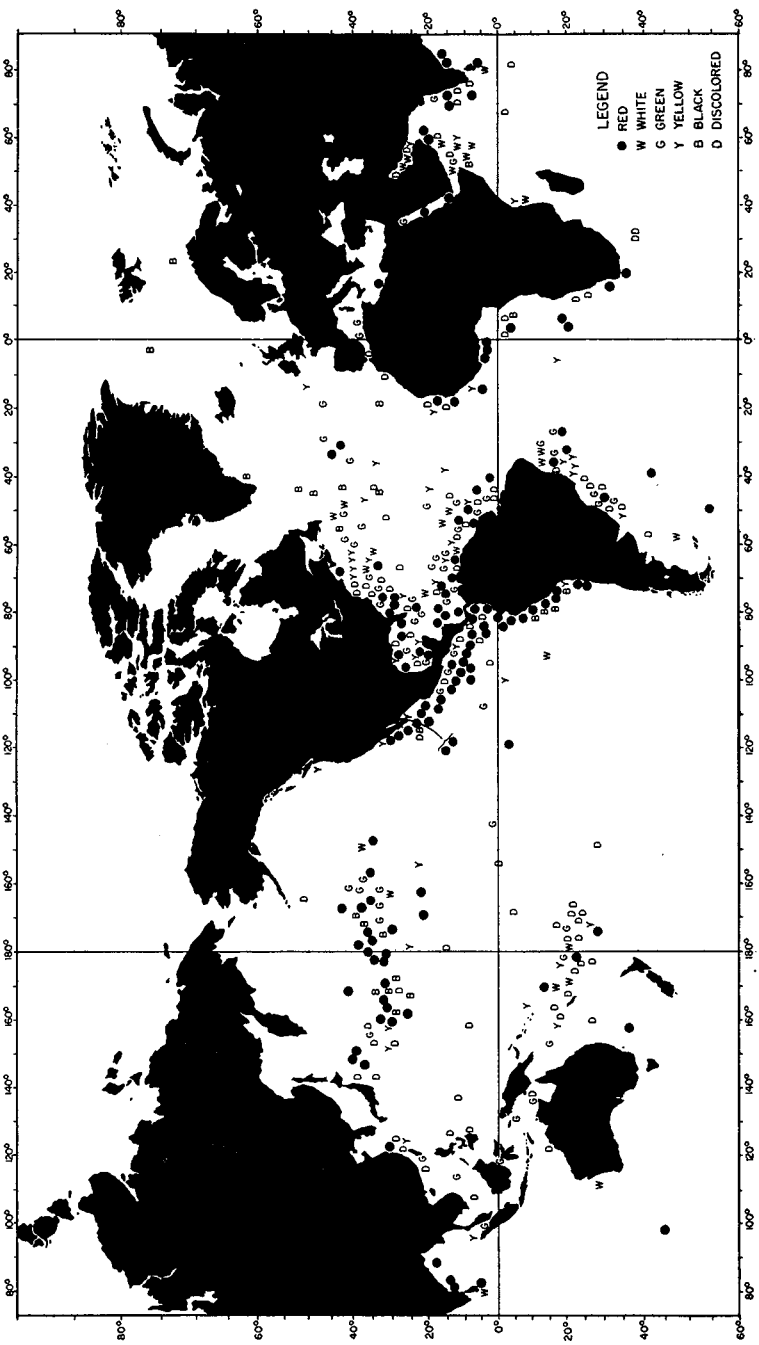

FIGURE 4.—*Distribution of discolored water in the sea*
Modified from Hayes and Austin (1951).

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(Kristensen, 1943; in litt.). A very strong poison was isolated from waterbloom of blue-green algae (Fitch *et al.*, 1934; Shelubsky, 1951) and of dinoflagellates (Sommer *et al.*, 1937; Sommer, Monnier, *et al.*, 1948; Sommer, Riegel, *et al.*, 1948; Riegel *et al.*, 1949). The dinoflagellate poisons were also isolated from plankton-eating invertebrates. Mussels can store great quantities of poison before they are killed; when eaten by man these mussels cause paralytic shellfish poisoning (Sommer *et al.*, 1937; Koch, 1938; 1939).

Experiments by Gunter *et al.* (1948, p. 320) with the dinoflagellate *Gymnodinium brevis* Davis collected during the Florida mortalities (no. 72), and by Otterstrøm and Steemann Nielsen (1940) with the flagellate *Prymnesium parvum* Carter collected during a fish mortality in Danish lakes, have shown that these organisms may kill fish in well-aerated aquaria. Reich and Aschner (*fide* Komarovsky, 1951, p. 221) have shown that *Prymnesium parvum* secretes a toxin which acts directly upon the fish, killing them in a matter of hours. A pure culture made by the Danish authors proved to be non-poisonous, and they suggest "that the poisonous element is a product of metabolism that is not found in large quantities in a young culture but in large quantities in an old culture, the largest amounts thus occurring in autumn." (Otterstrøm and Steemann Nielsen, 1940, p. 22.) It may also be that the poisons are not produced in aquaria but that they gradually concentrate in organisms living in highly productive waters where enormous masses of plankton decay during the course of the year. Bhimacher and George (1950) have shown that there can be successions of discolored organisms—for example, euglenoids developing in water containing great quantities of decaying *Noctiluca* (no. 80). With these successions the poisonous species may gradually develop, and this might explain why red water is not always injurious.

Another factor besides the poisonous nature of red water which may contribute to the mortalities coinciding with red water is the shortage of oxygen at the beginning of a red-water outbreak when red water develops after the death of great amounts of other plankton organisms. (*See* below.)

Red water occurs in very fertile parts of the sea, often during or after unusually warm weather; it develops in succession after a great production of other organisms. Products of decay of the latter might be one factor that sets the bloom in motion. Great outbreaks occur particularly in subtropical and tropical regions where the rate of overturn of organic matter is high; in fertile parts of high latitudes red water, at least of catastrophic porportions, does not occur or is very rare. Plenty of sunshine seems another requirement for red-water outbreaks. The areas where red water occurs are somewhat reminiscent of polluted waters; the dead fish will worsen the "pollution". Here it is important to note that pollution by human action also favors red-water outbreaks. Connell and Cross (1950, p. 22) assume that small amounts of sewage pollution favor the development of red water in Offatts Bayou. Braarud (1945, p. 405) states that in inner Oslo Fjord some phytoplankton species show a definite relation to the degree of pollution; in the region of highest pollution dinoflagellates occurred in enormous numbers.

The greatest outbreaks of red water probably occur toward the end of a phytoplankton season; in areas where upwelling occurs during part of the year only, red water usually develops toward the end or directly after the period of upwelling (very convincing examples are scarce, but see no. 48, 78, 79, 80, etc.). A rise in the temperature of the coastal water or an inflow of river water often precedes the development of red water. Near Peru (no. 48) red spots occur wherever warm water invades the cold Peru Coastal Current. Bloodlike patches caused by dinoflagellates are particularly frequent in El Niño years when abnormally high temperatures prevail in these waters (see no. 43). This may be due to the beneficial effect of a high temperature or of stratification; killing of the prevailing plankton is another possibility. In other regions (no. 58, 60, 68, 70, 72, 74) red water coincides with an inflow of river water and/or with rain in the hinterland. The relation of rainfall in the hinterland/red water in the coastal area has been ascribed to a fertilization by river water (no. 72, Slobodkin, 1953), to an inflow of sewage-polluted water (Connell and Cross, 1950, p. 362), to the beneficial effect of stratification (for the detrimental effect of a "dilution" of the population through vertical transport *see* Braarud, Gaarder, Grøntveld, 1953, p. 8; Slobodkin, 1953), or to the favorable effect of low salinity on mass development of certain species of dinoflagellates (Nordli, 1953). Killing of the prevailing plankton by a sudden change in salinity is another possibility. In some areas rain in the hinterland is due to cessation of upwelling in the coastal area and may mean a sudden rise in the temperature of the coastal water, disappearance of the fog, etc.

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Great mortalities apparently do not occur in very cold regions. Red water and/or paralytic shellfish poisoning of man occur as far northward as Norway (no. 58), Iceland (no. 57), Scotland (no. 60), and Canada (no. 44, 54); mass mortality is as yet unknown from these regions, except the Pacific side of Canada. Red water frequently occurs in New Zealand waters (no. 52), but catastrophic killing is unknown. The greatest destructions occur in fertile seas in low latitudes.

Many mortalities coinciding with red water in literature are ascribed to: (1) vulcanism, (2) a decrease in salinity, (3) lack of oxygen and production of H_2S, etc. This has some factual basis: (1) Discolorations of the sea often have been considered the result of vulcanism instead of being caused by accumulations of plankton. (2) High rainfall and subsequent influx of fresh water into the sea in some areas precede red tides. (3) Absence of oxygen and development of H_2S occur at least in some of the areas where red water has been observed (it is probable, but not certain, that the greatest oxygen deficiency is to be met with when the red-water organisms die and decay). Such a situation occurs in the South Russian limans, in the Sea of Azov, in the Southwest African coastal waters, and in other hypertrophic areas. The situation in the Sea of Azov is described in Chapter 25 and in nos.

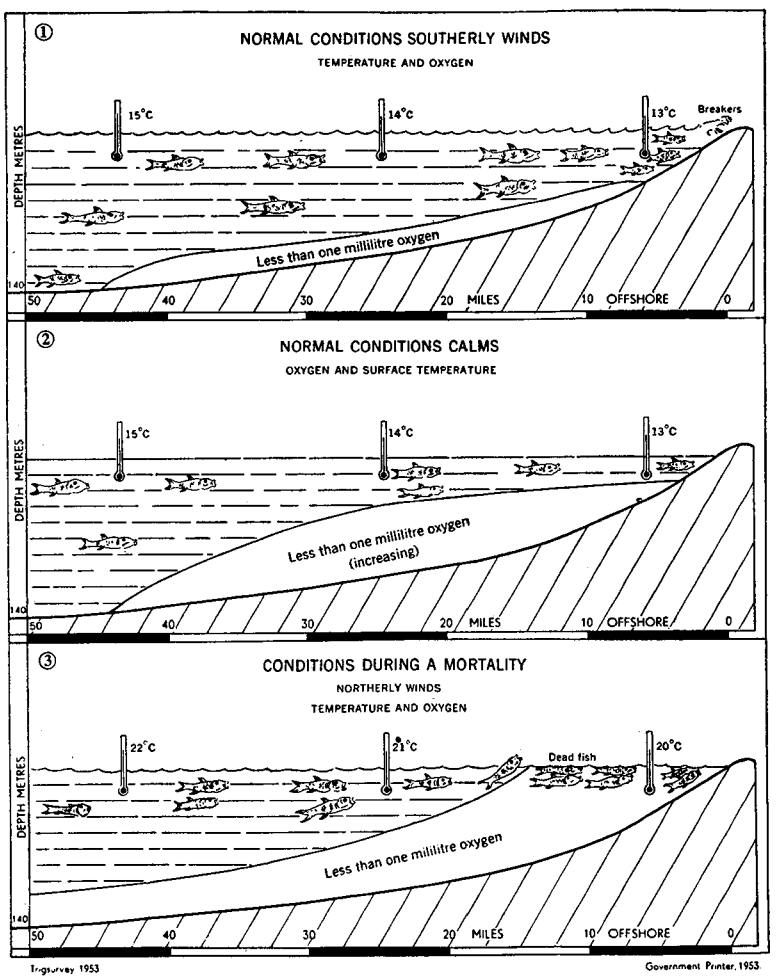

FIGURE 5.—*Temperature and oxygen conditions coincident with mortalities in Walvis Bay* From Copenhagen (1953).

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63, 83). Recent researches by the 1949 Belgian Oceanographic Expedition in January 1949 (Van Goethem, 1951), by the WILLIAM SCORESBY in March 1950 (Currie, 1953; Hart, 1953), and by the NAMIB in May 1950 (Copenhagen, 1953) have shown that a similar abnormally high consumption of oxygen and development of H_2S temporarily occurs in the Southwest African coastal areas. This led Brongersma (1951; 1952) to conclude that future source rocks of oil are developing in such hypertrophic areas (this assumption was also based on the peculiar resemblance between the sediment of the Southwest African coastal area and the Monterey shales). It led other authors (Currie, 1953; Hart, 1953; Copenhagen, 1953) to conclude that the great fish mortalities occurring in the Southwest African coastal waters are caused (at least in part) by H_2S and lack of oxygen (Fig. 5). If this is correct, the nature of the plankton during the mortalities is not material. Brongersma (1948) assumed that the fish mortalities near Southwest Africa are caused by dinoflagellate poisons, for several observations show that the plankton at the beginning of a mortality has a certain nature: mortality coincides with red water of dinoflagellates. Therefore, it seems reasonable to suppose that this red water is injurious. Virulent poisons found in dinoflagellates in other parts of the world support this hypothesis. However, there is still another possibility: it has gradually become apparent that heavy outbreaks of red water often occur toward the end of a phytoplankton season indicating that most of the oxygen will be used up in the lower-water layers of fertile areas. This, together with the fact that a change in temperature and salinity probably coinciding with killing of part of the prevailing plankton often precedes red tides, suggests a new possibility: the death of the prevailing plankton, bringing about lack of oxygen, causes on one hand mass mortality and on the other hand the development of red water. Determinations of oxygen at the beginning of a great mortality are yet to be made; such determinations together with researches on toxicity of the plankton may show which factor is most important. If lack of oxygen is most important, it is not correct to say that these mortalities are caused by, but they only coincide with, red water. For remarks on the so-called azoic region, *see* under Mass Mortality by Lack of Oxygen. Near the coast of Peru two phenomena occur: red aguaje and the Callao painter (no. 47).

At any rate, a red discoloration occurs during the mortalities near Southwest Africa. The nature of most discolorations mentioned by Brongersma (1948, p. 8) is unknown; therefore, further confirmation of her hypothesis, which was chiefly based on evidence from other similar regions, is needed. Unfortunately the WILLIAM SCORESBY visited this area in March and September–October 1950, whereas the great mortalities occur in the southern summer, particularly at Christmas time. The GALATHEA Expedition did visit these waters on December 25, 1950, when a great catastrophe occurred. At that time Walvis Bay and the adjoining coastal waters were covered to a considerable extent with a layer of what might be described as a thick brownish soup consisting almost entirely of a small dinoflagellate (*Glenodinium*) (Spärck and Steemann Nielsen, *fide* Copenhagen, 1953).

It seems highly probable that the periodical fish mortality near Temrjuk (southeast coast of the Sea of Azov) (no. 63) also occurs in waterbloom.

Highly eutrophic and hypertrophic regions.—Waterbloom does not occur in waters of low production (oligotrophic[1]). Heavy outbreaks of red water causing catastrophic killing are restricted to the most productive parts—*viz.* to highly eutrophic, and particularly to hypertrophic water.

Factors governing organic production in the sea are discussed in Chapters 6, 11, and 16; such production is closely dependent on the supply of nutrients to the well-lighted upper layers of the sea. This supply is high in regions where the nutrients are brought up from the depths of the oceans or from the depths of inland seas by vertical currents (convection currents, upwelling, strong tidal currents, etc.), or where they are supplied by certain rivers from the surrounding land.

In very cold climates convection currents reach to great depths. Here discolorations of the water caused by diatoms are of frequent occurrence. The temperature of the water is usually too low for outbreaks of red water (dinoflagellates, marine blue-green algae, etc.).

In warm climates convection currents do not reach to great depths, except in certain basins in very dry regions (inner part of Gulf of California, Red Sea) (Sverdrup *et al.*, 1946, p. 790). Fertility of the Red Sea is brought about not only by convection currents but also by upwelling. In the Gulf

[1] The only record of waterbloom in oligotrophic water is that by Borgstrom (1935), who records an unusual waterbloom due to the blue-green *Microcystis aeruginosa* in an oligotrophic lake; as a result of nitrogen deficiency the color of the alga was yellow.

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of California (sometimes called the "Vermilion Sea"), the seasonal phytoplankton cycle is dependent upon upwelling in the outer Gulf and upon convection in the inner part (Gilbert and Allen, 1943, p. 109; Sverdrup, 1940).

The names of these seas have some factual basis, for red discolorations by blue-green algae and by dinoflagellates occur repeatedly (no. 46, 77); mass mortality coincident with red water has been reported so far only from the Red Sea. It seems fairly certain that mass mortality also occurs in the Gulf of California.

Upwelling may occur in mid-ocean, but it is particularly important along certain coasts. Red water accompanied by mass mortality occurs in nearly all regions of upwelling, although there are a few gaps in our information. The most important regions of upwelling are the coastal waters of Southwest Africa, Peru-Chile, Northwest Africa, and California. Catastrophes associated with red water occur in all of them. Since 1948 (Brongersma, 1948), several new incidents have occurred. In 1948 catastrophic killing in red water was unknown from Northwest Africa, but an incident was reported in August 1951 (no. 65). The sediment near El Hadd (Southeast Arabia), where upwelling occurs in summer, shows a great similarity to that of the so-called azoic region near Walvis Bay (abundance of fish remains, H_2S, relatively high organic content, etc.). On the basis of abundant fish remains, Stubbings (1939, p. 112) suggests that a change in salinity causes a great destruction of life in this vicinity. A red-water occurrence near the cemetery of fish near El Hadd was reported in October 1950 (no. 78), and destruction here may have been caused by red water, as previously supposed (Brongersma, 1949; 1950).

Red water has also been reported from the Bay of Guanabara (Rio de Janeiro) (no. 70); according to Böhnecke (1943) there is upwelling in the coastal waters of this region. Another possible explanation of the fertility of this bay is that the nutrients are carried by rivers from the hinterland.

In 1948 Brongersma (p. 64) mentioned that mass mortality (cause unknown) occurs in the region of upwelling water near the coast of Venezuela. Clark (1929) states that it is caused by red water (no. 71).

Parr (1935, p. 62) supposes that upwelling may take place on the Florida bank and on the Campeche Bank. Red water and catastrophic killing occur in both these regions (nos. 72, 75). If Parr's supposition is correct, it is feasible to consider upwelling the initial cause of these red-water outbreaks. Determinations of the total phosphorus content in Florida coastal waters were made by Ketchum and Keen (1948), Chew (1953), and Graham *et al.* (1954, received too late for full discussion). The total phosphorus content of water containing dense *Gymnodinium* populations during the 1948 Florida outbreak was found to be 2½ to 10 times the maximum expected in the sea. This might be explained by a combination of upwelling on one hand and of active swarming or concentration of red-water organisms on the other hand, or to intense local regeneration from decaying plankton. A similar phenomenon is found in the Southwest African upwelling water (Currie, 1953, p. 7).

Other hypotheses proposed to explain the Florida red water are: (1) The high nutrient content is not derived from the open sea, but from the hinterland (Humm, 1952; Slobodkin, 1953; Anonymous 16, 1953). Slobodkin demonstrated that high rainfall in Southwest Florida often precedes red tides in the coastal water. Chew (1953) has shown that water of Gulf origin contains more total phosphorus than does water with greater river influence; this means that the high phosphorus content of the coastal waters apparently does not come from river runoff, but from the open Gulf. Hence, the interesting association of great rainfall with red tide probably must have another explanation. (Feinstein (1956) finds no direct correlation between Florida red tides and precipitation or runoff, but admits that some indirect relationship may occur.) (2) Leaching of bottom deposits rich in phosphates and nitrates (F. G. W. Smith, 1949). (3) Concentration of *Trichodesmium* plankton by winds and tides and subsequent death and decomposition should furnish sufficient nutrients for red water outbreaks (Graham, Amison and Marvin, *fide* Chew, 1953, p. 623). (4) H. B. Moore (*in* Chew, 1953, p. 624) postulates a convergence off the coast of Florida, concentrating a wide area of plankton into a relatively narrow zone. The sinking water in the convergence is thought to have no advective effect on the swimming dinoflagellates, which remain on the surface.

A strong upwelling of deeper-water layers occurs in the Straits of Messina; nevertheless, the mortality of deep-sea fish, repeatedly occurring in these Straits, is probably due to the direct influence of strong currents (no. 95).

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Some rivers carry an important amount of nutrients to the sea; near the mouths of such rivers the organic production is high (Thiemann, 1934; Hardenberg, 1931; 1948; Riley, 1937). The organic production becomes particularly high if such rivers flow into semiseparated parts of the oceans where nutrients derived from the land accumulate.

In the South-Russian limans, in the shallow parts of the Black Sea, and in the Sea of Azov, the organic production is very high. In the Sea of Azov there is waterbloom of blue-gree algae and of dinoflagellates from June through nearly the whole summer. (For a periodic fish mortality in this sea, *see* no. 63.) Mass mortality in reddish water has also been observed in the Black Sea (no. 64); the nature of the discoloration is unknown. Other semiseparated parts of the sea where waterbloom occurs rarely are the "haffs" of the Baltic (no. 59), some Norwegian fjords (no. 58), a Scottish Loch (no. 60).

In fresh and brackish waters mass mortality occurs chiefly during waterbloom of blue-green algae more rarely during that of flagellates and of dinoflagellates (literature in Brongersma, 1948, p. 39–41). Waterbloom of blue-green algae causing heavy mortality in fish ponds in the Jordan Valley recently has been described by Komarovsky (1951). Fish mortalities also occur during waterbloom of *Botryococcus Braunii* (Kützing) belonging to the Heterokontae (Pascher, 1939, p. 110, 184), which frequently forms waterbloom in fresh water (Fritsch, 1935, p. 476, Steinmann, 1923). This alga may be very abundant in brackish waters as well—*e.g.*, the Baltic (Woloszynska, 1935, Häyrén, 1940) and the Caspian (Zenkevich, 1951, p. 322). The occurrence of mass mortality during *Botryococcus* waterbloom is important, because *Botryococcus* frequently occurs in oil shales (Blackburn, 1936). In brackish waters catastrophes have also been observed during waterbloom of ciliates (Otterstrøm and Larsen, 1946).

In the sea, catastrophic killing is caused chiefly by red water of dinoflagellates; it is uncertain whether or not only certain species or genera may be injurious. Brongersma (1948, p. 42) gives only a few records of catastrophes in the sea caused by waterbloom of blue-green algae (no. 51). Destructions were mentioned by Chacko (1942, 1950), by Chidambaram and Mukundan Unny (1944) (no. 82), and by Aikawa (*fide* Galtsoff, 1949) (no. 49).

A red discoloration of the sea by ciliates has frequently been observed off the Cape of Good Hope (no. 69) and in New Zealand waters (no. 52); it is also recorded from the Gulf of Maine (no. 54) Iceland waters (no. 57), British Columbia (no. 44); near Valparaiso it was observed by Darwin (*fide* Hart, 1943). According to Bary and Stuckey (1950, p. 90) the causative organism in all these occurrences is *Cyclotrichium meunieri* Powers and not *Mesodinium rubrum* Lohmann, as has been stated by previous authors. The ciliate causing red water off the west coast of Florida at approximately 84° 30′ W. and 28° 30′ N. on June 2, 1952, is designated by Slobodkin (1953, p. 149) "probably *Mesodinium pulex* Noland or a closely related form." The red water in Santa Monica Bay in June 1945 contained, in addition to dinoflagellates a large number of ciliates (no. 45).

Brongersma (1948) omitted occurrences of ciliate red water, because records of mass mortality in the sea, caused by these organisms, are not known. Dr. John Hart (Plymouth, in litt.) remarks: "The ciliate *Mesodinium* was overwhelmingly dominant near the Cape of Good Hope on every occasion that I examined red water in this area; marine ciliates are constantly disintegrating so that they are quite unrecognizable in preserved samples, and this led to widespread failure to recognize its importance as a mass producer of visibly discolored water". As there is a record of mass mortality by ciliates in brackish water (*see* above), the possibility that the catastrophes near the Cape of Good Hope (no. 69) and in other places are caused by these organisms cannot be excluded. Bhimachar and George (1950, p. 348) assume that ciliates and euglenoids develop in water in which decaying *Noctiluca* occurs. They attribute the Malabar mortality to *Noctiluca* rather than to euglenoids, as had been supposed by Hornell (1917) (no. 80).

A red discoloration of the sea also may be caused by organisms other than phytoplankton: purple sulfur bacteria (Ellis, 1932, Heldt, 1952) and local concentrations of medusae, copepods and other crustaceans, and tunicates (Steuer, 1910; 1911; Galtsoff, 1949; Bary, 1953). Sulfur bacteria occur where saprophytic decomposition results in the production of hydrogen sulfide. A red discoloration by these organisms occurs in shallow land-locked bays and swamps with an accumulation of putrefying weeds and other plant remains; this has been recorded from the coast of Denmark, Jamaica (Ellis, 1932, p. 5), the Bay of Tunis (Cabasso and Roussel, 1942; Heldt, 1952), etc. In the Black Sea,

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the Sea of Azov, and the Caspian Sea, sulfur bacteria are important because they oxidize hydrogen sulfide accumulating in deep water and in shallow areas (Chapter 25; Kriss and Rukina, 1949). Purple bacteria are frequently associated with decomposing plankton; hence they may occur after outbreaks of red water of dinoflagellates.

The question whether purple bacteria are harmless is not settled; *see* the mortality near the mouth of the river Danube (no. 64). In the Bay of Tunis (no. 86) a red color caused by bacteria was observed after the mass mortality. Records of widespread mortality caused by green or brownish "waterbloom" of diatoms are not known except for the remark by Aikawa on catastrophes in Japanese waters (no. 49). Swarming of a colonial flagellate of the genus *Phaeocystis* is often responsible for a brownish discoloration of the sea in middle latitudes; the alga is very offensive to herring, which are never found in the areas where *Phaeocystis* is abundant (Savage and Hardy, 1935; Savage and Wimpenny, 1936). Catastrophes caused by abundance of *Phaeocystis* have not yet been observed.

Thick masses of jellylike slime produced by microscopic plankton or benthos have been observed in various seas: northern seas (Wille, *fide* Steuer, 1911, p. 354), northern part of the Adriatic (Cori, 1906; Zanon, 1931), coasts of Tunisia (Pottier, 1929; Feldmann and Fremy, 1935), Malabar, and South Kanara coasts (Bhimachar and George, 1950). The jellies become a great nuisance to fishermen as they prevent the nets from sinking, clog the meshes of the nets, etc. Fish avoid the jellies; the slime apparently does not cause great mortality.

In northern seas and along the coasts of Tunis the slime is produced by blue-green algae. In the Adriatic during warm weather, benthonic diatoms multiply with great rapidity on the bottom, forming masses of jelly; as a result of the oxygen produced by these algae, the jelly is lifted from the sea bottom and floats in the water (Zanon, 1931). Besides diatoms, dinoflagellates greatly contribute to the origin of these jellies (Cori, 1906). Along the Malabar and South Kanara coasts the sliming of 1948 was mainly due to the putrefaction of a superabundant population of the dinoflagellate *Noctiluca miliaris* (Macartney). *Noctiluca* attained its maximum in the year in the latter half of September; about the middle of October there was an abrupt decline in its numbers. During the peak period, pink patches of *Noctiluca* were very common; this pink water preceded the formation of thick slimy masses that caused an abrupt setback in the fisheries in the latter half of October. The slime consisted of dead and decaying *Noctiluca* mixed with fine clay. Red water often causes mortality on this coast (no. 80), but during this sliming of the sea only a few dead fish were found. There was no severe mortality of fish anywhere; apparently fish avoided such areas. However, there was considerable destruction of plankton (diatoms, fish eggs and larvae, etc.).

Animals killed by waterbloom.—In fresh and brackish water various aquatic animals are killed (fish, frogs, newts, snakes, etc.) (Deem and Thorp, 1939; Komarovsky, 1951; Kristensen, 1943, and in litt.; Liebert and Deerns, 1920; Otterstrøm and Steemann Nielsen, 1940; Prescott, 1948; Shelubsky, 1951), and terrestrial animals are killed when drinking water with poisonous waterbloom. Waterbloom of blue-green algae floats on the water and is swallowed by cattle "especially such as suck their drink at the surface like horses" (Francis, 1878). Nearly all records refer to domesticated animals (horses, cows, pigs, fowl, etc.) (Fitch *et al.*, 1934; Francis, 1878; Steyn, 1945a; 1945b; Stephens, 1948; 1949). Deem and Thorp (1939) mention the death of wild birds. Poisonous waterbloom of blue-green algae occurs particularly in warm, hard-water lakes where essential nutrients are abundant (Prescott, 1948). It is fairly certain that in the geological past (and probably also in certain places in recent time) the wild animals gathering to drink from warm, hard-water lakes were killed in many summers. In severe cases the animals die very soon, and their corpses accumulate on the shores of such lakes.

In the sea the animals killed consist of various groups of invertebrates and vertebrates. In severe cases probably the whole fauna dies. Crustaceans (crabs, shrimps, etc.) especially suffer greatly, also sponges, worms, mollusks (particularly cephalopods), etc. (no. 45, 47, 55, 66, 67, 72, 80; cephalopods no. 48, 68). The vertebrates that die are mainly fish; in most regions benthic species are killed first; if aquatic vertebrates other than fish are present, they may also be affected (sea turtles no. 72 year 1946, sea snakes no. 77). Birds and seals may die from eating the poisoned fish (no. 44, 47, 68); men are killed by eating poisonous mussels (paralytic shellfish poisoning); other vertebrates living on the sea shore also may die from eating poisonous marine mussels and other marine invertebrates (no. 44, 69, etc.).

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MASS MORTALITY IN SEA CAUSED BY LACK OF OXYGEN AND BY POISONOUS GASES (H_2S, ETC)

In the sea there is usually no lack of oxygen, but there are areas with an abnormally low-oxygen supply and areas with an abnormally high oxygen consumption. An abnormally low oxygen supply occurs in badly ventilated fjords; here a great amount of H_2S accumulates, and when on rare occasions (*e.g.*, once in a half century) this is raised to the surface widespread mortality of the fauna of higher water layers occurs (no. 84). Shortage of oxygen also occurs when very shallow waters in winter are covered with ice for a long time; then part of the fauna may be killed by lack of oxygen (no. 32). Shortage of oxygen by an abnormally high consumption occurs in hypertrophic shallow seas.

In all eutrophic lakes the oxygen content becomes very low during the summer stagnation; in hypertrophic lakes the oxygen content becomes zero for a long time, and H_2S is developed. In shallow seas with their much greater surface there is not such a long summer stagnation; here the stratification is often disturbed by winds. Therefore, there is usually no oxygen deficiency, but this nevertheless may occur in hypertrophic parts of the sea. Here the oxygen consumption is so enormously great that even during a short spell of calm weather the oxygen of the lower-water layers is used up, and the boundary O_2/H_2S rises above the sediment. As a result, widespread mortality of the bottom invertebrates occurs. This happens even in the very shallow Sea of Azov where a strong stratification occurs only during warm and calm days. In other hypertrophic waters the stratification and the oxygen deficiency last much longer—*e.g.*, in the South Russian limans. A similar phenomenon is described by Sadowsky (1930) from the Bay of Krasnowodsk on the eastern side of the Caspian, from Southwest African coastal waters (bays and open sea) by Van Goethem (1951, p. 88, 91) and Currie (1953, p. 7), from the Bay of Talcahuano by Falke (1939; 1950).

When strong winds bring new oxygen to the bottom water some time after the "bottom" mortality in the Sea of Azov, the benthonic fauna returns from all sides (Zenkevich, 1951, p. 299). This means that an azoic area occurs only temporarily and locally, and it may explain the controversies concerning the existence of an azoic area in Southwest African coastal waters. Many bottom samples taken in this area by the Marine and Biological Survey of South Africa in the years 1925–1928 smelled strongly of H_2S and were devoid of any bottom life (Von Bonde, 1928a, p. 12; 1928b, p. 18; descriptions of the samples in the annexures of Von Bonde's papers; Marchand, 1928; Copenhagen, 1934). More samples were taken by the WILLIAM SCORESBY (Currie, 1953, p. 7), by the GALATHEA Expedition, and by Copenhagen (1953). Currie states that the azoic zone covered a larger area than previously supposed. "A series of Baillie rod soundings revealed that it extended, at least in patches, between depths of 50 and 150 metres, for about 400 miles north of lat. 25° S. The map by Marchand (1928) (copied in Brongersma, 1948, p. 8) should not be considered to indicate one continuous azoic zone; apparently it is an azoic zone in patches, patchy in both place and time. The GALATHEA Expedition found evidence of bottom life at two profiles in the azoic zone. Prof. R. Spärck (Private communication) states that at two profiles at the latitudes of Sandwich Harbour and Conception Bay a considerable number of annelids and mollusks were found.

In the Black Sea hydrogen sulfide is found from about 180 m to the bottom. Along the upper layer of the H_2S zone there are places where H_2S is oxidized to H_2SO_4 by sulfur bacteria (for recent research and criticisms *see* Kriss and Rukina, 1949).

Antipa (1941, p. 83) observed yellow-reddish water bordered with stripes of white foam somewhat south of the river Danube. He was told by fishermen that reddish water may be observed twice a year in a flow of cold water. Fish die when arriving in this water, and the fishing nets are "burnt" by it. The cause of the reddish color has not been investigated. Antipa supposed that water is brought up from a depth of 180 m where H_2S is converted into H_2SO_4. Antipa's hypothesis was adopted by several geologists (Staesche and Teichmuller, 1944, p. 20). Archangelski (*fide* Leutwein, 1951, p. 34) states that acid water sometimes is brought to the surface by storms. Further research of this phenomenon is needed (nature of the color, bacteria ?, dinoflagellates ?). Is acid water really brought up from a depth of 180 m, or is nutrient-rich water brought up from the depth, causing a great production of phytoplankton and subsequent H_2S, and is this H_2S afterward oxidized to H_2SO_4 ? The mortality is listed here provisionally under noxiousness of waterbloom (no. 64). The statement of the destruction of the nets is of great interest, for such an annoying destruction of the nets also occurs in the red-water region near Walvis Bay where H_2S often occurs (communicated by the director of

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a Dutch factory of fishing nets). Why the nets are burned along the borders of the Black Sea and near Walvis Bay is as yet uncertain.

MASS MORTALITY IN SEA CONNECTED WITH SPAWNING RUNS

Mass mortality of the capelin (*Mallotus villosus* Müller) (no. 90) repeatedly occurs in many places in arctic seas. This mortality usually is described as physiological death after spawning (Porsild, 1902, p. 219; Andrée, 1920, p. 615; Weigelt, 1927, p. 143, 205; Scheuring, 1929, p. 655). It is not certain whether this interpretation is correct; perhaps it can better be classified under stranding. These fishes enter the tidal zone in huge shoals to spawn and are often thrown on the beach in countless numbers (Bigelow and Welsh, 1925, p. 142). Considerable numbers are left stranded on the beach during the act of "rolling" that precedes spawning (Sleggs, 1933, p. 38). Probably many others die when exhausted after spawning. In favor of physiological death is the statement by Hansen (1943, p. 121) that the great bulk of this species spawns only once or twice.

Certain squid are gregarious spawners, and at least one species (*Loligo opalescens*; see McGowan, 1954) dies after spawning. Unfortunately we know little about the biology of squids, and the possibility that observed mass mortalities may be a natural phase of the life cycle of the species concerned (*e.g.*, the mortalities of *Dosidicus gigas*, no. 48) cannot be dismissed.

MASS MORTALITY CAUSED BY STRANDING

When huge shoals of fishes enter the tidal zone, thousands may perish by stranding. This has been reported for clupeid fishes entering a bay in Alaska (Bower and Fassett, 1914, p. 27) (no. 91) Perhaps the destruction of the capelin (no. 90) should be classified under this heading.

MASS MORTALITY IN SEA CAUSED BY SEVERE STORMS

During severe storms hundreds of dead fish of various kinds may be thrown on the beach (no. 92, 93). Fishes living in the deeper parts of the littoral region are particularly affected, as they are not accustomed to much agitation. On Iceland hundreds of specimens of *Brosmius brosme* Müller and *Sebastes marinus* L. perish during every winter storm (Faber, 1829, p. 85, 128) (no. 92). Hundreds of dead *Sebastes* also were observed after storms in the coastal waters of northern Norway (Finmarken) (Gunnerus, *fide* Faber, 1829) and Greenland (Fabricius, 1780, p. 169) Severe storms may further cause great injury by covering the benthonic fauna with thick layers of mud (Engle, 1948) (no. 94) or sand, or, conversely, benthonic invertebrates are plowed from the bottom of the sea and thrown up on the beach. The latter occurred during a severe gale in the Netherlands (Swennen, 1953) (no. 93a) and repeatedly in the Black Sea (no. 93b).

In the Straits of Messina, where strong vertical currents exist, dead deep-sea fish often are thrown on the beach; this mortality attains catastrophic proportions after severe storms (no. 95). Storms may cause catastrophes in an indirect way by destroying spits of land (no. 23).

The catastrophes along the coast of Chile (no. 48) have been incorrectly attributed to storms by Abel (1922, p. 534).

MORTALITY IN SEA CAUSED BY VERTICAL CURRENTS

Strong vertical currents, both up and down, and whirlpools exist in the Straits of Messina (Marini, 1909; Lohmann, 1910); these are possibly the result of instability of deep internal waves (Defant, 1940). Dead or dying deep-sea animals often are thrown on the beach near Faro. After severe storms the mortality attains catastrophic proportions (no. 95). The death of thousands of myctophid fish on the California coast (no. 96) has been connected with strong upwelling; it is not certain whether this is correct.

Several incidents of which the cause is unknown are cited under no. 97–105.

SECTION II. PALEONTOLOGICAL SIGNIFICANCE OF CATASTROPHIC KILLING

The paleontological significance of mass mortality has repeatedly been emphasized, and repeatedly refuted with even more stress. In this section it is intended to show that at least some catastrophes are paleontologically important.

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The paleontological significance of mass mortality has been brought forward in connection with the following problems: (1) Cuvier's theory of catastrophes; (2) origin of highly bituminous shales and of petroleum; (3) origin of phosphorite; (4) origin of fossil deposits with abundant remains of vertebrates (and of certain invertebrates).

CUVIER'S THEORY OF CATASTROPHES (CUVIER, 1826)

In the first half of the nineteenth century mass mortality played an important part in discussions concerning Cuvier's hypothesis; after some decades, however, this hypothesis no longer found adherents; accordingly interest concerning a catastrophe causing mass mortality disappeared. It is not our intention to discuss the validity of Cuvier's hypothesis here, as the mortality records given in this paper are not catastrophes in the sense of Cuvier, but "anastrophes".

ORIGIN OF HIGHLY BITUMINOUS SHALES AND OF PETROLEUM

In early hypotheses on the origin of oil macroscopic organisms were supposed to be the chief source material. To explain the great quantity of petroleum, a mass mortality of these organisms seemed to be of importance. In highly bituminous shales most groups of macroscopic organisms (*e.g.*, mollusks and other benthic invertebrates) are scarce; fishes, crustaceans, insects, and plants are the principal macroscopic fossils observed. Several authors (Dufrenoy, Dieulafait, Posepny, Szajnocha, Murchison, *fide* MacFarlane, 1923, Preface, and 1931) have concluded that the sudden death of millions of fishes resulted in the accumulation of oil. Others (Schultz, 1920, p. 102; etc.) did not consider fish to be the chief source material but assumed only that their bodies had contributed to the oil supply.

According to the present concept, microscopic plankton organisms are the chief source material of oil. These are very short-lived; therefore, a catastrophe of plankton is wholly superfluous to explain the great quantity of material. The total annual production of plankton yields much more organic material than a momentary catastrophe of the plankton (Krejci, 1955, p. 97). The importance of mass mortality is, therefore, denied emphatically in modern petroleum literature. To prevent confusion, it may be emphasized that the writer does not agree with the opinion of MacFarlane and others that fish may form the chief source material. She wants only to state that recent mass mortality of vertebrates occurs in parts of the areas where future bituminous rocks are deposited. This does not imply that the vertebrates are the source material of the bitumen; it is a mere coincidence (caused by the fact that both occur in areas of high production). This coincidence may explain why vertebrates frequently occur in bituminous rocks.

Conditions leading to the formation of bituminous rocks are twofold: either the supply of oxygen to the lower-water layers is excessively low (persistent stagnation), or the supply of dead plankton and other oxidizable material is extremely high (hypertrophy). In eutrophic waters the production of both plankton and benthos is great and there is a direct relation between the two. Above a certain maximum, extensive "bottom" mortality occurs in certain times of the year, when the boundary O_2/H_2S rises above the sediment in the free water (*see* under Mass Mortality by Lack of Oxygen, and no. 83). Depending on the degree of hypertrophy and on the degree

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of the oxygen supply, all transitions from gyttja to true sapropelium will occur; in a fossil state such sediments will be slightly to highly bituminous. Hypertrophy occurs in shallow parts of the sea: (1) in inland seas and in their bays and lagoons (Sea of Azov, Bay of Krasnowodsk, South Russian limans (in the latter hypertrophy is combined in summer with a rather strong stratification), probably also the Gulf of California); (2) in the open oceans and their bays and lagoons (Southwest African coastal waters to a depth of 154 m (Marchand, 1928, Currie, 1953), Bay of Talcahuano (Falke, 1939, 1950)). A sediment resembling that of Southwest Africa occurs in the open sea near Cape El Hadd (southeast Arabia) at a depth of about 400 m (Stubbings, 1939, Brongersma, 1948, p. 94; 1949).

In highly eutrophic and particularly in hypertrophic water, poisonous red water and mass mortality of vertebrates and also of invertebrates, if present, repeatedly occurs. Present knowledge indicates that such mortalities usually occur close to the coast. This means that such catastrophes occur at least in parts of the regions where sediments are deposited under temporarily anaerobic conditions.

The similarity between the recent sediments of the Gulf of California, the coastal waters of Southwest Africa, and the Miocene Monterey shales is so striking that it suggests that the Monterey shales were deposited under hypertrophic conditions. Probably many other bituminous shales were deposited under hypertrophic conditions.

To those who believe there is a relation between highly bituminous shales and oil, the above consideration may throw some light on the origin of oil. Today several oil geologists assume, however, that oil need not be generated under sapropelium conditions, but that potential source rocks are deposited in reducing as well as in oxidizing environments. It is difficult (if not impossible) to furnish conclusive arguments against this hypothesis, but obviously reducing conditions are preferable by far, and this pertains particularly to the topmost layer of the sediment, as the greatest bacterial activity occurs here. If oxygen is present in the top layer, the hydrocarbons and the hydrocarbon pigments originally synthesized by living plankton (Knebel, 1949, p. 95) are in large part destroyed by hydrocarbon-oxidizing bacteria. If oxygen is absent these hydrocarbons are preserved; moreover, part of the nonhydrocarbon organics are transformed by anaerobic bacteria into hydrocarbons (ZoBell, 1949). Thus, reducing conditions in the bacteria-rich bottom water and top layer of the sediment promote the formation and particularly the preservation of hydrocarbons.

Formerly it was assumed that reducing conditions were restricted to waters with persistent stagnation; this condition is rare. This was not in agreement with the general opinion of the rather frequent deposition of source beds. As we know today that anaerobic conditions occur in hypertrophic shallow seas as well as in stagnant waters, Brongersma (1951) supposes that source beds are deposited in these areas. That means that source beds are deposited: (1) in regions of upwelling; (2) in certain inland seas where nutrients deriving from the land accumulate; (3) perhaps near the mouths of certain rivers coming from tropical highmoors (*see* no. 51a). If (3) is correct (but this is still very speculative), it might explain why a given formation may be carbonaceous (coal-bearing) in one part of a basin while grading into a bituminous formation (oil, oil–shale) in the other part of the basin (Knebel, 1946, p. 1949).

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Beerstecher (1954, p. 117) states that the marine conditions essential for productive source sediments are those that would predispose to large carotenoid accumulations. The dismutation and rearrangement of carotenoids by microbial action would easily account for the variety of substances found in crude oil and for the absence of any disparity in the amounts of odd- and even-numbered carbon chains. Moreover, the terminal cyclohexenoid rings of carotenoids provide an excellent answer to the problem of the sources of benzene and cyclohexane derivatives in petroleum.

Carotenoids are yellow to red pigments of aliphatic or alicyclic structure, composed of isoprene units; the carotenoid hydrocarbons are designated by the term carotenes; the oxygen-containing carotenoids usually are called xanthophylls (Goodwin, 1952). In marine plankton xanthophylls usually predominate over carotenes; in sediments the relative proportions of carotenes and xanthophylls often are the reverse (Fox, 1944). The reason is not clear; perhaps the xanthophylls are reduced to carotenes by chromogenic micro-organisms. Relatively rich carotenoid stores occur in red water. This was shown for the dinoflagellate *Prorocentrum micans* Ehrenb. by Pinckard *et al.* (1953).

As oil is of very frequent occurrence in the United States and neighboring countries, the frequent occurrence of red water and mass mortality in the seas bordering the United States, Mexico, and Yucatan is noteworthy (no. 44, 45, 46, 55, 72, 73, 74, 75, 76) (along the northern coast of the Gulf of Mexico these phenomena are rather rare at the present time). Today the situation in most of these waters is apparently eutrophic, but slight changes in the nutrient content, the depth of the water, etc., might be sufficient to alter eutrophy to hypertrophy, and thus anaerobic conditions would occur.

ORIGIN OF PHOSPHORITE

Murray (1890, p. 481; Murray and Renard, 1891, p. 397) postulated that phosphatic concretions are formed in places where great destruction of marine animals occurs. This hypothesis has been accepted by many authors and in recent time still finds some adherents (Collet, 1906; 1932, p. 56; Murray and Philippi, 1908, p. 185; Rosanov, 1928, p. 394; Grutterink, 1946, p. 32). Murray and Renard (1891), suggested that colloidal calcium phosphate supplied from decaying organisms is precipitated about a nucleus. They pointed out that calcium phosphate is an important constituent of some invertebrates and of vertebrate bones and teeth. One reason for the persistent popularity of Murray's hypothesis is the presence in some phosphorite deposits of numerous vertebrate bones. This applies particularly to the Senonian phosphorites of the Levant: Syria, Palestine, and Transjordan. A very high percentage of these consist of scales and bones of fish (Cayeux, 1939, p. 310; 1941). The phosphatic deposits of Egypt also are rich in vertebrate remains. Accumulations of vertebrate remains also occur in the Cretaceous and Tertiary deposits of Tunisia and Algeria, but in some of these deposits such remains are rare (Cayeux, 1941). More examples of the occurrence of vertebrate bones are not given here. In several other phosphorites vertebrate remains are very scarce or absent.

Phosphorite and changes in temperature.—In Murray's time the hypothesis was generally accepted that the southeastern side of the Agulhas Bank is dominated by the warm Agulhas Current, whereas

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the southwestern side is dominated by the cold Benguela Current. Large numbers of phosphatic concretions were found by the CHALLENGER in various parts of the ocean, but they were particularly abundant on the Agulhas Bank. The abundance of phosphorite in this and other regions led Murray (1898, p. 130) to conclude that occurrences of glauconite and phosphate nodules are intimately associated with a wide annual range in temperature at the surface of the ocean. He assumed that destructions of vertebrates occurred in such regions. He did not record catastrophes for the Agulhas Bank, but took their occurrence for granted. The tilefish disaster (no. 39), due presumably to a sudden change in temperature, greatly influenced Murray's opinion.

Dietrich (1935a; 1935b) has shown that the whole Agulhas Bank is dominated by the warm Agulhas Current. The cold water that is sometimes observed near the coast is not explained as a result of the prevalence of the cold Benguela Current; instead, these low temperatures are due to "dynamically caused upwelling" or to a shifting of the subtropical convergence by strong winds.

Murray's hypothesis has been criticized by several authors. Blackwelder (1916, p. 290) states that dead vertebrates float while distended by the gases of putrefaction, and both while floating and after lodgment upon the shore they are subject to the attack of scavengers, as well as to final decomposition by micro-organisms. "As a final result, but little of the original fish remains except the points of the teeth, which being almost wholly mineral matter, apparently contain too little nutritive substance either to attract the spoilers or to serve the purposes of bacteria. Under these circumstances, it is difficult to imagine how a layer of carcasses could be deposited in the open sea." This concept is taken over by other authors (Dietz, Emery, and Shepard, 1942, p. 832). The writer cannot wholly agree with Blackwelder's concept. It is true that bones of vertebrates containing much organic matter are eaten by various scavengers; hence, their scarcity in most places becomes explicable. It is not true, however, that all dead vertebrates float. Gunter (1941; 1947b, p. 671), discussing mass mortality by cold waves, states that there are indications that some fishes, possibly a considerable percentage of those killed, do not come to the surface but sink to the bottom. Baughman (1947a) states that during the 1947 catastrophe in Texas almost as many large fish remained on the bottom as were washed up by the waves. Moreover, there are certain places where dead fish occur in great quantity on the bottom; in most of these places mass mortality takes place. On the Agulhas Bank after fish destructions by cold there may be a solid mass of carcasses in certain bays or other places along the coast (J. L. B. Smith, 1949, p. 8). (A record of masses of dead fish on the Agulhas Bank near Mossel Bay is given under no. 41.) Probably destruction of vertebrates by noxious waterblooms also occurs close to the coast in parts of this region (no. 69), as well as killing by fresh water.

It is certainly not the writer's intention here to defend Murray's hypothesis that the phosphorus of most phosphorites is derived from bones of vertebrates, but only to give all data that may throw some light on these problems.

Bitumen deposited in stagnating bottom water and phosphorite.—Blackwelder (1916, p. 290) states that the abundance of phosphorus in phosphatic rocks need not be related to bones of vertebrates but may be explained in another way. He considers the quantity of phosphorus dissolved in sea water sufficient to produce in a few thousand years the thickest known phosphate beds. Consequently, one has only to account for the special conditions which cause it to be precipitated on the sea floor. Blackwelder (1916, p. 292) emphasizes that phosphatic rocks are sometimes highly bituminous, and that such bituminous rocks are deposited in water where the vertical circulation is not effective. Deeper parts of the Black Sea seemed to afford the required conditions; Blackwelder states, however, that phosphorite has not been found in the deep water sapropel of this basin.

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Recent researches.—The important researches by Dietz, Emery, and Shepard (1942, p. 832) have shown that in recent time phosphorite is formed in non-depositional areas on topographic highs off the California coast in association with glauconite sands. They state that these areas are among the most oxidizing environments of the sea floor. A very high oxygen supply also occurs in strong-gradient currents (Florida and Agulhas currents). Hence, the oxygen supply is nearly the reverse of that suggested by Blackwelder.

Emery and Dietz (1950) state that phosphorite is deposited in regions of high organic production. Phosphorus is an essential constituent of protoplasm. When dead plankton or other organic remains are decomposed, phosphorus gradually returns to the water in a soluble form. Great amounts of plankton sink to the bottom in areas of high production—*e.g.*, in the regions of upwelling water near California, Chile, etc. In the oxidizing nondepositional parts of these regions, a great amount of phosphate of planktonic origin returns to the bottom water within a very short time. At certain times of the year, the product of phosphate and calcium ions may exceed the solubility product of tricalcium phosphate in the bottom water, and this or related compounds are precipitated.

Much remains to be known concerning the origin of phosphorite. Is the nature of the plankton important? Plankton organisms with skeletons of calcium carbonate do not occur in fresh water but are most numerous in warm and saline water.[2] Two of the many problems to be solved are: Why do some fossil phosphorites occur in, below, or above bituminous deposits, and why do some fossil phosphorites show an abundance of vertebrate remains?

There are two possible explanations of the abundance of bones of vertebrates in some phosphorites: (1) They are a lag concentrate of fish formed during a long interval of nondeposition; the fish perished in a normal way, *viz.*, one by one; (2) They are the victims of mass mortalities; it is difficult to prove the latter assumption, but it is worth noting that mass mortality by cold and by noxiousness of waterbloom takes place in or near to the regions where phosphorite occurs on the bottom of Recent seas.

In Californian waters mass mortalities by red water take place near the coast, whereas most phosphorite occurs farther offshore; the only places where phosphorite occurs on the shelf is off Santa Monica and San Diego (Dietz, Emery, and Shepard, 1942, p. 829). In 1894 and 1901 catastrophes by red water occurred along the coast of southern California from San Diego to Santa Barbara, and in 1907 from San Diego to San Pedro. Catastrophic killing was observed particularly on the Santa Monica beach: the dead animals of the 1894 catastrophe were mainly observed on Santa Monica and Redondo beaches (Tanner, 1896); a catastrophe in red water occurred again in Santa Monica Bay in 1945 (no. 45).

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[2] As a rule calcite is present in fossil phosphorites and in the enclosing rocks. In areas of cold upwelling water several factors are unfavorable for the precipitation of calcium carbonate; the carbon dioxide content of the bottom water is increased by oxidative processes. If strong upwelling occurs all year, the low temperatures of the surface water cause limited production of calcareous structures, and the supply of calcareous material on the sea bottom is small. In the outskirts of these regions and in areas where upwelling occurs during part of the year only the conditions are more favorable.

Willcox (1953) and McKelvey *et al.* (1953) also assume that phosphorite is precipitated in high production areas; McKelvey *et al.* adhere in part to the purely chemical hypothesis of Kazakov (1937; 1950).

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On the Agulhas Bank mass mortalities by cold water (no. 41), by fresh water, and probably by red water (no. 69) take place near the coast. Some phosphate concretions collected by the CHALLENGER and other expeditions came from the Bank proper (Valdivia, sta. 104, Murray and Philippi, 1908, p. 107, 181), but the greater part came from the external slopes (Cayeux, 1934, p. 131). Whether mortalities by cold occur here or occurred here in the past, is unknown.

Phosphorite sometimes occurs below, above, or between bituminous layers. A well-known example is the following: "The nodules of the Falling Run member lie in a zone of temporary non-deposition of the bituminous shales during which phosphate concretions and a lag concentrate of fish bones, etc., were formed" (Rich, 1951, p. 2025). Rich considers these conditions closely parallel to those reported by Dietz, Emery, and Shepard for phosphatic nodules off the California coast: "there, phosphate nodules are very common in those parts of the ocean bottom, where, because of too active water movement sediment is not now accumulating". This assumption is highly plausible. Thus, when stagnating bottom water is considered the explanation of the presence of bitumen in underlying and overlying shales, it follows that there may have been persistent stagnation at one period, and nearly the reverse conditions in the preceding as well as in the following period. When hypertrophy is considered the cause of the bituminosity, the changes may have been less marked, and under such conditions the neighboring occurrence of phosphorite and bitumen is plausible as both occur in areas of high production.

ORIGIN OF FOSSIL DEPOSITS WITH ABUNDANT REMAINS OF VERTEBRATES

Some paleontologists assume that the accumulations of fossils, particularly of vertebrates, as they occur in certain deposits, are caused by catastrophes. A few examples are given relating to marine as well as to fresh-water deposits; the supposed causes of the catastrophes as indicated by the various authors are mentioned, although they probably are erroneous, as is also that given by the writer in 1934 concerning the bituminous Padang Highland marl shales. It is highly probable that these shales were deposited in a hypertrophic, warm, hard-water lake and that the fish were periodically killed by noxiousness of waterbloom.

It is certainly not intended here to give an enumeration of all deposits with abundant vertebrate remains, but rather to give representative examples:

(1) Bituminous Permian Kupferschiefer with abundant fish remains; catastrophic killing caused by submarine springs (Moret, 1940, p. 8).

(2) *Xyne grex* layer of California Miocene Monterey shales near Lompoc. In this layer millions of the fish *Xyne grex* Jordan lie side by side. They were killed suddenly; cause unknown (Jordan, 1920).

(3) Bituminous Liassic shales of Holzmaden. Drevermann (1931, p. 473) compares these shales with the sediment of Walvis Bay, where catastrophic killing repeatedly occurs. Supposed cause of the catastrophes: gases escaping from the sediment.

(4) Bituminous Oligocene shales of Aix-en-Provence (France, lake deposit). Fish are prodigiously abundant, often lying piled over and alongside each other (Haug, 1911, Pl. 127; MacFarlane, 1923, Fig. 47). They were killed by catastrophes caused by hot materials and sulfurous compounds thrown into the lake (Matheron, *fide* MacFarlane).

(5) Bituminous old Tertiary shales of the Padang Highlands (Sumatra, fresh-water lake). Fish

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are abundant in some of the layers: locality Sipang A, layers 3, 6, 22a; Sipang B, layers 33, 34, 36, 40, 43. Repeated catastrophes; causes calcareous mud (Sanders, 1934), H_2S (Musper, 1935).

(6) MacFarlane (1923; 1931) assumes that the fish whose remains occur in many bituminous deposits perished by catastrophes, a common cause of death being vulcanism.

(7) Weigelt (1927, p. 27) considers that all the vertebrates, of which the well-preserved remains form rich deposits, perished in an abnormal way.

(8) Phosphatic deposits in north Africa with abundant fish remains; fish killed by catastrophes (Grutterink, 1946).

Examples of abundance of invertebrate remains associated with catastrophes in literature:

(9) Devonian Hunsrück shales of Germany (only slightly bituminous). There has been much discussion whether or not the fossils of these shales perished by catastrophes. Here there are accumulations of certain invertebrates: echinoderms, arthropods (*Phacops*), and others.

Fish remains occur but are rather abundant locally only (a layer of 1.50 m near Gemünden according to Kutscher, 1931). Von Koenigswald (1930) assumes that the Hunsrück fossils were killed by catastrophes (H_2S). Lehmann (1939) likewise attributes them to catastrophes (vulcanism). Richter (1941) states that Lehmann's argument for catastrophic killing (high percentage of young individuals) is not valid.

(10) "Battlefields" of belemnites in the Liassic shales of Holzmaden. Abel (1922, p. 534) compares these battlefields with the catastrophes of squids along the coast of Chile (cause of death: storms) and with the spawning concentrations of *Loligo pealei* on the eastern coast of North America. Endogenous mortality as a natural part of the spawning cycle is described recently for *Loligo opalescens* on the California coast (McGowan, 1954). In this way hard parts of belemnites might have accumulated over many years. As the Chilean mortality (no. 48) coincides with a discoloration of the water by great masses of plankton and with mass mortality of fish, red water is more feasible. Spawning may be the cause of the concentration of the squids.

Vulcanism is often mentioned as a cause of catastrophic killing of fossil vertebrates (examples 4, 6, 9 in part, and several other examples not mentioned here). Richter (1941, p. 222) states that this is often without any foundation—*e.g.*, in respect to the fossils of the bituminous Cambrian Burgess shales. There is a temptation to accept vulcanism as a plausible explanation for a good preservation of fossil remains because it insures quick burial. Moreover, current opinion is that most recent catastrophes are caused by vulcanism. It has been shown in Section I that this is chiefly due to underestimation of other causes and to the fact that several recent catastrophes are erroneously ascribed to vulcanism.

Examples (3) and (10) both bear upon the Holzmaden shales. Drevermann cites for comparison the Walvis Bay catastrophes (supposed cause of death: H_2S), whereas Abel compares the battlefields of belemnites with the catastrophes of squids near the west coast of South America (supposed cause of death: storms). Apparently these authors compare the Liassic catastrophes with different recent phenomena. The causes of the recent catastrophes are, however, incorrectly interpreted by both. The cause of both the Walvis Bay and Chilean catastrophes (if a post-spawning death is not involved), is probably red water (nos. 68, 48). Hence, Drevermann and Abel compare the Liassic shales with the same recent phenomenon.

These examples, to which others could be added, show how an incorrect interpretation of recent catastrophes can lead to an incorrect interpretation of fossil deposits.

ABUNDANCE OF VERTEBRATE REMAINS AND CASTASTROPHES

Does abundance of fossil remains point to catastrophic killing? There are other possibilities: the fossil remains might have drifted together by currents, or they might accumulate in nondepositional areas during a long period. The reasons the

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writer believes that abundance of vertebrates in some fossil deposits is indeed caused by catastrophes are: (1) Vertebrate remains are scarce or absent in most recent sediments; most of the sediments in which such remains are abundant are found in regions in which catastrophes occur. (2) The sediments of some of these regions strongly remind one of certain fossil deposits.

Whether the abundance of invertebrates in certain deposits was caused by catastrophic killing has not been convincingly determined. *See* the Hunsrück shales, example (9).

As the oceans swarm with vast schools of fishes, and locally also with other vertebrates, a large number of vertebrate remains might be expected to occur in recent sediments. From an examination of bottom samples, it appears, however, that in most sediments vertebrate remains are strikingly scarce. Fish otoliths are the only remains that occur in many localities; this applies to a lesser degree to teeth of selachians, whereas bones and scales occur only on rare occasions.

Many authors (Murray and Renard, 1891, p. 267; Eastman, 1903, p. 189; Böggild, 1916, p. 31) have commented upon the astonishing rarity of bones in marine sediments. Most of the samples examined by these authors were dredged from deep water far from land; hence, they mainly prove that bones are almost lacking in oceanic sediments. However, they also seem to be very scarce in most sediments in the vicinity of the land (some data in Brongersma, 1949).

Considering that bones of vertebrates contain much organic matter and are eaten by various scavengers, their scarcity becomes explicable. Verrill (1884b, p. 1054) and Blackwelder (1916, p. 290) state that the bones of fish are rapidly consumed by echini and other animals. At the writer's request Dr. J. Verwey (Den Helder) fed *Psammechinus miliaris* (Gmel.) fish bones; these were very rapidly eaten.

Abundance of vertebrate remains in certain marine sediments.—Accumulations of selachian teeth occur in certain barren regions of the Central Pacific and in other oceans in great depths far from land; many of these teeth are accompanied by ear bones of whales. Many of these remains are to a certain degree impregnated with oxides of manganese or of iron (Murray, 1889; Murray and Renard, 1891; Eastman, 1903; 1906). An interesting record of numerous bones of whales and manganese nodules west of Dassen Island (Union of South Africa) was recently given by Copenhagen (1953). Great mortalities are not recorded from the places of these accumulations of selachian teeth and whale bones. A reasonable explanation for these accumulations is not yet available. As the rate of sedimentation in these areas is very low, bones might accumulate even if the quantity sinking to the bottom per unit time is small. An impregnation with oxides of manganese and of iron makes them indigestible and, therefore, favors their preservation.

Of the fish killed by catastrophes, some are cast upon the shore whereas others sink to the bottom of the sea and remain there. Those cast upon the shore usually have a very small chance of preservation. In very dry areas they are preserved a rather long time; dried mummies frequently are found on the borders of salt lakes (nos. 26, 27). When lying on the bottom of lakes or of the sea the chance for preservation is somewhat greater. Records of dead fish observed in these surroundings are the following:

After severe winters dead fish were observed on the bottom of Danish waters (Blegvad, in litt.) (no. 32). Masses of dead soles and other animals were observed on the bottom of the North Sea after the severe winter of 1929 (Lumby, 1931) (no. 33). Accumulations of fish of various species occur on the bottom of bays of Texas after cold spells (no. 37); probably many of them do not come to the surface but remain on the bottom (Gunter, 1941; 1947b; Baughman, 1947a, p. 31). Great numbers of dead fish in all stages of decomposition were observed on the Agulhas Bank; probably

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they were killed by cold (no. 41). Great numbers of vertebrates, killed by waterbloom, occur on the bottom of highly eutrophic and hypertrophic regions. Masses of dead *Mallotus villosus* (Müller) in all stages of decomposition were observed by Porsild (1902, p. 219) on the bottom of Disko Bay; they probably perished after spawning (no. 90). A large number of dead *Gadus polaris* was observed on the bottom of the Arctic Polar Sea (no. 97).

The occurrence of vertebrate accumulations on the bottom of the sea does not prove that bones or teeth will ultimately be preserved within the sediment. If the animals are killed by, and nearly at the same time covered with, a thick layer of volcanic ash (no. 1) or other fine-grained sediments, they have a good chance to be preserved. Further factors favoring the preservation of the bones of vertebrates are mass killing, impregnation with phosphorite, high salt concentrations (*see* the fish in Lake Assal, no. 31), and anaerobic conditions caused by hypertrophy or persistent stagnation. The comparatively small masses of fish occurring on the bottom after severe winters will be subsequently destroyed by scavenging invertebrates, bacteria, and other factors. When the mortalities attain catastrophic proportions the chance of preservation of remains increases. Not only are millions of vertebrates killed, but also a high percentage of the scavengers that might consume their carcasses. In nondepositional areas where phosphorite is precipitated, vertebrate remains stay uncovered for a long time, but as they are made indigestible by the precipitation of phosphorite they have a better chance to become fossilized.

In hypertrophic regions three factors favor the abundance of vertebrate remains: abundance of life, frequency of catastrophes by red water, and killing of the benthonic scavengers when the boundary O_2/H_2S temporarily rises above the bottom. Indeed there are extensive cemeteries of vertebrates, sometimes also of cephalopods, in these hypertrophic regions. Examples: (1) "Azoic" region near Southwest Africa; here fish skeletons may be brought up by the bucketful (Von Bonde, 1928a; 1928b, annexures; Marchand, 1928). (2) Vicinity of Cape El Hadd (Stubbings, 1939; Brongersma, 1949); in bottom samples collected by the JOHN MURRAY Expedition fish bones and scales and other fish remains were abundant. (3) Bay of Talcahuano; fish remains, sometimes even whole specimens, and cephalopods (Falke, 1939; 1950).

The scavenging benthos is absent in the deeper parts of basins with persistent stagnation (some Norwegian threshold fjords, deeper parts of the Black Sea, etc.). In these Norwegian fjords, catastrophes caused by H_2S occasionally occur (no. 84); the writer does not know whether remains of vertebrates that were killed by these catastrophes, or of those that died in a normal way, occur in the sediments of these fjords. Isolated bones occur in the deep-water sapropelium of the Black Sea. Murray (1900) found bones and scales in some of the samples collected during the Russian explorations in 1890 and 1891; *see also* Andrussow (1893). At certain places marvelously preserved fish occur; such remains were found in the samples collected by the expeditions of Shokalski in 1925 and 1926 (Archangelski, 1927, p. 208; Archangelski and Koptschenowa, 1930). It is uncertain whether the catastrophes that repeatedly occur along the very fertile borders of this sea (no. 63, 64, 103) have anything to do with the occurrence of these well-preserved fish.

It would be highly interesting to ascertain whether in deeper layers of the sediment something is preserved of the masses of dead fish observed on the borders of some salt lakes and lagoons (nos. 26–31), of the masses of dead *Mallotus* (no. 90) observed on the bottom of Disko Bay, of the dead fish in the Bay of Temrjuk (no. 63), etc.

Sediments of certain mass mortality regions reminiscent of fossil deposits.—It is very difficult to prove whether or not the fossils of certain deposits are the result of catastrophes. The extensive controversies concerning the fossils of the Hunsrück shales may be representative in this respect (literature in Kutscher, 1931; Ehrenberg, 1936; Richter, 1941). In some cases, however, proof may be furnished by the following coincidence: the sediment in some regions of catastrophe has characteristic features. If fossil sediments show the same combination of characteristics, it is fairly certain that during their deposition catastrophic killing occurred.

Example: In parts of hypertrophic regions the sediment contains much H_2S, the

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organic content is relatively high, remains of invertebrates are scarce, remains of vertebrates are abundant. The chief direct cause of the abundance of vertebrate remains is catastrophic killing by red water. Then ultimately all characteristics of the sediment as well as the red water are caused by hypertrophy. If a fossil sediment shows the same characteristics, it is nearly certain that hypertrophy prevailed; this implies that catastrophes occurred during its deposition. The sediments of some hypertrophic areas show a further characteristic: they contain a very high percentage of the siliceous frustules of diatoms. Diatom ooze and diatom mud occur in areas of high production. They occur in regions of upwelling as well as in very cold regions: in the open sea (W. Schott, 1936; W. Schott, in G. Schott, 1935; 1942; Brongersma, 1948, p. 84), and in inland seas (Gulf of California, Revelle, 1939; Sverdrup and staff, 1941, p. 493; Gilbert and Allen, 1943, p. 89).

The sediments of hypertrophic regions are much like bituminous shales. The occurrence of vertebrates is a nearly constant character of these deposits; vertebrates certainly are not always abundant, but in some places or in certain layers they are prodigiously abundant. Some examples of bituminous marine and fresh-water shales with abundant vertebrate remains have been given above; numerous examples relating to all geological periods since Silurian times are given by MacFarlane (1923; 1931) and by Deecke (1913).

The similarity between the Miocene diatomaceous shales in the Californian coast ranges and the Recent green muds of the Gulf of California and of Southwest African coastal waters is particularly striking, because all of them consist of a very high percentage of siliceous frustules of diatoms. Those of the Gulf of California are green, finely laminated, highly organic diatomaceous mud (Sverdrup and Staff, 1941, p. 493); the Southwest African sediment also is green and highly organic (Copenhagen, 1934; 1953); it is designated by Pratje (1939, p. 1669) as true diatom ooze.

The nature of the fossil fish in the Monterey shales points to open-ocean conditions and also indicates that the fish did not live in very cold regions (David, 1943). These features, combined with the presence of diatom ooze, show with certainty that the shales were deposited in regions of upwelling. At the present time upwelling prevails along the California coast, but the recent sediments are not notably diatomaceous, and the present situation apparently is not hypertrophic as in Miocene times but is more highly eutrophic. This may be due to a change in the depth of the water, the direction of the coast line, and the supply of terrigenous material. (Shallowness favors the productivity of the sea and the preservation of diatom frustules; the direction of the coast line influences the intensity of upwelling, and, therefore, the productivity.)

In some years the catastrophes in red-water regions are very great. During the enormous catastrophe of December 1924 the sardine schools had just entered Walvis Bay, and, therefore, the millions of dead fish consisted for the greater part of sardines (Anonymous, 10, 1926, figs.). In the *Xyne grex* layer of the Monterey shales (Jordan, 1920, fig. on p. 20), millions of a herringlike fish lie buried; this layer is an exact equivalent of the layer that was deposited in Walvis Bay in December 1924.

No absolute proof can be given at present that other deposits also originated in areas where catastrophes occurred, but some suggestions will be made.

Many authors hold that bituminous black shales were deposited under conditions

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prevailing in poorly ventilated basins (Pompeckj, 1901, for Holzmaden shales; Pompeckj, 1914, for Kupferschiefer; Krejci and Weiler, 1928, for Oligocene Menilite shales; Clarke, 1904, and Ruedemann, 1934, 1935, for black shales of eastern New York; etc.). In some cases the nature of the fish and of the other fossils indicates that this is not wholly correct. A very high percentage of the Kupferschiefer fish belong to benthonic species, as has been shown by Pompeckj himself. This proves that during part of the year oxygen was present in the bottom water. According to Dorn (1936), the richness of the fauna in the Holzmaden shales is not in agreement with the limited conditions of life in poorly ventilated basins. A few benthonic species occur among the fish of the menilite shales; some of the fish are definitely littoral species (Pauca, 1933; Fröhlicher and Weiler, 1952; more literature in these papers) proving that at least part of the menilite shales were deposited in very shallow waters. These arguments suggest that a comparison of these shales with basins with persistent stagnation is not wholly satisfactory. This is not intended to imply that these shales are not comparable with Black Sea conditions. In the Black Sea there are two peculiarities: persistent stagnation in the deeper parts, and a peculiarly high production along its borders (catastrophes in the Black Sea and adjacent seas under nos. 63, 64, 103).

The present concept of the seas in which the bituminous menilite shales were deposited in Oligocene times in Moravia, Galicia, Hungary, Romania, parts of the Black Sea, and the Caucasus is as follows: Along the northern border of the old Tethys was a ring of semiseparated seas connected with one another (Fröhlicher and Weiler, 1952, p. 30). Semiseparated parts of the sea may become more and more eutrophic; for semiseparated parts of the Baltic, Gessner (1933, p. 156) showed that with increasing isolation the nutrient content and the production increase. In certain regions this leads to hypertrophy. The seas in which the menilite shales were deposited are reminiscent of the Gulf of California, and in some degree also of the shallow parts of the Black Sea, the limans, and the Sea of Azov, but there must have been great differences in the supply of river water, and consequently in salinity, etc.

Von Koenigswald (1930) and Lehmann (1939) suppose that the fossils of the slightly bituminous Hunsrück shales (chiefly invertebrates: crustaceans, echinoderms, etc., see example (9) above) perished by catastrophic killing. If this is correct, an analogy of the Hunsrück shales might be found in highly eutrophic rather than in hypertrophic regions, or perhaps in hypertrophic regions where the anaerobic situation lasts a short time only; in such waters catastrophes of crustaceans, echinoderms, etc., by red water (nos. 45, 47, 55, 66, 67, 72, 80), and catastrophes of benthonic invertebrates by lack of oxygen (no. 83) repeatedly occur.

Deecke (1913, p. 83) states that the accumulations of selachian teeth in various greensands cannot be considered comparable to the recent accumulations of selachian teeth in the depths of the oceans. The fossil glauconite sands recorded by Deecke remind one in every respect of the recent glauconite sands (many containing phosphorite) occurring in nondepositional parts of some littoral regions (Agulhas Bank, topographic highs off California). One might try to find similar accumulations of selachian teeth in those parts of these areas where catastrophes repeatedly occur (nos. 41, 45, 69).

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Porsild (1902) compares the recent accumulations of *Mallotus* on the bottom of Disko Bay to the postglacial Marlekor concretions of Canada and Norway, which frequently contain the same species of fish. One might investigate whether concretions *in statu nascendi* occur in deeper layers of this bay, and whether the lengths of the fossil fish correspond with the year classes of the capelin that enter the tidal zone in order to spawn (no. 90).

SUMMARY

The life of most animals in the sea is terminated by their capture by other animals; those that die in other ways are sooner or later eaten by scavengers; exceptions are given below. The hard parts of some invertebrates are indigestible and may become embedded in the sediment. The hard parts of vertebrates are a source of food and are eaten by echini and other organisms. Vertebrate remains are therefore excessively scarce in most Recent marine sediments.

Where catastrophes occur the situation is different. One must distinguish between limited mortalities and mass mortality. It is questionable whether the hundreds of vertebrates killed by storms (no. 92, 93) leave evident traces in the sediment, but if killing attains catastrophic proportions the chance is much greater. Catastrophes are not rare; there are several places where killing of thousands of vertebrates repeatedly occurs. Besides vertebrates the scavenging benthonic invertebrates are often decimated; these will repopulate the whole area only after a long interval. Hence, not only the extent of a catastrophe, but also the interval between catastrophes in the same place is important. The principal causes leading to catastrophes are a sudden drop in temperature, waterbloom, and oversalinity; the intervals between these catastrophes in many places are very short, about 6 to 10 years. Where rivers enter into salt lagoons and salt lakes, a more or less severe mortality occurs several times a year. Lortet (1883, p. 137) states that dead fish are cast on the shore of the estuary of the river Jordan nearly daily; here the accumulation of smaller mortalities attains catastrophic proportions.

The chance of preservation further depends on the length of time elapsing before the victims are embedded and on the nature of the sediment. Vertebrates killed by and shortly afterward embedded in fine-grained volcanic ash have a good chance. Such conditions will occur more often in slack river arms and in quiet bays affected by rivers than in the open sea; here the ash fallen over a great land area accumulates; fish suffocated in rivers of "liquid ash" are mentioned under no. 1. Further factors favoring the preservation of vertebrate bones are phosphatizing, anaerobic conditions, etc.

If dead vertebrates are cast upon the shore their chance to be preserved is small. The dried mummies lying on the shores of some salt lagoons and salt lakes (nos. 26, 27) remain undecomposed a rather long time; decay is slow in such excessively dry regions.

Many authors assume that all vertebrates float after death and finally are thrown on the beach. This is not entirely correct, although vertebrates are often cast up. Fishes of deeper waters even may be found on the shore; cause of death: vulcanism (no. 2, year 1919), earthquake (no. 10, 17, 20), cold (no. 39, 40, 42), strong vertical

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currents (no. 95, 96); *see also* Whitley (1943, p. 175). It is not true, however, that all dead vertebrates float; many remain on the sea bottom. Here their chance to be preserved is greater, but even on the bottom hardly anything is preserved under normal circumstances. In a few localities bones, scales, and whole skeletons are found; in most of these places catastrophic killing repeatedly occurs. It is, however, uncertain whether something is ultimately preserved of these accumulations lying on the bottom. Researches on the sediments of these regions are needed for a solution of this problem—*e.g.*, in the sediment of bays of the Gulf of Mexico where thousands of vertebrates repeatedly are killed by cold (nos. 37, 38); in the sediment of the Bay of Disko and other arctic bays where thousands of specimens of *Mallotus villosus* Müller perish after spawning (no. 90); in salt lakes near the entrance of rivers, where fish perish by a strong increase in salinity (nos. 26–31).

It is fairly certain that bones of vertebrates are preserved in the sediment of hypertrophic regions (cause of mass mortality: waterbloom; causes of preservation: temporarily anaerobic conditions, quick embedding in the porridgelike mass of dead plankton), and in areas where phosphorite is precipitated (causes of mass mortality in areas where phosphorites occur: cold (no. 41) and waterbloom (no. 45); cause of preservation: covering with phosphorite).

True sapropelium develops in basins with persistent stagnation; moreover, sediments near sapropelium occur in shallow seas and bays where a not too great oxygen supply is combined with hypertrophy. In some parts of the latter areas (chiefly in bays, sometimes in the open sea near shore) catastrophic killing by red water occurs. As the areas where sediments near sapropelium are deposited and where catastrophes occur overlap in part, a high percentage of the vertebrates occurring in bituminous shales may have been killed by catastrophes.

Phosphorite is precipitated in nondepositional parts of more or less fertile regions. Whether phosphorites originate in enormous masses of decaying plankton or sometimes in enormous masses of decaying fish as well is an unsolved problem. The only contribution to this problem made in this chapter is that mass mortality of vertebrates repeatedly occurs in or near areas where phosphorite is abundant. In the highly fertile California waters, it is tempting to connect the frequent occurrence of phosphorite with excess phosphate derived from great masses of decaying plankton; mass mortality of fish occurs in part of the area where the phosphorite is found. This may be the mere coincidence of both occurring in areas of high production. On the Agulhas Bank the plankton production is probably lower. At the present time mass mortalities occur repeatedly near the shore of South Africa, whereas most phosphorite occurs along the borders of the Agulhas Bank. If part of the Agulhas Bank lay above sea level in the geological past, the shore line was nearer to the borders of this Bank, and, if other conditions were the same as today, widespread mortality would have occurred in these areas.

The similarity of sediments in regions where catastrophes occur with certain fossil deposits indicates that catastrophic killing has played a part in geology. In this chapter only a few instances of analogous sediments could be given; it is to be hoped that researches in other regions of catastrophe may reveal more analogies.

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APPENDIX

CATALOGUE OF MASS MORTALITIES IN THE SEA (FIG. 6)

A. Mass Mortality Caused by Vulcanism

(For catastrophes erroneously ascribed to vulcanism, see no. 12, 47, 48, 68, 72, 77, 90, 101.)

No. 1. Afognak, Alaska.

1912, 6–9 June. An eruption of Katmai volcano (58°16′N, 155°W) covered a large area with ash up to depths of ten inches, eastward across Shelikof Strait to Afognak and Kodiak islands. On Afognak fish mortality was high in the streams, which ran almost liquid mud, suffocating the fish. Many dead fish were washed to the bays with sand and mud. Ash was washed to the streams for several months and even in August several hundred migrating salmon perished in the muddy water. Ocean water, except near streams, was only slightly discolored for a few days, but the eruption nevertheless affected marine organisms: many dead sea urchins were observed on the shores or drifting about in bays and straits, and there was a considerable loss of mollusks, particularly clams and cockles (Bower and Fassett, 1914, p. 62, 64).

No. 2. Hawaii.

1859, 23 January. A stream of lava from Mauna Loa. Probably there was also a submarine eruption, as dead fish were found west and east of Molokai. The lava stream from Mauna Loa did not reach the sea until January 31 (Sapper, 1917, p. 98).

1919. A stream of lava from Mauna Loa flowed into the sea. In that area the offshore water is very deep. A large number of fish and other animals were killed; many deep-sea fish were found floating in the water (Jordan, 1921).

1950, 2–7 June. Over 100 million yards of lava flowed from Mauna Loa into the sea. On June 3 a windrow of dead fish, 2–6 feet wide, "extending as far as the eye could see," was observed about two miles offshore from the flow. There were lesser accumulations inshore. Between 300 and 600 fish killed by this flow were collected, some of them known to live in depths of more than half a mile. Common shore forms were not collected. By June 7 the fish had for the most part disappeared (Gosline *et al.*, 1954).

No. 3. Tanna Volcano, New Hebrides.

1878, 11 February. Heavy eruptions occurred on Tanna and in the nearby sea, causing a floodwave. So many fish were thrown on the beach that the pigs could not eat them all, and many fish decayed on the beach (Anonymous, 4, 1878; Fuchs, 1880, p. 98).

No. 4. Southeast of Island Juan Fernández, Chile (34°55′S, 77°38′W).

1867, October. The crew of a ship felt seven shocks; afterwards they sailed for two hours through milkwhite water covered with dead fish (Rudolph, 1887, p. 347).

No. 5. Oshima, Japan.

1421. During eruptions near this island the water of the sea became hot and the fish died (Sapper, 1917, p. 139).

No. 6. San Ferdinandea, Mediterranean.

1831, 8 June. On the ninth of June, 1831, a volcanic island appeared near southern Sicily in the Mediterranean, and disappeared in December, 1831. This island has been called: San Ferdinandea, Hotham Island, Graham Island, Julia, etc. On June 8 Captain Francesco Trefiletti observed volcanic phenomena in this place (water spouting in the air, clouds of smoke, etc.). Dead and dying fish floated on the surface as far as nearly two miles from the eruption. On the 12th, fishermen of Sciacca gathered a great number of freshly killed fish in this part of the sea (Poggendorff, 1832, p. 72; Hoffmann, 1839, p. 93). This mortality has been confused with one in the middle of the Atlantic, (no. 101). Walther 1927, p. 325; also Weigelt, 1927, p. 37) mentions that Captain Parsons, one day before the appearance of San Ferdinandea, observed such quantities of dead *Syngnathus anguineus* that it was impossible to pull up a ship's bucket without four or five dead fish. Captain Parsons was not one of the captains who observed the appearance of San Ferdinandea (see Poggendorff, 1832, p. 97). Moreover, *Syngnathus anguineus* (= *Nerophis aequoreus* = *Entelurus aequoreus* (L.)) does not occur in the Mediterranean (Duncker, 1915, p. 34). The story about Captain Parsons appears in the original description of no. 101.

No. 7. Gulf of Naples, Italy

Eruptions of Vesuvius caused great destruction. This occurred on the following dates:

1631, 16 December. Fish floated on the water and covered the beach (Lo Bianco, 1906, p. 79).

1794, 17 June. A stream of lava flowed into the sea; the water became very hot, and enormous numbers of "cooked" fish floated on the surface (von Buch, 1867, p. 400).

The ash rain of 1906 caused great destruction among benthic invertebrates. 1906, April, the fish had disappeared (Michael, 1906, p. 134; Lo Bianco, 1906, 1907), and the bottom was covered with a layer of ash devoid of benthic animals. At the end of May the ash had become mixed with the underlying sand and mud, and this bottom layer contained numerous larvae of mollusks, worms, and crustaceans.

No. 8. Krakatoa, Indonesia.

1883, 26–28 August. An enormous mass of hot ash and pumice was flung out by the successive eruptions. Sluiter (1889, 1890), who visited the island in 1880, some years before the eruption, observed small coral reefs at various points; in 1883 these were all killed "by being smothered with a thick layer of ash which covered the whole seabed and suffocated all the animal life" (Dammerman, 1948, p. 9).

After the last and heaviest eruption the collapse of the volcano left an enormous hole in the ocean bed, into which the sea rushed, causing a terrific floodwave. On the coasts of South Sumatra and West Java this reached heights of 20 to 35 meters. When the water withdrew, many dead fish, turtles, and two specimens of *Halicore* were lying on the beach of Benkulen (Verbeek, 1885, p. 63).

No. 9. Acid rivulet flowing from Idjen crater lake, E. Java, Indonesia.

Guillemard (1894, p. 111) describes "a lake in the crater of Taschem, in eastern Java, which is so strongly impregnated with sulphuric acid that no fish can live in it, or in the river which flows from it, and where the river empties itself into the sea it destroys or drives away all fish for a considerable distance." The crater of Taschem is the crater of the Idjen (Junghuhn, 1853, p. 102). Guillemard's statement is probably based on a record by Leschenault (1811, p. 433).

The crater lake of the Idjen, with 40 million m^3, contains the greatest accumulation of strongly acid water in the world (Van Bemmelen, 1949, I, p. 216; II, p. 240). The outlet of this lake is a rivulet called Banjoepait, which is also strongly acid (Woudstra, 1921, p. 155). Today the situation is not wholly comparable with that at the beginning of the 19th century, as a dam closes the outlet of Idjen lake, and a quantity of water

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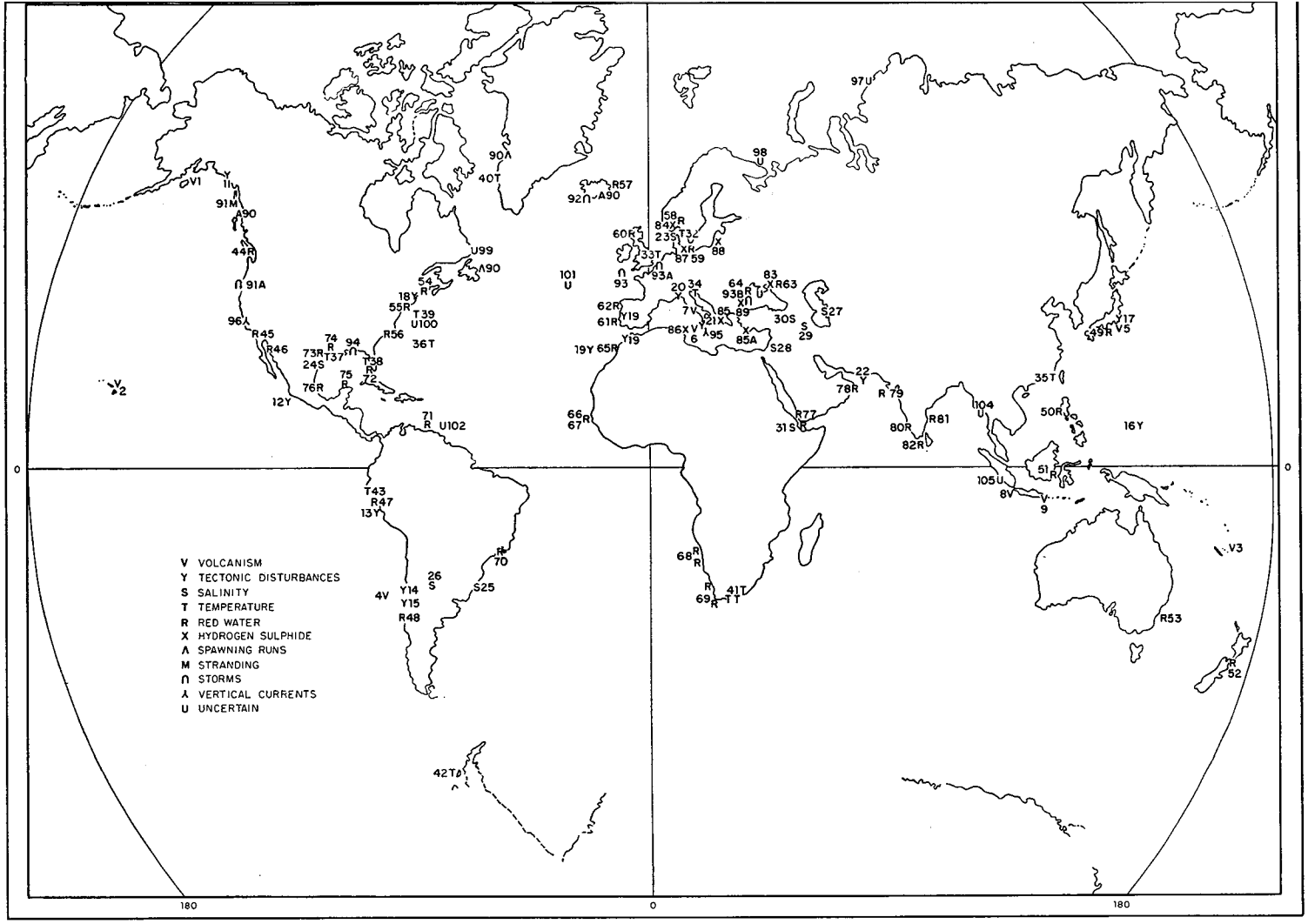

FIGURE 6.—*Location of various types of mass mortalities itemized in the Appendix*

sufficient to be neutralized by another rivulet is allowed to flow out of the lake into the Banjoepait. Once or twice a year the sluices are opened and the excess water from the lake kills all freshwater fish in the rivulets (Prof. R. W. van Bemmelen, in litt.). It is improbable that the rivulet causes much injury to marine fauna as seawater is a buffer solution; but catastrophes may occur when the whole content of acid crater lakes is suddenly thrown out during eruptions.

B. Mass Mortality Caused by Tectonic Earth- and Seaquake

(The tilefish disaster (no. 39) is erroneously ascribed to a seaquake.)

No. 10. Lake Baikal, U. S. S. R.

1904, 29 September. After an earthquake of intensity VII many dead or stunned fish from the deepest parts of the lake (greatest depth 1350 m) arrived at the surface (von Sieberg, 1923, p. 82).

No. 11. Alaska.

1899, 10 September. An enormous earthquake occurred. Shock: many dead fishes, probably killed by the shock, were thrown up on the shore in Disenchantment Bay (Martin, 1910, p. 359). Uplift: numerous dead barnacles, mussels, and limpets were found attached to uplifted ledges 18 feet or more above the present sea level (Davison, 1936, p. 164).

No. 12. Manzanillo, Pacific coast of Mexico.

1932, 3 June. Great waves flooded the shore; when the water withdrew thousands of dead fish lay on the beach (Zelízko, 1934, p. 92). Zelízko states that the flood waves were caused by an undersea volcanic eruption. This is not correct; they were caused by a tectonic seaquake. The epicenter was about 16°N. 104°W. (communicated by the Royal Netherlands Meteorological Institute).

No. 13. Callao, Peru.

1828, 20 March. After a heavy earthquake there was much commotion in the harbor. The odor of H_2S and dead fish were perceptible. It is not certain whether the fish were killed by the shock or by the H_2S (Rudolph, 1887, p. 202). The sediment of this harbor contains a great quantity of this gas.

No. 14. Valparaiso, Chile.

1822, 19 November. A great earthquake occurred. Shock: An evident shock was observed 120 miles from Valparaiso some distance off shore from San Antonio, where a ship was severely shaken; the captain afterwards saw great quantities of dead fish of many kinds floating about. Uplift: Part of the sea coast was uplifted and laid bare and dry with beds of oysters, mussels, and other shells still adhering to the rocks; the effluvia was very offensive (Davison, 1936, p. 79).

1906, 16 August. Uplift: Elevation by this earthquake was not quite as great as in 1822. At several points in the Bay of Valparaiso, the rocks on the seashore were coated with a white band of dead invertebrates (mostly *Balanus*) (Davison, 1936, p. 86).

No. 15. Concepcion, Chile.

1835, 20 February. A great earthquake occurred. Uplift: Part of the bottom of the shallow sea was uplifted and exposed; near the Island of Santa Maria, 25 miles southwest of Concepcion acres of the rocky flat were covered with dead shellfish, the resulting stench was abominable (Davison, 1936, p. 92).

No. 16. Umata Bay, Island of Guam.

1849, 24 January. An earthquake was followed by a flood wave. When the water retreated, hundreds of dead fish lay on the beach (Rudolph, 1895, p. 585).

No. 17. Sagami Bay, Japan.

1923, 1 September. The great Kwanto earthquake, which laid half of Tokyo in ruins and destroyed Yokohama, also did considerable damage to the fauna of Sagami Bay. According to Imamura (*fide* Davison, 1931, p. 75) there were three successive earthshocks; the epicenters of two of them were in the bay. No other known earthquake has caused such remarkable distortions of the seabed. In the central portion of Sagami Bay "the area of distortion is of vast extent, and the seabed has subsided as much as 460 feet at the northwest end, 590 feet near the center, and 656 and 690 feet at the southeast end. In the northeast portion, the greatest uplift measured is 820 feet, and in the southwest portion, 328 feet" (Davison, 1931, p. 94). Such enormous changes of the sea bottom must have been accompanied by great alterations of the fauna, but very little is known about it. Many deep-sea fish of the cod family (*Physiculus*) were found floating dead near the center of Sagami Bay. According to Yatsu (1926) these fish were undoubtedly killed by the sudden rushing of water into the newly formed depression at the bottom of Sagami Bay. Further, some dead deep-sea fishes drifted in a northeasterly direction off Oshima (Kaburaki, 1928, p. 1527).

Uplift: Besides alterations in the bottom of Sagami Bay, intense upheavals and subsidence along the coasts of Sagami and Tokyo Bay occurred. Uplift of coastal rocks caused serious destruction to sponges, hydroids, sea-anemones, worms, *Mitella*, barnacles, bivalves, snails, star-fishes, sea-urchins, etc. (Kaburaki, 1928, p. 1525). Oval holes bored by *Lithophaga nasuta* indicate the former beach line. At some places there are four different horizontal belts of bore holes, indicating that there have been four sudden uplifts in the last centuries (Imamura, 1926, p. 264). As a further result of the uplifted bottom many clear-water-loving associations were subjected to the turbid upper water layers. Either they were exterminated or were re-established farther out in cleaner water (Gislén, 1931, p. 415).

Flood waves, poisonous gases escaping in the neighborhood of estuaries, and landslides also destroyed many littoral organisms. Man directly and indirectly augmented the injury: gases from the enormous fires contaminated the water, and oil from storage tanks caused much damage to mussel beds and algae, etc. (Kaburaki, 1928, p. 1523). The damage would have been less had it occurred in the geological past.

No. 18. Atlantic coast of U. S. A.

1755, 18 November. An earthquake in Massachusetts and New Hampshire caused much commotion in the water of the harbors; great quantities of dead fish were observed (Rudolph, 1887, p. 290).

No. 19. Lisbon, Portugal and neighboring areas.

1755, 1 November. The great Lisbon earthquake caused great flood waves, observed in areas far beyond the limits of the disturbed area. At Salle on the north coast of Africa, the sea flowed into the heart of the town, leaving great quantities of sand and fish in the streets. In Madeira great quantities of fish were left by the flood waves on the shore and in the streets of the village of Machico (Davison, 1936, p. 21).

No. 20. Riviera, particularly near Nice, Mediterranean.

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1887, 23 February. Shock: On the day of a disastrous earthquake that did great damage along the Western Riviera, and during the following days, many deep-sea fish were taken dead or half dead in shallow water or found stranded on the beach (Giglioli, 1887; Bellotti, 1887).

No. 21. Straits of Messina, Italy.

1908, 28 December. Directly after the earthquake many dead fish floated on the surface of the water, including large specimens of *Cerna gigas*, *Labrax lupus*, and *Pagrus vulgaris* (Anonymous, 9, 1909; Condorelli-Francaviglia, 1909; for particulars concerning the earthquake see Davison, 1936, p. 201).

No. 22. Arabian Sea.

1945, 5 December. During a great earth- (better sea-) quake numerous dead fish were seen in a circular area in the sea, about 400 miles west-southwest of Karachi; observed from an aeroplane by Lieut. Cdr. (A) G. F. Venema, verb comm,; epicenter at 24°30'N 63°E communicated by the Royal Netherlands Meteorological Institute.

C. Mass Mortality Caused by a Change in Salinity

(For catastrophes in sea erroneously ascribed to salinity change, see no. 72, 80.)

No. 23. Limfjord, Denmark.

1825, 3 February. During a heavy storm the narrow bar that separated this fjord from the North Sea gave way and fresh water fish suddenly perished from inrushing salt water (Forchhammer, 1841, p. 11).

No. 24. Laguna Madre, Texas.

The Laguna Madre is part of the coastal lagoon, separated from the Gulf of Mexico by a narrow barrier called Padre Island. Certain features of this lagoon were described by Price and Gunter (1942), Burr (1945a, 1945b), Gunter (1945b), Hedgpeth (1947a, 1947b, 1953), Collier and Hedgpeth (1950, p. 161). "Because it lies in a semi-desert area, and has no river drainage into it, it becomes much saltier than sea water. In some years, when rainfall is inadequate and the summer is especially dry and hot, the Laguna, especially the upper half, becomes excessively salty because of evaporation, and the fish die in large numbers" (Hedgpeth, 1947a). During dry years the salinity approaches three times that of normal sea water. Invertebrates are probably also killed, but they have not been recorded. The dates of the mass mortalities have not been exactly documented, but mass mortality seems to occur approximately every 10 years; some mortality from oversalinity occurs every year (Gunter, 1947b, p. 672).

No. 25. Lagoa dos Patos, Argentine.

The salinity varies during the course of the year. In summer when the rivers are low and evaporation is great, sea water enters the southern part, sometimes as far north as Mostardas. The water in the lagoon does not get oversaline as in Laguna Madre (no. 24); in summer the salinity is somewhat less than that of sea water, in the southern part of the Lagoa dos Patos, gradually decreasing towards the north. von Ihering (1885, p. 176, 182) was told by the lighthouse keeper of Mostardas that in midsummer the fresh water fish often get "dizzy"; great numbers die and are thrown on the beach, he supposes that they are killed by a change in salinity. It is uncertain whether this is correct. Strong phosphorescence has been observed in summer (von Ihering, 1885, p. 176); this might be caused by a mass development of dinoflagellates.

No. 26. Mar Chiquita, northeast part of the province of Cordoba, Argentina.

Photograph of the dead fish in von Freyberg (1927, p. 308); see further Kanter (1925). The salinity varies from 7 to 36‰ (von Freyberg, 1927, p. 305). Several species of fish live in the brackish Rio Dulce. These fish are sometimes carried alive by the Rio Dulce to the middle of the lake and thrown in a wholly fresh state on the southern shore. According to von Freyberg (1927, p. 308) they are well preserved in the highly saline water; dried mummies are frequently found on the shore.

No. 27. Gulf of Kara Bugaz, U. S. S. R.

This is a shallow lagoon on the eastern side of the Caspian Sea. The salinity of the water of the Gulf in 1902 was 16.4%, as compared with 1.27% for the Caspian as a whole (Sverdrup, Johnson and Fleming, 1946, p. 148). The Gulf is separated from the Caspian by a bar 60 miles long, with a shallow entrance only a few hundred meters wide and about 5 km long. The water in this channel always flows in one direction, and builds a delta into the Gulf just as a true river does (Knipovich, 1922, p. 400). Along the borders of this delta and of the western part of the Kara Bugaz there are great masses of dead *Ruppia* plants and algae. Fish entering the Kara Bugaz through the channel perish in great quantities; their remains are thrown on the beach or sink to the bottom (Andrussow 1897, p. 29; Kusnetzow 1898). Apparently these remains do not reach the inner parts of the gulf; only a single bone was found in bottom samples taken by a Russian expedition (Lotze, 1938, p. 110). Fish mortality occurs chiefly in spring, and also in summer and in the fall; it ceases altogether in winter (Andrussow, 1897, p. 29). Enormous numbers of dead fish may be found in March. Recent literature concerning the Kara Bugaz is not available to me.

No. 28. Dead Sea, Israel and Jordan.

Salinity: surface 22.7%; near the bottom 33.3% (Fulda, 1938, p. 204).

Fish cannot live in the Dead Sea, but some species of *Cyprinodon* abundant in salt springs near the borders of the lake have been collected alive in the "sea" close to the entrance of rivulets (A. Günther, 1864, p. 490; Tortonese, 1938). They probably perish when going out too far into the sea. According to Barrois (1891, p. 45; also in Lortet, 1883, p. 137, 162, 164, 177, 178; 1884, p. 444) an enormous number of dead fish of various fresh water genera and dead mollusks lie on the shores of the delta of the river Jordan and of the Dead Sea. The river water floats on the supersaline water and mixing proceeds slowly. The fish perish when the salt content of the upper water layers becomes too high.

No. 29. Lake Urmia, (L. Rizaiyeh), northwest Iran.

Salinity 22% (Kaehne, 1923, p. 127).

According to R. T. Günther (1899, p. 355) the salinity is fatal to any fresh water fish of the inflowing rivers and the lake is therefore an efficient barrier to the distribution of fish from one river to the next. Quantities of dead fish are sometimes observed near some of the river mouths (see also A. Günther, 1899).

No. 30. Lake Van, Turkey.

The salinity of this lake is 2.26%, (Lotze, 1938, p. 4). A species of fish (*Alburnus tarichi* Pall.) lives in this lake in winter (Deyrolle, 1872); in May to June it retires into the tributaries. According to Lortet (1884, p. 439) thousands of fish perish when the salinity becomes fatal. Brant (1841, p. 397) and Deyrolle (1872) state only that the fish are caught in great numbers when

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they ascend the streams. It seems doubtful whether Lortet's statement is correct.

No. 31. Lake Assal, Somaliland.

Mean salinity 32.4%; lower concentrations near the borders of the lake and at the surface. Fish cannot live in the lake. At its eastern border are springs with a salinity of sea water or somewhat lower. Streams flow from these springs into the highly saline lake. Small fish in the rivulets are sometimes carried into the lake and perish. One may observe undecomposed dead fish lying on the salt (Degoutin, 1922; p. 15; Fulda, 1928; Lotze, 1938, p. 69).

D. Mass Mortality Caused by Temperature Change

No. 32. Waters around Denmark, particularly in the severe winter of 1929.

The mortality of littoral animals has been studied by Blegvad (1929). The benthos living between 0 and 1 meters depth is killed in great quantities during ice winters, especially in places exposed at low tide. Certain species, as *Mytilus edulis*, are frozen in the ice, others (*Aricia armiger*, *Nereis diversicolor*, *Cardium edule*) may be frozen stiff at low tide; others (*Mya arenaria*, *Macoma baltica*, *Arenicola marina*), probably die from lack of oxygen. Great mortalities occur, particularly when there is a continuous ice period. Such conditions prevailed from January to March 1929.

Johansen (1929) studied the 1929 mortality of large animals around Denmark. In every severe winter, when certain waters are covered with ice, a striking number of dead fish and other animals can be observed here and there. They are found partly frozen in the ice, partly drifting in the water among ice fragments and partly cast upon the shores; often they are first seen when brought up from the sea bottom after the ice has disappeared. Many animals are not killed directly by the low temperature, but by lack of oxygen, or presence of H_2S when eutrophic waters are covered with ice for a long period. In 1929 there was a great mortality among porpoises (*Phocaena communis* Less.), obviously because they could not break through the ice to breathe. Wholesale destruction of fish occurred only in small areas. The eels suffered most damage; many of these were killed by intense cold, whilst others suffocated through lack of oxygen.

No. 33. Eastern and southeastern parts of the North Sea.

Severe winter of 1929. Large numbers of dead and decaying fish, chiefly soles, (*Solea vulgaris* Quensel), were found in the trawl catches in the last half of March and throughout the whole month of April, 1929. "In addition to the Sole, other kinds of fish mentioned as having been destroyed are Brill, Cod, Conger, Dab, Plaice and 'Miller's Thumb (*Cottus*)' " (Lumby and Atkinson, 1929, p. 311). Crabs were also found dead on the bottom. The distribution of dead fish and low surface temperatures are given by Lumby and Atkinson (l. c.), and Lumby (1931); unfortunately observations of bottom temperature are lacking. At any rate the temperatures were very different from those to which the fish are accustomed. It is highly probable that they were killed by the low temperature (Johansen, 1929; Lumby and Atkinson, 1929; L., 1930; Dannevig, 1930, p. 195). There was a similar occurrence in the cold winter of 1946/1947.

No. 34. Northern part of the Adriatic.

Severe winter of 1929. As a result of the abnormal cold in February 1929, the temperature of the surface water in March fell as low as +5.90°C, and even below +5°C in the Gulf of Trieste. There was widespread mortality of squids (*Sepia officinalis*), and of *Dentex vulgaris* and other fishes; littoral fish were particularly affected (Vatova, 1934).

No. 35. Pescadores Islands, West of Formosa.

In cold winters when the air temperature falls below 10°C on some days, vast quantities of shallow water fishes and some invertebrates are killed near the Pescadores. The species are nearly always the same: *Niphon spinosus*, *Hexagrammus otalii*, *Lethrinus* and *Sepia*. Temperature observations were not made during these mortalities, but it seems probable that the animals were killed by low water temperature. They are washed ashore when the air temperature is about 4 or 5 degrees below the mean lowest. A similar freezing of fishes has been reported from Yamaguti and Wakayama prefectures in Japan at about the same time (Hayasaka, 1934).

No. 36. Bermuda Islands.

Cold winter of 1901. During February and the first part of March, 1901, the weather was unusually wet. The air temperature fell at one time as low as 7°C. The continued low temperature cooled sea water beyond the limit of endurance of many tropical fish. Vast numbers died and were washed ashore, particularly in the first week of March. Two of the commoner shallow water species, the hamlet grouper and the squirrel fish, were most affected. Deeper water fish were apparently unaffected. Certain crabs, corals, and large specimens of *Octopus* also perished (Verrill, 1901).

No. 37. Texas.

Excellent work on the effect of cold winters on the fauna along the Texas coast has been done by Gunter (1940; 1941; 1945a, p. 103–108; 1947a; 1947b), by Gunter and Hildebrand (1951), and by Collier and Hedgpeth (1950, p. 146–147); for a popular account with photographs of the 1947 catastrophe, see Baughman (1947a).

Mass mortality occurs particularly in the shallow bays (Laguna Madre, Galveston and Copano Bays), where the water cools off faster, and gets colder than the open waters of the Gulf.

Mortalities were observed on the following dates: 1845/1846, winter, the beach near Corpus Christi was thickly strewn with fish and green turtles (Collins, 1884, p. 276); 1852, January (Bartlett, 1856, *non vidi*; *fide* Nunez Ortega, 1877, and Gunter, 1945a, p. 103); 1881, winter (Johnson, 1881); 1924, December (Higgins and Lord, 1926); 1930, January, many fish died in Galveston and Copano Bays and the Laguna Madre (Burr, 1930, *fide* Gunter, 1945a, p. 104); 1940, January, many fish and several species of crustaceans were killed (Gunter, 1941); 1942, January, light cold wave and a very limited mortality (Gunter, 1945a, p. 105); 1947, January, a major freeze and a very heavy mortality, particularly in the Laguna Madre (Collier and Hedgpeth, 1950, p. 147), from San Antonio Bay in Texas to the 8th Pass of the Laguna Madre in Mexico, fish by the millions littered the shore in windrows (Baughman, 1947a, p. 12); 1949, January and February, very cold weather; only a few dead fish were seen, no major catastrophe (Collier and Hedgpeth, 1950, p. 147); 1951, January 28–February 3, the Texas coast was struck by a record-breaking cold wave; there was great destruction of marine life (besides invertebrates and considerable numbers of dead fish, pelicans and a dead turtle were observed), but probably this cold spell did less damage than those of 1940 and 1947 (Gunter and Hildebrand, 1951). Photographs of various mortalities were given by Burr (1930), Baughman (1947a), and Gunter and Hildebrand (1951).

No. 38. Southern and Western Coasts of Florida.

A vast destruction of fish occurs during most freezes (Storey and Gudger, 1936). Southwest Florida lies on the northern

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fringe of the tropical zone and many species of fish are at or near the northern limit of their distribution. Tropical fish are first affected during cold waves (Storey, 1937). Many fish migrate as soon as the waters start chilling, but others cannot or do not migrate; the surface fish are probably often paralyzed before they can react. Hence, the mortality is high among needle fish and hound minnows (Storey and Gudger, 1936, p. 646). Catastrophes observed: 1856, 24–25 December; 1868, 25 December, this mortality extended as far north as Tampa Bay (Packard, 1871); 1886, 12 January, fish affected from Key West to Punta Rassa, in the most severe freeze on record (Willcox, 1887; Finch, 1917; Storey and Gudger, 1936, p. 645); 1894–1895, there were two freezes during this winter, that of December 29–30, 1894, being the more destructive to fishes; moreover, several manatees (*Trichechus latirostris* (Harlan)) died (Bangs, 1895) (with the possible exception of the 1886 freeze the largest mortality probably occurred on this date); 1898, 3 January, high mortality among fish; 1904 or 1905, 1917, 1934 (Storey and Gudger, 1936); winter of 1939–1940 (Miller, 1940; Galloway, 1941).

No. 39. Mass mortality of the tilefish (*Lopholatilus chamaleonticeps* Goode and Bean) between Cape May and Nantucket, east coast of U. S. A.

1882, March and April. Vessels crossing the northern edge of the Gulf Stream reported passing through countless numbers of dead fish. A high percentage of these were tilefish. They appeared on the surface of the water in an area 170 by 25 miles (Bumpus, 1898, p. 577). The tilefish was discovered in 1879; for three years it was abundant in the area lying inside the Gulf Stream, near the parallel of 40°N, and between 70° and 71°20′W, in depths from about 90 to 125 fathoms. Here, as well as farther south and west, in the spring of 1882, dead tilefish were seen floating (Collins, 1883b). No tilefish were caught in this area until 6 August 1892; in 1898 they had become abundant again (Bumpus, 1898; 1899).

Macovei (1938, p. 51) states that there was a mass mortality in the Gulf Stream in 1882 and in 1892; the second date may be a mistake, confused with the tilefish reappearance in 1892.

The tilefish disaster was presumably caused by a sudden (but only temporary) invasion of the bottom along the warm zone by unusually cold water (Collins, 1883b, 1884; Lucas, 1891, p. 648; Libbey, 1895; Bumpus, 1898; Bigelow and Welsh, 1925; Bigelow, 1927, p. 514, and 1931, p. 91). In the years preceding the tilefish disaster, Verrill (1882, 1884a) found a peculiar invertebrate fauna in a band of warm water along the border of the Gulf Stream; after the disaster this fauna had also disappeared (Bumpus, 1898). Scheuring (1936, p. 359) believes that the tilefish were killed by cold water thrown up by a seaquake.

No. 40. Sukkertoppen and other places along the west coast of Greenland.

1899, 11 February. Four miles off Sukkertoppen an enormous quantity of dead or dying redfish (*Sebastes norvegicus*) was seen rising to the surface in an area, 4000 feet long and about 1000 feet wide (observed by R. Müller, see Jensen, 1922, p. 98). *Sebastes norvegicus* Cuv. et Val. is synonymous with *Sebastes marinus* (L.), see below.

1937–1938, winter and spring. Quantities of cod (*Gadus callarias*), sea cat (*Anarrhichas*), Norway haddock (*Sebastes marinus*), and lumpsucker (*Cyclopterus lumpus*) came up to the surface dead and were washed ashore near Sukkertoppen (Jensen, 1939, p. 73).

In Amerdlok Fjord in the Holsteinborg district in 1938 from the end of May and through the whole of June, during trawling for deep water prawns, a large number of large dead or dying cod came up in the trawl, a phenomenon not previously observed in the history of this fishery. The water temperatures are chiefly dependent on which of the two main currents, Polar or Irminger, is the stronger. Warm periods alternate with cold periods. According to investigations by Hansen unusually low temperatures occurred in 1937, and especially in 1938, everywhere in the waters of the fjords and along the coasts (Jensen, 1939, p. 73; Hansen, 1949, p. 9).

No. 41. Cape Province, Union of South Africa.

Extensive fish mortality occurs repeatedly in various places along this coast (Gilchrist, 1906, 1914; J. L. B. Smith, 1949, p. 8). The chief cause is a sudden decrease in the surface temperature, coinciding with strong southeasterly winds. Near Knysna and along the Schoenmakerskop coast, widespread mortality occurs annually or every few years (Gilchrist, 1914, p. 25; Dr. J. Pringle, in litt.). Brongersma (1948, p. 59) supposed that the Knysna and the Schoenmakerskop mortalities were caused by red water, but this seems to be incorrect. When the cold water invades the warm coastal water, limited areas of red water have been observed (Dr. P. Korringa, personal communication), but these are apparently harmless.

Mass mortalities were observed at the following places (they undoubtedly occur much more often than appears from the records given below):

East London, 1903, 26 September. Tons of dead fish were cast up; the beach was strewn with them from Christmas Vale to the Keiskama mouth; "there had been a heavy southeast wind blowing for four days, and these fish came ashore on the last day of the gale" (Gilchrist, 1914, p. 24). A similar mass killing was observed once or twice in the 25 years preceding 1903; one had been observed about two and a half years earlier near the mouth of the Igulu.

Port Elizabeth. Mortality has been recorded from this region at different times: 1886, 16 December, Cape Recife; 1902, 23 December, Jeffreys Bay (Gilchrist, 1914, p. 22, 24). Thousands of dead and living fish were washed ashore near Schoenmakerskop in 1946 (Sapa, 1946); during this occurrence the water was unusually cold.

Knysna. Mortality occurs almost annually in very cold water. "It appeared generally after a continuous or strong southeast wind" (Gilchrist 1914, p. 28). The area affected extends from Cape St. Francis to Cape St. Blaize. A small mortality was observed by Gilchrist on February 7, 1914.

Mossel Bay, September 20, 1903. "The bottom of the sea was covered with dead and rotten fish, and at times the net was quite full of these". Dead fish were also floating about in the sea and in the bay (Gilchrist, 1914, p. 25, 26). A cold mist had enveloped the bay and extended far out to sea.

No. 42. Bellinghausen Sea, Antarctica.

1952, 22 March. An enormous number of dead fish, all *Pleurogramma antarcticum* Blgr., floated on the surface west of Adelaide Island in 67°03′–67°05′S, 71°03′W. The density of the fish was greatest about 18 miles from the border of the pack ice. The depth of the sea in that place is about 510 m. Within 3 miles of the pack ice dead fish were not observed. The surface temperature was −1.5 to −1.8°C. These fishes usually live at a depth of 280–540 m. The temperature of the water layer wherein the fishes lived was +1° to +2°C. Dead specimens of the same species also have been found by other expeditions in antarctic seas (Popovici and Nani, in press). Probably the fish are killed when the cold surface water sinks through the warm circumpolar water to the bottom.

No. 43. Peru. Mass mortality in unusually warm water.

According to present opinion part of the Equatorial Countercurrent turns south in the northern winter, and is called El Niño (Sverdrup, *et al.*, 1946, p. 704). In disturbed years it

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extends far south along the coast of Peru, causing great catastrophes: "the organisms in the coastal current, from plankton to fish, are destroyed on a wholesale scale." These authors also state that "El Niño" is not the only current that brings warm water to the coast of Peru with subsequent destruction of organisms. High temperatures occurring near the coast at other times of the year (due to offshore oceanic water approaching the shore) may have a disastrous effect on the fauna as well, although the effect is less severe. Schweigger (1943, 1945a, 1945b, 1949) states that two different phenomena are involved. One is the development of a strictly coastal counter current, called El Niño by Peruvian fishermen, originating in the Gulf of Guayaquil and flowing southward in the northern winter along the most northern part of the Peruvian littoral. The other phenomenon (erroneously called El Niño by oceanographers outside Peru) is the movement of warm oceanic water from the north and west towards northern Peru and sometimes far southward along the coast (see also G. E. Hutchinson, 1950, p. 13). The high temperatures due to El Niño or to offshore water approaching the coast in normal years along the northern coast of Peru are harmless according to Schweigger (1949, p. 130, 230). On the other hand, these high temperatures favor the appearance of red water; thus they may be indirectly noxious. In abnormal years when high temperatures prevail even far southward, great catastrophes occur (R. C. Murphy, 1926, 1936). Such abnormal years were 1891, 1925, 1941. As great red water outbreaks occur particularly in such years, part of the mortalities are caused by noxious waterbloom.

E. Mass Mortality in Sea Caused by Noxious Waterbloom

Unless mentioned otherwise, the catastrophes occur in red water caused by dinoflagellates. Nos. 63 and 64 are provisionally placed under this heading; further information is needed. The examples include some apparently harmless occurrences of red water, but consecutive numbers are given to all examples to facilitate reference to the text.

Several mortalities produced by waterbloom are ascribed to other causes. These include the records erroneously mentioned under:

a. Vulcanism: No. 47, Forbes (1858), T. J. Hutchinson (1873), Anonymous, 3, (1874). According to some of these authors the catastrophes are caused by H_2S of volcanic origin. No. 48, Cienfugos (1895). No. 68, Koch *in*: Gilchrist (1914, p. 21), Weigelt (1930, p. 309). No. 72, Stearns (1878). No. 77, Ilg (1902, *fide* Höfer, 1902), Abel (1912, p. 39), Weigelt (1927, p. 37).

b. Decrease in salinity: No. 72, Agassiz (*in* Shaler, 1890, p. 158), Höfer (1902, p. 631), Abel (1912, p. 37), Beeby Thompson (1925, p. 38), Weigelt (1927, p. 63 and 204), Stutzer (1931, p. 309). No. 80, Denison (1862, p. 453), Anonymous, 2 (1862, p. 320), Jones (1882), Geikie (1893, p. 648), Stutzer (1931, p. 309).

c. H_2S: No. 47, Burtt (1852, 1854), Walther (1927, p. 325), Weigelt (1927, p. 37). No. 68, Marchand (1928), Classen (1930), Kaiser (1930), Copenhagen (1934).

d. Gases escaping from mud volcanoes: No. 68, Stromer von Reichenbach (1912, p. 305), Weigelt (1927, p. 39).

e. Oil springs: No. 47, Tanner (1896).

f. Disease: No. 68, Chapman (1868, p. 393), Arbuthudt (1882, p. 38), Stutzer (1931, p. 309).

g. Storms: No. 48, Abel (1922, p. 534).

Pacific Ocean and adjacent seas.

Red discolorations in the sea often occur along the coasts of Mexico, Central America, the northern part of South America, Japan and New Zealand (Fig. 3, see also map in Hayes and Austin, 1951). Records of mass mortality in red water are unknown from the Pacific coast of Central America, probably because only a few investigators in these countries are interested in these problems. Patches of red water frequently occur along the western coast of North America, but great outbreaks of red water and mass mortality are apparently rare. In these waters the number of dinoflagellates is particularly high in summer; in many years they make mussels and other invertebrates highly poisonous. Paralytic shellfish poisoning of man occurs along the whole Pacific coast of North America (Sommer *et al.*, 1937; Anonymous, 12, 1942; for recent literature see Sommer, Monnier, *et al.*, 1948; Sommer, Riegel *et al.*, 1948; Riegel *et al.*, 1949).

No. 44. British Columbia and Washington.

Patches of red water due to the dinoflagellate *Gymnodinium splendens* Lebour have repeatedly been observed in lower Puget Sound (Nightingale, 1936); they caused some damage to oysters. Kincaid (1951, *fide* Korringa, 1952, p. 280) reports that red tide, caused by extreme abundance of *Gonyaulax*, occasionally leads to serious losses among oysters (*Crassostrea gigas*) on the beds in the northern part of Willapa Bay. Dr. K. Bube (*fide* Weigelt, 1927, p. 206) observed great destruction of fish near Seattle: whether this was associated with red water is unknown. Clemens (1935) observed red water of ciliates (*Mesodinium rubrum* Lohmann) near Nanaimo (British Columbia) on April 28, 1933; damage was not recorded. According to Bary and Stuckey (1950, p. 90) the causative organism is not a *Mesodinium*, but *Cyclotrichium meunieri* Powers.

An unusual number of dead birds was noted in May 1942 on the beaches of Washington State and, large numbers of dead birds were seen floating ten to twenty miles off the Washington coast and about 30 miles offshore in Hecate Strait, British Columbia. This coincided with a sudden outbreak of paralytic shellfish poisoning; three humans died, and cats and chickens died along the Washington beaches after eating the viscera of razor clams. This coincidence led McKernan and Scheffer (1942) to conclude that the sea birds also were killed by toxic dinoflagellates; they assume that small fish and crustacea near the area of the red tide had been feeding on a diet rich in organisms of the *Gonyaulax* type, and that birds subsequently feeding on the fish and (or) barnacles or other shellfish were the victims of secondary poisoning. This assumption is highly probable. The occasional destruction of birds along the coasts of Peru (no. 47) and southwest Africa (no. 68) is probably from the same cause.

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No. 45. California.

Great outbreaks of red water and mass mortality occasionally occur along the coasts of southern California; apparently they are rare. Red water has not been observed farther offshore than 30 miles; it occurs particularly in summer. The chief organisms concerned are *Prorocentrum micans* Ehrenb. and *Gonyaulax polyhedra* Stein; catastrophes of fish and invertebrates have been observed in red water of the latter. It is uncertain what organism caused the 1945 catastrophe in Santa Monica Bay; the plankton contained an unusual number of the dinoflagellate *Polykrikos schwartzi* and a large number of ciliates (tintinnids) (Sommer and Clark, 1946, p. 100).

Dates: 1746, red water observed by Gonzag (Isachenko, 1914, p. 243, *fide* Galtsoff, 1948, p. 4); 1894, end of February, mass mortality of fish (Tanner, 1896); probably again in summer (Peckham, 1897); 1901, mid July red water and great mortality of fish and invertebrates (Torrey, 1902); 1907, early in August, red water and mass mortality (Kofoid, 1911, p. 244); 1917, 4 June, red water, no damage; 1917, September, red water and mass mortality (Allen, 1921, p. 543); 1933, red water, according to Allen (1933) no damage, Bonnot and Philips (1938, p. 59) state that dead fish were found about September 5 off San Francisco in patches of "dirty brown stinking water" and the same condition was observed from Fort Bragg to Crescent City between September 12 and 19; 1938 and 1939, red water, no damage (Allen, 1938, p. 55; 1941, p. 627; 1942). During the first half of June, 1945, red water occurred in abundance off southern California from San Luis Obispo South to Los Angeles; on June 19 dead and dying fish and invertebrates (shellfish, lobsters, etc.) were observed in Santa Monica Bay (Pope, 1946; Sommer and Clark, 1946). Red water occurred from San Diego to Long Beach in July, 1952; no major mortality was reported but the shellfish disappeared from beaches at La Jolla.

No. 46. Gulfo de California, Mexico.

In this Gulf the plankton production is enormously great. Red water probably occurs often in spring. Records of mass mortality are not known, but it is highly probable that in some places they occur.

A yellow discoloration in the southern part is recorded by Streets (1878).

1937, 20 March, the large dinoflagellate, *Noctiluca scintillans* (Mac.) Kofoid and Swezy occurred in enormous numbers near Angel de la Gardia Island; there were 3 million specimens per liter (Allen, 1937). 1939, March, the dinoflagellate *Gymnodinium catenatum* Graham occurred at all stations North of 29°N. On one of these stations this species was responsible for the occurrence of red water; here the abundance was almost a million cells per liter (Graham, 1943). This dinoflagellate was first believed to be *Gonyaulax catenella* Whedon and Kofoid, and was so reported by Allen (1942); Gilbert and Allen (1943) refer to the organism as *Gymnodinium* spec.; 1940, December, small patches of red water were observed (Sverdrup and Staff, 1941, p. 493).

No. 47. Peru.

Red water frequently occurs (Carillo, 1892; Coker, 1910; Lavalle, 1917a, 1917b; Stiglich, 1925; E. R. Gunther, 1936, a, b; Schweigger, 1949). Blood red spots occur wherever warm water invades the cool Peru coastal waters. Red water occurrences are particularly frequent in abnormal years when warm water is carried far southwards along the Peruvian coast. Scott (*in* R. C. Murphy, 1926, p. 36) mentions the frequent occurrence of red patches in the abnormal year 1891, and Schweigger (1949, p. 233) in 1941, another abnormal year.

The Peruvian name for red water is red aguaje. Aguaje has been synonymized by several authors with the Callao painter. Lavalle (1917b; Brongersma, 1948, p. 52; Schweigger, 1949, p. 234) states, however, that aguaje is a red discoloration of the sea, whereas Callao painter is a development of H_2S (cf. the occurrence of two phenomena, red water and a development of H_2S near the coast of southwest Africa). The Callao painter apparently occurs in those places where enormous masses of plankton and other organisms decay. Lavalle (1924) remarks that mass mortality of fish and guano birds occurred in connection with red aguaje in 1923 (also in Schweigger, 1949, p. 234). Other occurrences of mortalities in red water are mentioned by Stiglich (1925) and Rahm (1937, p. 1246), see further Brongersma, (1948, p. 52). The confusion in literature of the Callao painter, red aguaje, and mortalities makes it difficult to get a correct idea of the frequency of the mortalities. Schweigger (1949) states that they are rare. For mortality in this area caused by a sudden increase in temperature see no. 43.

No. 48. Chile.

Mass mortalities of fish and of squids (*Dosidicus gigas* (Orb.)) repeatedly occur along the coasts of Chile; they are particularly frequent in the Bay of Talcahuano and the adjacent Bay of Arauco. Among the inhabitants of Chiloe the mortality is well known; they use the dead squids for manure. In the Bay of Talcahuano some mortality occurs almost annually, between the end of February and mid-April. In some years the mortality attains catastrophic proportions; mass mortality was observed on the following dates: 1895, 7–11 February; 1916; 1930, April; 1932. An excellent description of this phenomenon has been given by Falke (1939, 1950; see further d'Orbigny, 1835–43; Cienfugos, 1895; Pfeffer, 1912; Schneider, 1930; Wilhelm, 1930, 1932; E. R. Gunther, 1936a; Brongersma, 1948, p. 62). The catastrophes coincide with an enormous production of phytoplankton; it is highly probable that they are caused by red water. The oldest reference to great numbers of fish being occasionally found on the shores of Chile is made by Molina (1808, p. 156). Schwabe (1951) connects the mortalities in the nearby Bay of Vincente with a strong stratification caused by differences in temperature and by a supply of fresh water discharged by a steelmill.

No. 49. Japan.

Red tide, "Akashiwo", is well known among Japanese fishermen. It occurs repeatedly in many parts of the neritic waters of Japan (Hirasaka, 1922). It is often accompanied by a great mortality among fishes, mollusks, and crustaceans (shrimps!) (Nishikawa, 1901). It is the most dreaded enemy of the pearl oyster (Mitsukuri, 1905, p. 284).

Galtsoff (1949, p. 111) reports: "According to Aikawa, between 1899 and 1934 there were twenty-four recorded occurrences of discoloration of water in Japan, sixteen of which were accompanied by mortalities of fish and shellfish. Of these instances, three were caused by *Noctiluca*, nine by other dinoflagellates, five by diatoms, and one by blue-green algae. The cause of the others was not determined. Ago Bay (34°17′N and 136°47′E) was the place of the most frequent outbursts of red tide, which appeared there seven times, causing some damage to pearl oysters, and inflicting particularly severe losses in the winter of 1933–34. Next in frequency was Tokyo Bay, where discoloration was recorded three times. The records summarized by Aikawa show that in Japan red tide may take place at any season of the year". Paralytic shellfish poisoning is recorded from Japan by Hashimoto and Mori (1951).

No. 50. Philippine Islands.

Red water causing great fish mortality repeatedly occurs along the coasts of Bataan province on the west coast of Luzon (H. M. Smith, 1908). An enormous mortality occurred at Manila in 1767, 22–24 September, (Le Gentil, 1781, p. 107).

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No. 51. Balikpapan, East coast of Borneo.

In October 1940, during a very severe drought, mortality caused by waterbloom of blue-green algae (*Trichodesmium erythraeum* Ehrenb.) was observed in small pools on the beach at Balikpapan (Mohler, 1941). Normally *Trichodesmium* occurs farther offshore, avoiding the brackish water near the coast (Delsman, 1939, p. 155).

No. 52. New Zealand.

Red water is of frequent occurrence in New Zealand coastal waters but deaths of fish and invertebrates attributable to it are as yet unknown. Extensive studies on red water were begun in 1948 (Bary and Stuckey, 1950; Bary, 1951, 1953). Between 1948 and 1951 ten blooms of the ciliate *Cyclotrichium meunieri* Powers occurred near Wellington and the Cook Strait region; they predominated in late summer and autumn, but winter blooming (August, 1948, June and July, 1949) also occurred. Red water caused by the dinoflagellate *Gymnodinium sanguineum* Hirasaka was observed in Kenepuru Sound (July, 1949) and in Queen Charlotte Sound (February and March, 1950). In the latter sound yellow water caused by a minute, as yet unidentified, dinoflagellate also occurred in March 1950. Besides red water caused by ciliates and dinoflagellates, a red discoloration in New Zealand waters is brought about by crustaceans and tunicates (Bary, 1953, p. 393).

No. 52a. Banka Strait, near the mouth of the Musi river, Southeast coast of Sumatra.

Redbrown water and fish mortality has been observed along the coast of Banka; it was ascribed to the influence of the Musi river; the nature of the discoloration is unknown (Dr. J. van Slooten, Tanah Merah, personal comm.). During the wet monsoon in 1938 Prof. Dr. J. Dufour (Delft, in litt.) observed a mass mortality of fish on the Sumatran side of Banka Strait near the mouths of the Musi river; whether it coincided with a discoloration of the water is unknown. Plankton production is great in the sea near the mouths of the southeastern Sumatran rivers (Hardenberg, 1931); according to Dr. J. Hardenberg (personal comm.) the production is greatest at the end of the wet monsoon, near the Musi about April.

No. 53. Port Jackson (=Sydney Harbor), East coast of Australia.

Red water appears almost annually for a short time in Port Jackson and Broken Bay (Whitelegge, 1891a; 1891b; Dakin and Colefax, 1933, p. 196; 1940, p. 61). In most years it is not injurious; only exceptionally kills invertebrates; such catastrophes occurred in 1866 and at the end of March 1891.

Atlantic Ocean and adjacent seas.

Red water often occurs in the warmer parts of the Atlantic: along the north coast of South America and the southeastern part of the United States, further northwards red water is rather rare. In the Gulf of Mexico red water occurs frequently along the lower west coast of Florida, and probably along the coasts of Yucatan and Mexico; along the northern Gulf coast red water is rare. It occurs frequently along southwest Africa, probably also along northwest Africa.

In the seas bordering northern Europe red water is rare. Only streaks of dirty red water caused by *Noctiluca miliaris* occur rather frequently on warm and calm summer days. They were observed by Pratje near Helgoland, by Suriray near Le Havre (France), by Verhaeghe near Ostend (Belgium), by Theel and Aurivillius on the Swedish coast of the Skagerrak (Pratje, 1925). In some semiseparated parts of the north European seas waterbloom is a more common phenomenon.

Organic production is very high in the shallow parts of the Black Sea, the Sea of Azov, and the limans. In the limans waterbloom of blue-green algae occurs from June through nearly the whole summer; red water caused by dinoflagellates, e.g., *Exuviella cordata* Ost., has also been observed.

No. 54. Southeastern Canada and Maine.

Mass mortality in red water is not recorded from Canada. Yet dinoflagellates may be abundant, for paralytic shellfish poisoning caused by *Gonyaulax tamarensis* Lebour has been reported by A. L. Murphy (1936) Gibbard, Collier and Whyte (1939), Medcof et al. (1947), and Needler (1949).

A strong discoloration of the sea was observed on August 1, 1882 along the coast of Maine and the Bay of Fundy; off Monhegan and Mount Desert Island the water had a color of diluted milk (Collins, 1883a, p. 282). According to Bigelow (1926, p. 404) this was probably caused by dinoflagellates. Mackerel passing from the blue into the white water became disabled; a mortality was not recorded. During the warmest days of August 1931, red water caused by the ciliate *Cyclotrichium meunieri* Powers was observed in Frenchman Bay (Gulf of Maine, between Mt. Desert Island and the mainland; Powers, 1932); mortality was not recorded.

No. 55. Narragansett Bay and other bays along the eastern coast of U.S.A.

Red water occurs rather infrequently along the eastern coast of U.S.A., but in some bays it is more common (Prof. T. C. Nelson, in litt.). Galtsoff (1948) observed swarming of dinoflagellates along the northern coast of Massachusetts, along the coast of New Jersey, and in the bays and rivers of Maryland and Virginia; mortalities were not observed.

In Narragansett Bay widespread mortality of fish and crustaceans occurred at different occasions: 1886, 18 June, 1 July (Knowles, 1887); 1898, September (Mead, 1898); 1900, September (Sherwood and Edwards, 1902). An oily scum was noticed on July 1, 1886; red water was observed during the 1898 and 1900 occurrences. Since 1911 there have been only two occurrences of red water (Prof. C. J. Fish, in litt.).

In Delaware Bay red water caused by *Amphidinium fusiforme* frequently occurs; catastrophes have not been recorded (Martin and Nelson, 1929; Prof. T. C. Nelson, in litt.).

No. 56. Southeast coast of North Carolina.

In July 1886 the coastal waters were covered with an oily scum; it extended for several miles out to sea and affected the rivers for a long distance inland. This phenomenon caused a great mortality among fish (Knowles, 1887). It occurred at nearly the same time as the catastrophes in Narragansett Bay. Probably the oily scum consisted of great masses of plankton.

No. 57. Iceland.

Red water occurs rather frequently in gulfs bordering the

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island; catastrophes by red water are unknown to me. In 1649 in several gulfs the water appeared all on fire during the night, and on the following day the sea was as red as blood (Carter, 1858, p. 261); this occurrence was apparently due to dinoflagellates. On 18 July 1904 red water caused by a ciliate species (*Mesodinium* spec.) occurred in Seydisfjord (Paulsen, 1909, p. 27; 1934).

No. 58. Norway.

Red water of dinoflagellates and paralytic shellfish poisoning have been recorded, but catastrophes are still unknown. In October 1938 red water caused by *Gonyaulax polyhedra* Stein was observed near Tvedestrand (Braarud, 1938). On various occasions a red discoloration caused by *Gonyaulax tamarensis* Lebour and other species was observed in the inner Oslo Fjord (Braarud, 1950). The inner Oslo Fjord is the only place in Norway where paralytic shellfish poisoning repeatedly occurs (In 1901 and in 1935; Braarud, 1950). *Ceratium* species also cause red water (Nordli, 1953).

No. 59. Baltic.

Waterbloom of blue-green algae is rather common at some places in the Baltic (Sjöstedt, 1922), especially in such semi-separated parts as the Baltic lagoons (Kurisches Haff, Stettiner Haff, etc.). This so-called "Haffblüthe" occurs annually, and in severe cases may bring about great fish mortality (Anonymous, 7, 1896; Schiemenz, *in* Seydel, 1913, p. 90). In the harbor of Rostock (Baltic coast of Germany) a great fish mortality occurred in October 1917 in yellowish bloom of *Heterocapsa triquetra* (Ehrenb.) Stein (=*Peridinium triquetrum* (Ehrenb.) Lebour) and *Glenodinium foliaceum* Stein (Lindemann, 1924; 1926).

No. 60. Loch Long, Scotland.

In June 1925 patches of brownish water containing *Peridinium triquetrum* (Ehrenb.) Lebour were observed; they were not injurious. The *Peridinium* increase coincided with low salinity and high temperature of the surface water. In the surface samples the numbers per liter varied from 32000–56000 (Marshall and Orr, 1927, p. 857; Anonymous, 11, 1933).

No. 61. Portugal.

At Cape Espichel (at a distance of 16 km from the river Tagus, West Portugal) red water was observed by Montagne (1846) on 3 and 4 June 1845; he described the red water organism as *Protococcus atlanticus*. At Praia Branca (near Lourinha, W. Portugal) red water and strong luminescence occurred in September 1944; 85% of the plankton consisted of the dinoflagellate *Gonyaulax polyhedra* Stein (Santos-Pinto, 1949).

No. 62. Bay of San Simon, near Vigo, northwest Spain:

Red water caused by *Gonyaulax polyhedra* Stein was observed by Diez del Vall (1947). Red water apparently occurs rather often, for it has a special name among Galicians: "purga de mar".

No. 63. Bay of Temrjuk, in the southeastern part of the Sea of Azov.

Mortality of fish repeatedly occurs in summer in times of high plankton production. Large numbers of fish appear at the beach in a very weak condition, a high percentage perishing afterwards (Knipovich, 1926, p. 85; 1927, p. 89). Knipovich assumes that they perish from lack of oxygen; considering the similarity to catastrophes in other high production areas the phenomenon is listed here provisionally under noxiousness of waterbloom. Future research may show whether this is correct. For destruction of benthonic invertebrates, chiefly in the deeper parts of the Sea of Azov, by lack of oxygen see no. 83.

No. 64. Black Sea, somewhat south of the delta of the Danube River.

1913, 21 July, Antipa (1941, p. 83) observed yellow reddish water between Zaton and St. Georghe. The reddish water was bordered with stripes of white foam. Antipa was told by fishermen that twice a year there comes a flow of cold water of a reddish color. Fish perish immediately, and the nets are destroyed when immersed in this water. The nature of the reddish discoloration is unknown. Provisionally this mortality is placed under noxiousness of waterbloom.

Africa.

No. 65. Cape Blanco, the cape meant here lies at a short distance north of Cape Cantin, French Morocco.

1951, 17 August. Red water and a great catastrophe of fish occurred in this region (Dr. J. Furnestin, Director of the Zoological Station at Casablanca, verbal communication).

No. 66. Dakar, Senegal.

Mass mortality of fish (chiefly Clupeidae and Engraulidae) occurs nearly every year between February and April in the southern part of the peninsula, near Dakar. The mortalities were very great in 1939, on 17 February 1944, and 25 March 1946. In 1946, besides fish, a great number of invertebrates were killed (worms, echinoderms, crustaceans, mollusks, etc. (Cadenat, 1946, and in litt.).

No. 67. Joal, Senegal.

Mass mortality of fish and invertebrates (actinians, crustaceans, mollusks) occurs rather periodically at the end of the dry period (June–July) (Dr. J. Cadenat, in litt.). The cause of mortalities no. 66 and 67 is not yet ascertained, but it seems probable that they are caused by red water.

No. 68. Southwest Africa.

Red water and mass mortality occur very often in Southwest African coastal waters. The victims consist chiefly of fish, also of cephalopods and other invertebrates. Classen (1930) and Copenhagen (1953) consider that some mortality occurs every year, sometimes even four or five times a season. In many years the mortality attains catastrophic proportions (1838, 1851, 1880, 1924, 1943, 1950). The mortalities occur in the southern summer; the great mortalities nearly always occur in December or January, and particularly at Christmas time. For details and literature see Brongersma (1943, 1947, 1948); in recent years valuable work has been done in this region by Copenhagen (1953), by the WILLIAM SCORESBY during March and September-October 1950 (Currie, 1952, 1953; Hart, 1953), and by the GALATHEA Expedition (Spärck and Steemann Niel sen, *see* Copenhagen, (1953); see also Berger (1949, *non vidi*). A red discoloration of the sea was noticed during the mortalities of 1860, 1880, 1924, 1927, 1928, and 1950, December 25. On the latter date the sea inside Walvis Bay, and the adjoining coastal waters, were covered to a considerable extent with a thick brownish soupy layer consisting almost entirely of a small dinoflagellate (*Glenodinium* sp.) (Spärck and Steemann Nielsen, *see* Copenhagen, 1953). Mortalities were observed on the following dates: 1837, April (Alexander, 1838, p. 79); 1849? (Chapman, 1868, p. 393); 1851, shortly after the 5th of December (Andersson, 1858, p. 268); approximately at Christmas time (Chapman, 1868, p. 393); 1880, 21–23 December at Swakopmund, an enormous catastrophe commenced one day later in Walvis Bay, whereas a minor mortality was observed at Sandwich Harbour (Gilchrist, 1914, p. 20; Pechuel-Loesche, 1886, p. 824); 1881, Christmas time (Pechuel-Loesche, 1886, p. 824);

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1882, January, Arbuthudt (1882, p. 38); 1883, December (Stapff, 1887a, p. 55); 1884, December (Stapff, 1887b, p. 208); 1920, 10 December (Reuning, 1925, p. 91); 1924, December (Reuning, 1925, p. 91; Anonymous, 10, 1926, p. 24), this is the same as the "1925" mortality mentioned in Weigelt (1930, p. 340, see Brongersma, 1948, p. 10); 1925, 23–34 December (von Bonde, 1928a, p. 42); 1927, January (Classen, 1930); 1928, February (Marchand, 1928, p. 3); 1929 (Schnakenbeck, 1930, p 410); 1933, December and 1934, January (Copenhagen, 1953); 1938, November (Brongersma, 1943); 1943, about January (McConnell in Brongersma, 1948, p. 11); 1944, December, 1947, December, 1948, January, February and December, 1949, January, 1950, January, February and March (Offen, in Copenhagen 1953); the small 1950 March mortality was also observed by the WILLIAM SCORESBY (Currie, 1953; Hart, 1953); 1950, December 25 (Spärck & Steemann Nielsen, in press); 1951, February and March (Copenhagen, 1953).

The mortalities repeatedly occurring among fish, birds, and seals at the Guano Islands off the coasts of southwest Africa and the Cape Province (Gilchrist, 1914, p. 13, 14; Mr. R. W. Rand, in litt.) probably have a similar cause. An enormous mortality occurred among seals about 1825 in the Southwest African coastal waters (Morell, 1841; Schultze, 1910, p. 166). In 1902 or 1903 the penguins came out of the water and dropped dead in large numbers (Gilchrist, 1914, p. 14).

No. 69. Cape Province, Union of South Africa.

Along the Atlantic coast of the Cape Province and along the eastern side of the Cape Peninsula red water is very common; red water was often observed in False Bay. The red discoloration usually is caused by ciliates, only occasionally by dinoflagellates (*Gymnodinium*, *Noctiluca*, etc.) (Hart, 1934a; 1934b, p. 170; 1938, p. 129; 1943, p. 661).

Records of mortality probably caused by red water are the following: Stumpnose Bay (north of Saldanha Bay), about 1869, a great mass of Geelbek fish were found swimming in a disabled condition in dark red water. Saldanha Bay, about 1907, mass mortality in red water. Table Bay, 1837, millions of fish and many whales were killed; many persons died from eating the dead fish; about 1888, strong phosphorescence and shellfish poisoning of a man and several baboons. The baboons lay dead on the beach near Simon's Town with calm shells in their paws (Gilchrist, 1914).

America.

No. 70. Bay of Guanabara, Rio de Janeiro, Brazil.

Red water consisting chiefly of *Glenodinium trochoideum* Stein occurs almost annually; it is often accompanied by mass mortality of fish and crustaceans. Red water occurs in various months of the year; it was observed in June, 1913 (Faria, 1914, p. 29); January 24, 1945 (Oliveira 1948, p. 728); August 26, 1946 red water and strong phosphorescence at night (Oliveira, 1948, p. 729); April 16, 1948 (Oliveira, 1950, p. 390). Mass mortality occurred in 1913, 1946, and 1948. In August 1946 the western shore of the Bay of Gunabara was covered with dead fish over an area 8 feet broad and 3 nautical miles long. Red water caused by *Prorocentrum* sp. has also been observed, *e.g.*, in June and July 1949. This water was not injurious to the fauna (Oliveira, 1950, p. 390). Red water appears with the first rains after a long dry period.

No. 71. Venezuela.

On the coast of Venezuela opposite Margarita Island, mortality occurs every summer in dark colored water in the hottest period (August, September or October). The phenomenon is locally known as "turbio" or turbid water. At the time of the turbio enormous numbers of sea-birds and small cetaceans congregate in this region to feed on the more or less disabled fish. Great numbers of fish run ashore and die, especially small herring-like fish (Clark, 1903, p. 285 and 1929). Clark (1929) concludes that the catastrophe is caused by red water.

No. 72. Florida.

Mass mortalities of fish and of invertebrates occur repeatedly along the west coast of Florida. These are caused either by cold (no. 38), or by red water. The phenomenon described for the years mentioned below is similar in all reported aspects and in all probability the mortalities in these years are caused by red water. This phenomenon is localized on the lower west coast. The mean interval between catastrophes is about ten years. Red water and mass mortality may occur at any time of the year, but most often in the fall. Years of very great catastrophes were 1878, 1880, 1916, and 1946/1947. Gunter, Williams, Davis and Smith have shown that the 1946–47 occurrence was due to a vast flowering of a dinoflagellate species which turned the water yellow and killed an estimated billion fishes (Anonymous, 13, 1947; Gunter, Smith and Williams, 1947; Gunter, 1947b; Baughman, 1947b; Anonymous, 14, 1948; Gunter, Williams, Davis and Smith, 1948; Gunter, 1948; F. G. W. Smith, 1949). The dinoflagellate was described by Davis (1948) as *Gymnodinium brevis*. Galtsoff (1948, 1949) published two interesting papers on red water, and on the Florida red tide especially. The 1946/47 outbreak gave rise to studies on the causes leading to red water, which are still underway (1956).

During the occurrences of red water in 1916, and in 1946–1947, an odorless but acrid gas caused stinging in the nasal passages and coughing, among the inhabitants of the sea shore (Taylor, 1919; Woodcock, 1948). This is significant, for coughing also coincided with catastrophes on the coast of Texas (no. 73) and near Vera Cruz (no. 76). Some people suffered to such an extent during the Florida outbreaks that they were obliged to leave the region.

Mass mortalities were observed on the following dates: 1844, 1854 (Ingersoll, 1882, p. 75); 1878, September until January 1879 (Jefferson, 1878; Jefferson, Porter and Moore, 1878; Porter, 1882); 1880, August–December (Anonymous, 5, 1881; Glazier, 1882; Ingersoll, 1882; Moore, 1882; Walker, 1884); 1882, 20 July (Anonymous, 6, 1883); in 1883 there apparently was no great mortality, Brongersma's (1948, p. 57) mention of 1883 as the date of the 1880 mortality described by Walker (Slobodkin, 1953, p. 150) being erroneous; 1885, October (Glennan, 1887); 1908 (Taylor, 1919); 1917, October–November (Taylor, 1919); 1946, 20 November until August 1947 (for literature see above). The red tide appeared in November 1946 near Naples; dead and dying fish were seen floating in the vicinity of Naples and about 10 miles offshore. The death of fish increased and the red tide moved northward, until by the end of January 1947, the bays and beaches of Fort Myers, Sanibel Island and neighboring areas were strewn with millions of dead fish; turtles, clams, crabs, shrimps, and barnacles were also killed. Towards the end of March, 1947, a brief recurrence of the red tide took place, without sign of damage; in April fish mortality occurred again; during the summer (June 20 and July 18) the red tide broke out again with even greater loss than during the winter, extending northward almost to Tarpon Springs. The red tide finally disappeared towards the end of August. Red water and concomitant mortality recurred in 1952, October 25 (Slobodkin, 1953, p. 150) and November 11 (Anonymous, 15, 1952; Chew, 1953, p. 610) off the west coast of Florida; 1953, January 3 off Dry Tortugas and January 22 off Smith Shoal (Chew, l. c.).

No. 73. Coast of Texas.

During June, July and August 1935, great numbers of dead and dying fish were observed on the Texas coast. The mortality coincided with the development of a gas similar to that observed during the Florida occurrences of red water (no. 72)

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(Lund, 1935, *non vidi*; *fide* Gunter, 1947b, p. 673; 1951). Gunter (1947b, p. 673) assumes that this mortality was caused by red water.

No. 74. Offatts Bayou, saline lagoon on the bay side of Galveston Island, Texas.

This is a small basin with a maximum depth of about forty feet. The depth in the channel at the entrance of the lagoon is about twelve feet. Mortality has occurred during every summer since 1936, except 1940, in the upper end of the bayou. Fish, shrimps, oysters, and crabs die. The crabs (*Callinectes sapidus* Rathbun) have been reported to leave the water and crawl ashore. In connection with the mortalities the water "boils" with escaping gas. The color of the water has been described as milky, red and black (Gunter, 1942b). In the summer of 1949 Connell and Cross (1950) found that the mortality coincided with red water caused by a *Gonyaulax* species. Nearby residents and fishermen have reported the appearance of red tides and accompanying phenomena for almost every summer during the past 15–20 years, and have reported that the fish did not die in the "red water" but died quickly when the redness settled and the water became "white" or "milky". Connell and Cross state that dinoflagellates may produce potent toxins; they further suppose that anaerobic conditions were important factors contributing to the mass mortality of fish (for a critisicm of this paper see Hedgpeth, 1951). Gunter (1951) states that the presence of *Gonyaulax* does not explain the "boils" which evidently come up from the bottom and seem to start in the deepest part of the bayou. It remains to be shown whether or not the Offatts Bayou dinoflagellate is poisonous.

No. 75. Northern coast of Yucatan, Mexico.

1648. An enormous fish catastrophe occurred on this coast, causing a very bad odor that was evident as far as Merida (Nuñez Ortega, 1879, p. 190). In the fall of 1907 an enormous mass of dead fish was observed in yellow water near Progreso (8 miles off the coast). Millions of dead fish drifted ashore on the Progreso beach (E. M., 1908). Beeby Thompson (1925) mentions a mortality in the same waters, the sea being covered with an oily scum. As an oily scum is often derived from dead plankton, it is probable that the fish perished by noxiousness of waterbloom.

No. 76. Vera Cruz, Mexico.

Mass mortality caused by waterbloom probably occurs repeatedly. 1797, 10 November a catastrophe of fish took place; several people died from eating these fish (Nuñez Ortega, 1879). This author (1877, 1879) remarks that troublesome coughing occurs in certain years among the inhabitants of Vera Cruz; this coughing coincides with fish catastrophes. Catastrophes and/or coughing occurred in 1853, 1861, 1868 and 1871. This coughing reminds one of similar occurrences during the Florida red water outbreaks (no. 72) and during the mass mortality in 1935 on the Texas coast (no. 73).

Indian Ocean.

Red discolorations have been observed in the Red Sea, along the coasts of southeast Arabia, and along the coasts of India and Ceylon.

A red discoloration caused by dinoflagellates and an olive brown discoloration caused by euglenoids both occur repeatedly in the coastal waters of India, particularly in certain parts of the west coast. The color imparted to the sea by the euglenoids is not red, but resembles hay decoction (Jacob and Menon, 1948; Bhimachar and George, 1950, p. 347). Waterbloom caused by blue-green algae frequently occurs in the warm Gulf of Mannar, occasionally causing mortality among fish and invertebrates.

No. 77. Red Sea and French Somaliland.

Red water caused by blue-green algae and by dinoflagellates both occur in the Red Sea. In 1902 mass mortality in red water was observed in the southern part of the Red Sea and along the coast of French Somaliland (Ilg, 1902, fide Höfer, 1902, p. 634). 1947, 23 August, mass mortality occurred in red water near Kamaran Island off the coast of Yemen; besides fish a great number of crayfish, small crabs and prawns were killed; a red discoloration occurs annually, mortality in some years only. Sea snakes were also killed. (Mr. C. H. Inge, in litt.).

No. 78. From Bab el Mandeb to Cape el Hadd, Southeast Arabia.

The name "Red Sea" was applied by ancient Greek authors to all coasts of Arabia. In summer red water often occurs in the vicinity of Aden. A yellow discoloration of the sea has been observed from the air on several occasions between Bir Ali and Mukalla (Mr. C. H. Inge, in litt.). Near Cape el Hadd red water has been observed on various occasions in the fall: September 27, 1936 between Cape el Hadd and Cape Madraka (Helen Landau Hayes, U. S. Navy Hydrographic Office, in litt.); 1950, 24 October from 20° 5′ N, 59° 3′ E to 20° 36′ N, 59° 25′ E (Mr. H. Kessels, officers of M. S. Slamat, in litt.).

The occurrence of red water in this area is important because a cemetery of fish has been found in nearly the same region by the John Murray Expedition (stas. 54, 55, 56, 57, 58, 59, 77, 79, Stubbings, 1939); from about 21° 50′ to 22° 25′ N and from 59° 49′ to 60° 10′ E. It was hardly to be expected that the localities of red water and those where the fish cemetery was found would coincide, for the occurrences of red water were observed by chance in the track of cargo steamers.

No. 79. Kathiawar, northwest coast of India.

1849, 27 October, a catastrophe of fish was observed in red water (Carter, 1858).

No. 80. Malabar and South Kanara coasts, west coast of India.

Red water is of a regular yearly occurrence along certain stretches of the coast line, but its intensity varies within wide limits. Red water and mortalities occur in a certain season only, from the last week of August to early in November. Hornell (1917; Hornell and Ramaswami Nayudu, 1924) observed that the dead fish floated in water discolored by euglenoids and assumes that the mortality is caused by the euglenoids. Bhimachar and George (1950) assume that the fish are killed by noxious dinoflagellates, and that the euglenoids developed in water containing great amounts of decaying dinoflagellates. Mortality was observed on the following dates: 1507, 25 ? August (Hornell, 1917, p. 65); 1861, 1 November (Denison, 1862, p. 453); 1871, end of October (Jouan, 1875, p. 23); 1908, November; 1916, last week of August, 25 September and 9–15 October; 1922, 22 September (Hornell, 1917); 1944, 3 November; 1945, 10 miles off Cochin in the open sea over an area of 10 miles in diameter; 1946, 20 September and 31 October mortality near West Hill (Jacob and Menon, 1948). Sliming of the sea due to putrefying masses of *Noctiluca* occurred in the second half of October, 1948; during this phenomenon there was no mass mortality of fish (Bhimachar and George, 1950).

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No. 81. Madras, southeast coast of India.

Pink water containing great masses of the dinoflagellate *Noctiluca miliaris* frequently occurs in summer. Mortality among fish and invertebrates occurred in June 1935; mortalities have been observed in other years (Aiyar, 1936).

No. 82. Gulf of Mannar, India.

A small mortality was observed by Hornell (1917, p. 55) near Tuticorin in red water of dinoflagellates. Mortalities in waterbloom of blue-green algae occur rather often: *Trichodesmium erythraeum* Ehrenb. is very common and is seen in dense swarms during the months of April, May, July, October and November. When it gathers at the surface in dense swarms the sea is colored brownish yellow and emits a strong smell of chlorine. On such occasions, which last usually 3 to 7 days, heavy mortality of marine animals takes place (Chacko, 1950, p. 172).

1942, 17 May, great mortality occurred in a tide-pool on the southern (Ceylon) side of Krusadai Island, the casualties being particularly heavy among holothurians and fish (Chacko, 1942); 1944, May, along the southern shore of Pamban dead fish and crabs were thrown ashore (Chidambaram and Mukundan Unny, 1944). In both cases *Trichodesmium erythraeum* was responsible for the injury. Mortality has been observed between Colombo and Hikkaduva as well; a great mortality of *Diodon hystrix* occurred in November, 1933 (P. E. P. Deraniyagala, in litt.).

F. Mass Mortality Caused by Lack of Oxygen and by Poisonous Gases, with a Remark on a Catastrophe Supposedly Caused by H_2SO_4

No. 83. Sea of Azov, U. S. S. R.

The Sea of Azov occupies an area of 37600 km². It is excessively shallow, its mean depth being 6.8 m, the greatest depth 13¼ m. Many small fresh water lakes have a much greater depth. Shallowness combined with a comparatively great surface make good vertical circulation possible, with consequent oxygenation of the lower layers. In summer high temperatures combined with a slightly lower salinity of the surface water cause a rather strong stratification and the bottom layers are not oxygenated during warm and calm days. As the organic production and the amount of dead organic material sinking to the bottom are excessively high, the oxygen is fully used up during these short times of stagnation; the boundary O_2/H_2S rises above the sediment. This occurs particularly in the deeper parts of the sea and causes widespread mortality of the bottom fauna (Zenkevich, 1951, p. 299). The mortalities in the Bay of Temrjuk appear to be caused by poisonous waterbloom instead of oxygen deficiency (no. 63). Compare the occurrence of two phenomena: red aguaje and the Callao painter near the coast of Peru (no. 47).

No. 84. Badly ventilated Norwegian fjords.

Not all Norwegian threshold fjords are badly ventilated; some of them are periodically or continuously ventilated (sill depth rather great and sill short). Others are only occasionally ventilated (e.g., once in a half century). In the deeper waters of the last type there is no oxygen, whereas hydrogen sulphide is abundant. On the rare occasions when these fjords are ventilated there is a rapid inflow of sea water over the sill. This cold and saline water sinks to the bottom of the fjord. The H_2S-poisoned water is raised to the surface and causes catastrophic death of the whole fauna inhabiting the higher water layers.

Example: Hellefjord, 1905. The deeper layers were not ventilated since 1850 and contained an enormous amount of H_2S in 1903. In the winter of 1905 there was a strong odor of H_2S around the fjord and the entire fauna was destroyed (Dahl, 1906; Strøm, 1937, p. 56).

No. 85. Bay of Aetolikon, Greece.

15–16 December 1881. The Bay of Aetolikon is a small and rather deep basin semiseparated from the Bay of Mesolungion. During the night of the 15th to the 16th of December there was a heavy northeast storm and the water of the basin was much agitated. Some inhabitants of the village of Aetolikon felt an earthquake; others did not. Suddenly there was such a strong odor of H_2S that the people nearly suffocated. Afterwards many fish were found dead. Walther (1894, p. 937) concludes that the H_2S was of volcanic origin. According to von Rath (1882a, b) the occurrence has nothing to do with vulcanism. The indirect cause of the mortality, therefore, is uncertain. Possibly there was H_2S in the deeper layers of the Bay of Aetolikon, and a sudden renewal of the bottom water as a result of the severe storm may have brought the H_2S poisoned water to the surface. Another possibility is an evolution of H_2S from the sediment as a result of an earthquake (*vide* no. 13, 17). See further Fuchs (1883, p. 100).

No. 85a. Lake of Köcegiz near Fethiye, Turkey.

This lake is connected with the Mediterranean by a narrow canal. During severe storms the H_2S poisoned bottom water is brought to the surface, causing mass mortality of *Mugil* and other marine fishes. Millions of fish were killed during a storm in February 1937; a similar phenomenon occurred in June 1953 (Dr. Nümann, *fide* Prof. C. Kosswig, in litt.).

No. 86. "Lake" of Tunis.

This "lake" is a semiseparated part of the sea. The phenomenon of red water coinciding with a disagreeable odor and mass mortality of fish is well known among inhabitants of Tunis. This combination reminds one somewhat of mortality in red water consisting of phytoplankton; a disagreeable odor also has been perceived during dinoflagellate red water. According to Cabasso and Roussel (1942, p. 203) and Jeanne H. Heldt (1952) the red discoloration is, however, caused by bacteria and appears after the mortality. They assume that the fish are killed by oxygen deficiency and development of H_2S. The phenomenon is described by Cabasso and Roussel (1942, p. 203): During June-July in very hot years the lake gets a disagreeable odor, which usually vanishes after some days, but in certain very hot years it may last for several weeks. If this occurs a great mortality sets in. After the beginning of the mortality the water turns a wine-red color. Some days afterwards the mortality as well as the disagreeable odor diminish.

From water samples taken in the discolored area Cabasso and Roussel cultivated two microorganisms: *Vibrio desulfuricans*, producing H_2S by reduction of sulphates, and a sulfur purple bacterium, *Beggiatoa roseo-persicana*, oxidizing H_2S. They assume that the fish perish by the noxious action of the first organism and that the situation is ameliorated when the H_2S content decreases under influence of the second.

No. 87. Bay of Eckernford, Baltic.

1931, 5 November. In some parts of the Baltic (Bay of Kiel, Bay of Eckernford, and some other localities) there are places with a so-called infectious or dead bottom. In these places mortalities of fish and invertebrates repeatedly occur. The sediment in these places is black, and usually has a bad smell (Jaekel, 1931, 1933). On the 5th of November 1931 there was a great fish mortality in the harbor of Eckernford; the oxygen content in the lower water layers was low (2.0 to 2.9 mg/l) (Jaekel, 1931, p. 427). Mortality was observed also outside of the harbor in the Bay of Eckernford; besides fish, many in-

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vertebrates were killed; particularly crustaceans (*Carcinus maenas*), starfishes, and worms. Outside the harbor, abnormalities in the oxygen content were not observed. Jaekel (1933) and Meyer (1932) suggest that the cause of death is oxygen deficiency. Meyer compares the Eckernford mortality to the mass mortalities near Walvis Bay (no. 68), believing that they have the same cause. In accordance with Kaiser's (1930) hypothesis for an explanation of the mortalities at Walvis Bay, Meyer supposes that H_2S bubbling up from the black sediment is one of the principal factors at Eckernford also. Jaekel (1931, p. 428), however, points to the fact that the mortality also occurred near Hohwacht, where the bottom does not consist of black mud.

No. 88. Kurisches Haff, Baltic.

Mass mortality of fish occurs nearly every summer; the animals killed are chiefly "Stinte" (*Osmerus eperlanus* L.) and "Kaulbarsche" (*Acerina cernua* L.). Jüngst (1937) supposed the fish were killed by oxygen deficiency, but he did not determine the oxygen content; his observation of the dead fish was incidental to another purpose. An annual mass mortality in summer in this bay, chiefly of the same fish (Kaulbarsche) is ascribed by Szidat (1927, 1928) to parasitic worms.

No. 89. Liman of Varna, Bulgarian coast of Black Sea.

1940, 24–26 July. A great mass mortality occurred. This liman is a small basin. In summer H_2S occurs in the lower water layers; sometimes this is raised to the surface and occasionally brings about killing of the fish living in the surface waters (Paspalev, 1941, *non vidi*; Caspers, 1951a, p. 670, 1951b, p. 37). The explanation of these authors is feasible; nevertheless it seems worthwhile to examine the composition of the plankton during the mortality (compare with the mortalities in Offatts Bayou, no. 74).

G. Mass Mortality in Sea Connected with Spawning Runs

No. 90. Mortality of the capelin (*Mallotus villosus* Muller), Arctic.

The capelin has an arctic circumpolar distribution. In spring and early summer these fishes enter the tidal zone in huge shoals in order to spawn. In this period enormous numbers are killed. Mass mortality has been observed in the following places and on the following dates:

Iceland: large numbers are destroyed annually (Faber, 1829, p. 177); Agassiz (1851, p. 42) erroneously attributes this mortality to volcanism. Newfoundland: in Northern Bay, 1 July 1839 (Jones, 1882) and in Harbour Grace, August 1853 (Collins, 1884, p. 282). Alaskan Islands: Metlakatla, August 1897, they were killed in incredible numbers (Jordan, 1925, p. 349). Greenland: Bay of Disko (Porsild, 1902; Weigelt, 1927, p. 143), according to Weigelt (1927, p. 205) mass mortality occurs near Disko and Lodden; the latter probably is erroneous, as Lodden is the German name for *Mallotus*.

H. Mass Mortality Caused by Stranding

No. 91. Klawak, west coast of Prince of Wales Island, Alaska.

1913, January. An enormous amount of the Pacific herring (*Clupea pallasii*) crowded into a bay near Klawak. Hundreds of thousands, perhaps millions, were stranded and suffocated. When the tide receded they were left in a solid mass over the beach to a depth, in places, of several feet (Bower and Fassett, 1914, p. 27; Rounsefell, 1930, p. 273).

I. Mass Mortality in Sea Caused by Severe Storms

91a. California

Along some 25 miles of the California coast between Arcata and the mouths of the Eel and Mad rivers (appr. 40°30′ N). Large numbers of ducks, and occasionally some geese, are killed as a result of being engulfed by high waves and rolled into the surf, where their plumage becomes sanded and their internal organs are disarranged by the pounding waves. Drowning seems to be the actual cause of death. These catastrophes usually occur in moderately rough seas and heavy offshore fog following severe storms. It is estimated that between 6,000 and 9,000 birds were killed in this manner from Nov. 1 to Dec. 31, 1952 (Wooten, 1954).

No. 92. Iceland.

During every winter storm many fishes are cast on the shore near Örebacke.

1654. 1500 specimens of *Holocentrus sanguineus* Faber (=*Sebastes marinus* (L.)) were collected on the beach after a severe storm. Faber, visiting the island in 1821, observed that several hundred specimens of this species were thrown up after every winter storm together with great numbers of *Gadus brosme* Müller (=*Brosmius brosme* Müller) and of *Gadus mustela* L. (Faber, 1829, p. 83, 85, 128).

No. 93. Scilly Islands, England.

1874, 13 April. During a severe storm hundreds of fish were thrown on the beach (G. M., 1874).

No. 93a. Netherlands.

1953. In the night of 31 January–1 February a severe northwestern gale combined with spring tide caused flooding of extensive areas in the Netherlands, Belgium and England. Several thousand men, cattle, and other terrestrial animals were drowned. Several species of invertebrates that rarely are found on the beach were ploughed from the bottom of the sea by the agitation of the water, and in the Netherlands during the following days a large number of living specimens was cast upon the beach. Thousands of *Cardium crassum* were observed near Scheveningen, and thousands of *Venus striatula* near Bloemendaal-IJmuiden, etc. (Swennen, 1953).

No. 93b. Romania.

Thousands or even millions of specimens of the decapod crustacean *Upogebia littoralis* Risso are repeatedly cast on shore dead or alive after north or east storms, sometimes together with great amounts of aquatic plants, and with dead mollusks (*Mytilus galloprovincialis* and *Cardium*). *Upogebia* is a poor swimmer, living in burrows between 8 and 15 m. During storms the sand at this depth apparently is tossed about and the animals are driven from their burrows. Mass mortality occurred on the following dates in the vicinity of Constanza: 1935, 7–8 November; 1938, 15 November; 1939, 5–9 May (Popovici, 1940).

No. 94. Gulf of Mexico.

1947, 19 September. A severe hurricane did considerable damage to the shallow water fauna in Alabama, Mississippi, and Louisiana. Of the oysters on the Mississippi reefs 9 to 95% were killed. The most severely affected portion was the inshore beds from Bay St. Louis west to the state line; here oysters were either killed or had disappeared. Mud was washed a foot or more over some of the reefs (Engle, 1948, *fide* Gunter, 1953, p. 32).

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J. Mortality in Sea by Vertical Currents

No. 95. Straits of Messina, Italy.

Dead or dying deep-sea animals are often thrown on the beach near Faro. In the course of time Mazarelli (1909; *fide* Issel, 1911) collected 43 species of deep-sea fish and some deep-sea invertebrates; see also Jespersen and Täning (1926). The majority of these animals normally live at a depth of several hundred metres. Mazarelli states that the vertical currents need not reach the depth at which the fish live; he supposes that the fish move into higher water layers on their own accord, and that they are carried from these layers to the surface by vertical currents. It is a peculiar fact that certain species were seen in particular months of the year. Most specimens were collected between May and October, a period with strong south and southeast winds; few animals were thrown up in the other part of the year when northeast winds predominate.

The number thrown up after severe storms was particularly great; hundreds of dead deep-sea fish were collected by Giglioli near Messina after a severe storm on September 26–28, 1878 (Palacky, 1888).

No. 96. Pebble Beach, California.

1952, 17 October. The beach at Stillwater Cove, Pebble Beach (36° 33′ 59″ N, 121° 56′ 28″ W) was littered with thousands of dead myctophid fish, all of the same species (*Tarletonbeania crenularis* Jordan and Gilbert) and all of the same general size. There was a sudden drop in the temperature of the surface water in the week preceding the mortality. This drop was due to intense upwelling. Possibly the upwelling was responsible for the mortality (Aughtry, 1953).

K. Mass Mortality in Sea, the Cause of Which is not Certain

No. 97. North Polar Sea off the coats of Taimyr, Siberia.

1878, 13 August. Immense numbers of dead *Gadus polaris* were observed on the bottom of the sea in the vicinity of an island, by Nordenskiöld (1882, p. 292); he supposed they were killed by lack of oxygen, when the water was covered with ice.

No. 98. Murman coast.

1789, end of July. Fishermen sailed many leagues through huge numbers of dead haddock and coalfish between Fisher's Island and Sweetnose (68° N) (Abbs, 1792; Collins, 1884, p. 275). The cause of the mortality is unknown.

No. 99. Cape Charles Harbor, Labrador.

1876, 1 August. An enormous quantity of dead haddock floated on the surface of the water. Unusual numbers of icebergs were grounded in the vicinity. Were the haddock killed by cold? (Collins, 1884, p. 275).

No. 100. Atlantic, off the coast of U. S. A.

1884, 20 July. Many dead cephalopods (*Alloposus mollis* Verrill) were observed in nearly the same area as the tilefish in 1882 (Murray, 1898, p. 129). Were they killed by cold? [Or, endogenous post-spawning death?].

No. 101. Atlantic, somewhat north of the Azores. (Fig. 7).

Great numbers of dead needle fish, probably all belonging to

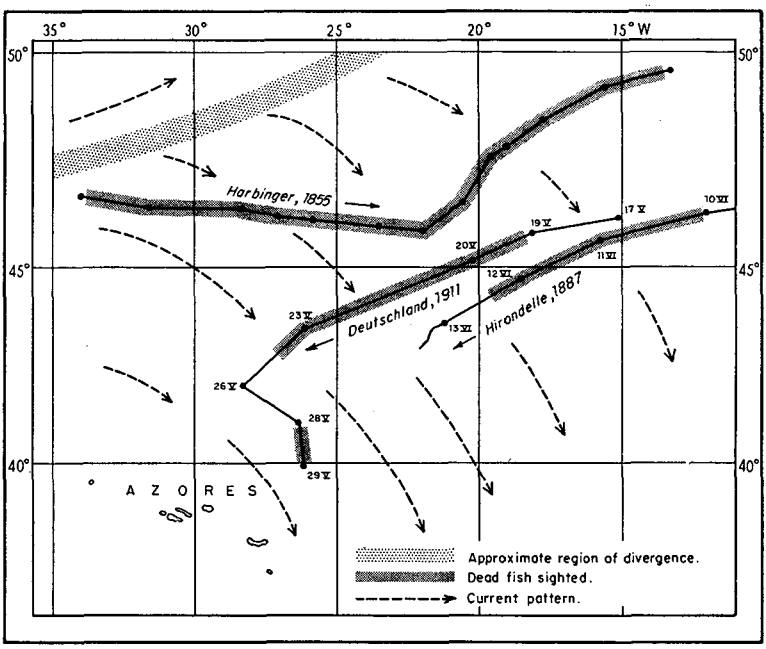

FIGURE 7.—*Mass mortality of needle fish north of the Azores (no. 101)*
Generalized current pattern after Schott (1942, Pl. XXII)

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the species *Entelurus aequoreus* (L.), were observed in different years. Dates: 1855; 1887, on the days preceding June 12th and particularly on the latter date; 1911, 19–24 and 28–29 May.

In 1855 a great quantity of dead fish mentioned under the name *Syngnathus anguineus* (=*Entelurus aequoreus* (L.)) was observed over an extensive area by Captain Parsons in the track of the ship. Dead fish occurred from 46° 49′ N, 34° 10′ W to 49° 36′ N, 13° 17′ W. The supposed cause of death is vulcanism, but no volcanic phenomena were observed. The catastrophe near San Ferdinandea (no. 6) has been quoted for comparison (Symonds, 1855; Anonymous, 1, 1856); this is probably the reason that these two catastrophes have been confused in later literature (see no. 6).

In 1887 a great number of dead fish mentioned as "Syngnathe" was observed in nearly the same area on one of the expeditions of the Prince of Monaco. On June 12th abundance of dead fish coincided with abundance of living macroplankton: Salpae. Pouchet (1887, p. 493; 1939, p. 219) supposes that the fishes lived as commensals of the Salpae in deeper water and that they were killed when dragged along to the surface by their hosts. This explanation is unlikely.

In 1911 (May 19–24 and 28–29) a great number of dead needle fish mentioned as *Nerophis* (formerly *Entelurus aequoreus* was often mentioned under the name *Nerophis*) were observed about 20°–30° W and 45°–40° N (Lohmann, 1912a, p. 32; 1912b, p. 82; 1912c, p. 419; 1920; Andrée, 1920, p. 616). There were two maxima in the occurrence of *Entelurus* (more than 80 per cent of these specimens were dead); these maxima coincided with maxima of living macroplankton (Tunicates (Salpae), Coelenterates, etc.); one of the two maxima coincided with a maximum of living microplankton (chiefly naked Monadinae and Gymnodinians), at the place of the other maximum a high percentage of the microplankton was dead.

Lohmann states that the fish lived in shallow seas among algae; he supposes that they floated with the algae to the open sea and perished when the algae sunk to deeper layers. There are, however two forms of *Entelurus aequoreus*: a littoral form, and a form of the high sea. The latter occurs from the 1000 m depth line off the European coast westward to about 35° W and southward to about 30° N; sometimes it occurs in very great quantities (Duncker, 1915, p. 33 and 1926, p. 18). According to Duncker (1915, p. 34) there are diaphanous specimens in all large collections that probably were dead before they were collected; such specimens were described by Cope (1875) as a separate species under the name *Osphyolax pellucidus*. This may be an indication that dead specimens are repeatedly found floating in the sea.

Like the *Centriscus* species (no. 104), needle fish are not good swimmers and like *Centriscus* they cannot escape with the sudden onset of unfavorable conditions. During cold waves in Florida (no. 38) needle fish suffer greatly, for they cannot escape to deeper water when the surface temperature changes suddenly. The unfavorable conditions need not exist over the whole area where dead *Entelurus* specimens were observed; if they are killed north of the Azores, the dead fish will drift in an easterly direction with the currents (for the direction of the currents in this part of the ocean see Schott, 1942, pl. XXII), and thus these leathery fishes that do not decay very soon may be transported over great distances. The coincidence of dead fish maxima with macroplankton abundance indicates that dead fish occur in an area of high production. This might be an indication that their cause of death is noxiousness of plankton blooms, although this is a mere hypothesis. The cause of this mortality is still wholly uncertain.

For the sake of completeness, records of reddish water observed in this area are given: a large area of rust-discolored water was observed at 44° 57′ N, 33° 34′ W on May 18, 1926; vermillion red water occurred over a wide area from 44° 59′ N, 36° 37′ W to 45° 19′ N, 35° 48′ W on April 9, 1932 (Helen Landau Hayes, in litt.).

No. 102. Tobago, an island northeast of Trinidad.

1872, August. A high number of starfishes and other marine animals were killed all along the southern shore of this island (Rawson, 1872).

No. 103. Black Sea.

About 1928. An enormous mortality occurred near Sebastopol (Jg., 1928). A catastrophe in the western part of the Black Sea is recorded by Popovici (1943)

No. 104. Pegu, Burma.

1809, September. An enormous quantity of dead *Centriscus scutatus* was observed by Dussumier over more than 20 miles along the coasts (Quoy and Gaimard, 1824, p. 191). The cause of death is not mentioned. *Centriscus* species are not good swimmers (Mohr, 1937). It is very difficult for such fish to escape the sudden onset of unfavorable conditions (changes in temperature, red water outbreaks, etc.). Researches on the real cause of this mortality are highly needed, because species of *Centriscus* occur in many Tertiary deposits (literature in Fröhlicher and Weiler, 1952).

No. 105. Southwest coast of Sumatra, Indonesia.

1775, November. Vast quantities of dead and dying fish were thrown on the beach during an excessively dry season; for at least a month the fish continued to be thrown up. The drought was so severe that many rivers did not flow (Marsden, 1781). The phenomenon reminds one of that on the East coast of Borneo (no. 51).

Further records of fish mortalities the cause of which is not certain are given by Adams (1868), Anonymous, 8 (1905), Dawson (1859), and Lahille (1912, *non vidi*).

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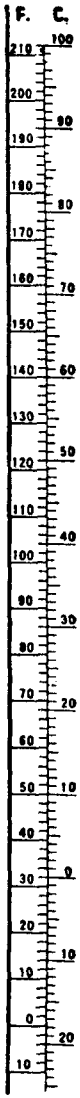

Nautical Miles	*Kilometers*
1	1.8
2	3.7
3	5.6
4	7.3
5	9.2
6	11.1
7	13.0
8	14.8
9	16.7
10	18.5
20	37.0
30	55.5
40	74.1
50	92.5
60	111.2
70	129.6
80	148.0
90	166.7
100	185.1
200	370.0
300	556.0
400	741.0
500	916.0

Feet	*Meters*	*Fathoms*
1	0.31	0.16
2	0.61	0.33
3	0.91	0.50
4	1.22	0.67
5	1.51	0.82
6	1.83	1.00
7	2.14	1.16
8	2.44	1.33
9	2.74	1.50
10	3.05	1.66
20	6.10	3.33
30	9.14	5.00
40	12.19	6.66
50	15.24	8.23
60	18.29	10.00
70	21.34	11.66
80	24.38	13.33
90	27.43	15.00
100	30.48	16.66
200	60.96	33.33
300	91.44	50.00
400	121.92	66.66
500	152.40	83.33
600	182.88	100.00

Statute Miles	*Kilometers*
1	1.6
2	3.2
3	4.8
4	6.4
5	8.1
6	9.7
7	11.3
8	12.9
9	14.5
10	16.1
20	32.2
30	48.3
40	64.4
50	80.5
60	96.6
70	112.7
80	128.8
90	144.8
100	160.9
200	321.9
300	482.8
400	643.7
500	804.7

Kilometers	*Nautical Miles*	*Statute Miles*
1	0.5	0.6
2	1.1	1.2
3	1.6	1.9
4	2.2	2.5
5	2.7	3.1
6	3.2	3.7
7	3.8	4.4
8	4.3	5.0
9	4.9	5.6
10	5.4	6.2
20	10.8	12.0
30	16.2	18.6
40	21.6	24.9
50	27.0	31.1
60	32.4	37.3
70	37.8	43.5
80	43.2	49.7
90	48.6	55.9
100	54.0	62.1
200	107.9	124.3
300	161.9	186.4
400	215.9	249.0
500	269.9	310.7

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