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BOTANICAL LIMNOLOGICAL METHODS WITH SPECIAL REFERENCE TO THE ALGAE

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INTRODUCTION

Productivity is the fundamental problem in the biology of freshwaters. The techniques for studying this are concerned with the sources of energy and nutrients, and the resulting changes in natural populations deduced from photosynthetic production or population composition and density. Such changes can be estimated

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by sampling the populations or by other means. Interpretation of the observed behaviour may require information from experimental populations and help from mathematical analysis.

The literature reviewed here is concerned almost wholly with microscopic plants and so with algae. Higher plants and the larger algae, often all classed together as macrophytes, are not specifically considered, although several sections, e.g., on temperature, light, chemistry and photosynthesis, contain relevant discussion. Such vegetation consists very largely of plants rooted in what "may be regarded as soils of a special type" (428), and the techniques for assessing production are largely those used for terrestrial vegetation. Frequent reference is made to techniques of oceanography, since many problems are common to this and limnology. We have also thought it profitable to discuss some general methods of approach as well as specific points of technique.

It is convenient to list here some general sources of information on limnological methods. These include the book by Welch (733) and a recent compendium in Russian (467), various special publications of the American Society of Limnology and Oceanography (e.g., 18, 85, 114, 463) and the more comprehensive communications on methods (e.g., 252, 392, 429, 430, 432, 457) issued by the International Association for Limnology. The well known series edited by Abderhalden contains some detailed but now largely outdated reviews, e.g., 2; 682 is, however, still of great value. Brief discussions of methods in relation to the theoretical background of the subject are given in various books (203, 240, 385, 569, 616a, 650, 734, 747). Important meteorological, physical and chemical constants and variables may also be found (110, 232, 276, 614).

The literature on methods is immense, and many investigators utilise those which, though they may not be original, are variants of more or less well known ones. This account is therefore not comprehensive. It was completed in January 1957.

IDENTIFICATION

It is beyond the scope of this article to discuss the techniques for identifying material; they are contained in the pertinent floras, faunas and monographs. Standard taxonomic works for freshwater algae include 214, 465, 491, 509, 606, 607, 611, 612, 613,

669, 673, 742, 744. Yet it is right to emphasize, first and foremost, that the best limnological methods may be wasted if the organisms concerned are misidentified. This is not necessarily a matter of correct nomenclature or taxonomy. Identification means " establishing the identity ", and it may be possible to do this for organisms on whose nomenclature the experts are not agreed—a not unusual situation in phycology. An assurance is needed that the plant studied or discussed is so like that described by someone else that it can be reasonably given the same name. The " someone else " is ideally the author of the botanical name of the plant. This ideal frequently cannot be realised and another standard must be applied.

As an example, we may consider the diatom *Asterionella,* one of the most widespread and abundant planktonic algae often discussed or studied by limnologists during the last 60 years. *Asterionella formosa* Hassall is the original or type species, but Hassall's description and figures are such that it is impossible to distinguish it for certain from the later described *A. gracillima* (Hantzsch.) Heiberg, and no type material exists so far as is known. The literature on both species is large, yet there is more than a suspicion that in many cases two authors, who each consider one of the pair, are in fact talking about the same organism. Reference to the original accounts, standard floras, check lists and other papers shows that there is a diversity of views among the specialists over characters of taxonomic importance, specific delimitation and nomenclature in the genus. Not uncommonly an " expert " is asked to name plants, but it is clear that, unless it is known, or it is reasonable to infer, whose description or material supply the basis for his determinations, the published list of species may still be unsatisfactory. What is a limnologist to do, when he has neither the time nor inclination to try to elucidate the confusion himself? The best plan seems to be to use a taxonomic work in which the form of *Asterionella* that he wishes to discuss is, in his view, clearly described and figured, and to state that he is doing this (e.g., 376, p. 390; 606, p. 334). In addition he should preserve specimens and, perhaps, a clone culture. If he still feels in doubt he can publish his own figures and description, including any useful physiological or ecological criteria. If samples are preserved, it may be

possible to relate earlier data on allegedly different species to current investigations.

It may be that a limnologist is concerned with physiological differences between algae belonging to the same species or taxon of lower rank. Plants which are not distinguishable on morphological grounds may have important physiological and so ecological differences. Here the taxonomists and their published works may be of no assistance. So far, this difficulty does not seem to have led to any serious errors in limnology (but see 564 concerning ecotypes and 191 on *Cocconeis placentula*), though this may be a reflection of our ignorance. Fortunately, descendants of most of the algae upon which physiological investigations are made are now usually preserved in one or more of the culture collections maintained at various institutes, some of which are listed at the end of the references. Such cultures form part of the apparatus available for limnological use. The algae are probably correctly named, though the curators of these collections are often dependent on the workers who made the original isolation for identification, so that checks are desirable. Indeed, Pringsheim (495) says: " it sounds unbelievable, but it is true, that almost every strain of *Euglena* employed in the many physiological investigations bears a wrong name . . . the definition of the species of *Chlorella* used in physiological work is not much better ". Perhaps the most remarkable example is to be found in oceanography where the much used *Phaeodactylum tricornutum* Bohlin (*Nitzschia closterium* f. *minutissima* Allen et Nelson) is almost certainly not even a diatom (72, 248) and does not have its main development in the plankton of the open sea (e.g., 69, 72, 137 and unpublished observations of the first author), so that many of the ecological inferences made from studies upon it are open to doubt. Moreover, it appears that sometimes this alga is referred to as *Nitzschia closterium* (e.g., 269, p. 136), a true diatom. Similar considerations apply to quantitative ecological inferences from such freshwater algae as *Chlorella* (cf. 257).

It is most desirable that when plants are mentioned they be named in full. Statements which say that *Navicula,* a genus with about one thousand species, favours such and such conditions are obviously wrong for Naviculae are to be found in almost every habitat and area in the world. Any other such generalisation about

genera with several to many species is open to doubt. Yet sometimes limnologists go even further and announce that whole classes prefer these or those conditions.

PHYSICAL ENVIRONMENT AND ENERGY SUPPLY

TEMPERATURE

Temperature measurements occupy a central position in limnology, as temperature changes affect not only many physiological processes but also, via the density of water, the fundamental stratification of a water body. Although the underwater distribution of temperature is less complex than its distribution in many terrestrial habitats (reviewed by 188), the sites for measurement are often remote and may demand specialised instruments. In some cases the measurement of small temperature differences ($< 0.5°$ C.) may be critical for interpreting the stratification of a waterbody. This applies particularly to warm tropical waters, where small temperature differences have disproportionately large effects on the density of water and hence on the stability of stratification (cf. 54, 160, 569, 656). However, readings to less than 0.05° C., a value obtainable with a variety of instruments, including those mentioned below, are but rarely required in any freshwater.

Mortimer (429) gives a recent and more detailed review of temperature measurement in limnology, describing the principal types of apparatus used and their relative advantages in various situations. Desirable qualities involved are accuracy and speed of operation. In shallow waters a simple form of mercury thermometer enclosed in a water sampler (e.g., the Ruttner sampler, 571, readings to 0.05° C.) is often very effective and gives temperature data together with other samples. In deeper waters the sampler may require more thermal insulation, as in the insulated water bottles originally developed for marine studies. Another instrument is the classic reversing thermometer, from which "it is no exaggeration to say that almost all temperature observations in limnology and oceanography have been and still are being made" (429). It is particularly suitable when readings of high precision are required from widely spaced and often considerable depths. Here a messenger causes a reversal through 180°, breaking the mercury column, at the depth required, and a reading is made after

hauling to the surface. To obviate this time-consuming operation, several instruments utilising electrical properties have been devised, in which readings from a submerged sensitive element are recorded on a galvanometer at the surface. Thermocouples have been occasionally used, with the measuring junction freely exposed and the reference junctions kept at a constant temperature in a vacuum flask. A recent development has been the thermistor, used also in terrestrial ecology and introduced into limnology in 1947; a full description is given by 432. The sensitive element is a mixture of metallic oxides sintered together, whose electrical resistance changes rapidly with temperature, and with a suitable voltage source, bridge circuit and galvanometer enables a rapid exploration of the thermal structure of a water-body to be made. Recalibration from time to time is, however, usually necessary for precise work. Use of this convenient instrument is rapidly spreading. Another advantage lies in the possibility of its incorporation in continuous temperature recorders (432).

A rapid self-recording instrument is the relatively complex bathythermograph (described briefly in 429; for this and other instruments suitable for work on large bodies of water, see 714), which is unique in that it can be operated from a moving vessel and has been much used in recent oceanographic work. However, time is required for interpreting the traces obtained, and the cost (at present about $400) is prohibitive for the average limnologist.

LIGHT

Measurement of light intensity in natural waters is less simple than that of temperature, and its application to botanical problems has led to some confusion, an unfortunate situation in view of the close relation linking light intensity with photosynthesis and, ultimately, plant growth. The most extensive review of the principles of light penetration underwater, and its measurement, is the book by Sauberer and Ruttner (587). Less exhaustive but very useful accounts are given in 3, 25, 26, 29, 289, 479, 569, 583, 586, 594, 650, and the best illustrated summary is probably in 112. The most fundamental measure of light penetration is obtained by the quantity commonly called " extinction coefficient ", or " absorption coefficient " in older literature (cf. 477); unfortunately these terms have different meanings in general optics. As measurements of

light penetration in natural waters are normally made in a vertical direction, from which the average light path may diverge considerably (751, 772), the terms are best prefaced by the word "vertical" (487, p. 194). Another less fundamental measure, the percentage transmission per metre, is widely used by Continental authors. Means for its estimation from a nomogram (720) and rapid interconversion with extinction coefficients (587) have been described. The vertical extinction coefficient or percentage transmission can be readily obtained from a semi-logarithmic plot of light intensity against depth, and for optically homogeneous water the former can be quickly calculated by dividing 3 by the depth interval required to reduce the light intensity of 5% of its initial value (this relation is a special case of the general equation defining the coefficient: 651). The extinction or transmission value measured depends upon the average path length of the light (as opposed to the vertical depth), which in turn is affected to some extent by the solar elevation. The latter relation has been conveniently summarized in graphical form (749, figs. 8, 10; 751, fig. 1).

The penetration of light under water has been measured by a variety of photo-sensitive elements, including several types of emission photocells, thermopiles and the selenium (barrier layer) rectifier cell. Modern forms of the last are relatively cheap, sensitive and easily incorporated into photometers for underwater use; they are now used almost to the exclusion of other instruments. Their properties and those of emission photocells are summarized in 727. Measurements can readily be carried out down to depths associated with 1% of the surface intensity and with a suitable amplifier to about 0.0002% (749). With photometers incorporating photomultiplier tubes, even greater sensitivity is possible (117a, 312a). The more cumbersome thermopile has been less often used —apart from the well known work of Birge and Juday (see 64 for apparatus) that of 22, 584, 639, 640 and 692 may be mentioned— but has a great advantage in recording radiant energy directly. Use of photoelectric measurements for underwater light intensities in absolute (energy flux) units is much more involved and has been but rarely attempted (see 283, 292, 359, 360, 651, 654). Particularly with the selenium rectifier cell, errors may arise from non-linearity in the response at high light intensities, especially when used with a galvanometer in a circuit of high electrical re-

sistance (see 727, fig. 1. 19). If present in measurements of light penetration with depth, they often simulate the effect expected from an upper water stratum of higher transmission (cf. 700, fig. 3). These errors, often neglected, can be avoided by the use of a galvanometer in a circuit of low resistance (< 50 ohms) and a suitable neutral density filter over the sensitive cell (29). In measurements a diffusing opal glass is also generally required; this may be combined with the neutral filter (e.g., 478, 483).

Measurement of light penetration underwater is normally made by lowering the sensitive element contained in a water- and pressure-proof photometer casing (for design, see 29, 182), and at suitable depth intervals recording the photo-current; similar records can be made when raising the photometer. Shading from the vessel (estimated in 485) can be reduced by the use of a boom. A more rapid " balance-by-depth " method has been described in 37, but involves some loss of accuracy and is not suitable for optically heterogeneous waters. Other modified methods (26, 182, 183) are suitable for use in strong seas where the use of a galvanometer as previously described is difficult. Under some conditions errors may arise from displacement of the photometer cable from the vertical, due to water currents (182), and the " wire angle " may then require interpretation (650, p. 358). A photometer fitted with a float and intended for measurements immediately under ice has also been designed (773).

Since the rate of extinction of light in natural waters varies with the wavelength (" the " extinction coefficient for a water is a common misapprehension), its measurement is best made in relation to narrow spectral bands isolated by colour filters. A useful series of glass filters is manufactured by Schott und Gen. (Jena), and for these much experience from Continental work is available (e.g., 289, 303, 585, 586, 587). For some colours, combination of two filters may be valuable. Although such glass colour filters transmit a fairly wide spectral band, the effective width is narrowed when combined with a selenium rectifier cell (for whose spectral response see 492) and used beneath a layer of water which also acts as a colour filter. Allowing for these modifications, it is possible to estimate an approximate " extinction midpoint " on the scale of wavelength for measurements with each cell-filter combination in water of a given type. Examples are provided by 289, 303,

304, 585, 586, 651, 654; for some Schott filters commonly used, a convenient table is available (303). The spectral region 400–700 mμ is readily covered, and the total radiant energy therein—available for photosynthesis (511, pp. 1152–1158)—can be found as fractions of the surface intensity for various depths. The calculation is possible by using either an approximate summation procedure (283, 651, 654, 656) or a fuller integration (see 650, p. 105). Measurements in the near ultraviolet are also possible with the usual type of photometer, but for shorter wavelengths (strongly absorbed by glass) special equipment (289, 302) is needed. Penetration of infra-red radiation has rarely been measured specifically, as it is less active physiologically; it cannot be measured by the selenium rectifier cell, and it is strongly absorbed by water. When a number of filters are used, much time is saved if they can be interchanged without bringing the photometer to the surface, and several devices to accomplish this have been described (64, 586, 683, 757).

It is not possible to assign very accurate working values to the "extinction midpoints" of photocell-filter combinations mentioned above, owing to the fairly wide spectral bands transmitted and especially (303) to the shift in the midpoints with depth. The latter is the result of the filtering effect of the water which is increasingly felt with increasing depth. Improved methods are desirable here. Much more selective transmission is possible with interference filters, but additional difficulties attend their use (see, however, 592). In consequence detailed examination of absorption spectra of natural waters has usually involved laboratory measurements with spectrophotometers, Pulfrich photometer or other instruments. Certain scattering effects (35, 36) usually prevent direct application of the results to calculating a light gradient in nature. However, valuable knowledge has been obtained of the properties of pure water useful as a reference point (cf. 3; 112, fig. 9), modifications due to various fractions in natural waters (e.g., 116, 124, 279), and the very variable and relatively little known behaviour for ultra-violet radiation (289 and references therein; 358, 415). Information on the numbers and types of particles present has also been derived from measurements of scattering (94a, 290, 291a) and absorption (93, 94).

Many measurements of light penetration have been—and con-

tinue to be—made with the selenium cell and opal glass without filters. Results are commonly expressed as a percentage of the surface intensity; actually the intensity just below the surface is often a preferable reference, as reflection from the water surface (controlled by other factors) is thereby excluded. "The" extinction coefficient may be deduced if, as often happens, the cell response declines exponentially with depth. Such a coefficient is neither unique nor readily interpreted, except that it relates to average behaviour in a broad spectral region delimited by the maximum sensitivity of the cell and the minimum extinction (over the spectrum) in the water. In many inland waters these two determinants coincide in the yellow-green spectral region, so that the coefficient measured is a somewhat high approximation to the minimum vertical extinction coefficient over the visible spectrum. The latter can be better determined from measurements in spectral bands isolated by colour filters, and is probably the best single optical characteristic of a water (651, 655). An alternative characteristic, the mean extinction coefficient over the visible spectrum (289, 292), is a more abstract quantity and one less easily determined.

Measurement of the intensity of light incident on a water surface may be required in three connexions. First, measurement of the underwater gradient of light intensity will be distorted if the surface intensity changes appreciably (e.g., with clouding) during the operation. Such changes can be measured, and compensated for, by readings of surface illumination from a deck photometer (29), used with colour filters if these are being employed in the underwater measurements. A neutral filter is also usually needed for reasons given earlier. The underwater and deck photometers can be conveniently connected with the galvanometer through a reversing key. A second application of measurements of the surface-incident intensity consists in their combination with data on the underwater light gradient to calculate absolute intensities at various depths (e.g., 148, 283, 399, 651, 654, 656). Surface loss by reflection and upward scattering (19, 132, 587) may be allowed for by a factor which is usually uncertain but fairly small (commonly about 10% for average daily conditions: cf. 283, 654). Underwater intensities must be expressed in units of energy flux (e.g., kiloergs/cm^2. sec. or cal./cm^2. min.) and not of illumina-

tion (e.g., lux or foot-candles) as spectral modification occurs with increasing depth. Filters designed to simulate such modification in seawater are described in 291. With suitable calibration, readings from selenium rectifier cells can be used to calculate intensities of incident radiation in energy units for various spectral regions (293, 488, 656). Third, a knowledge of daily and seasonal changes of incident light may be of great ecological value. Such information is most fully provided by the continuous recording of a photo-current (e.g., 30, 31, 416a, 750). Counters recording illumination—or radiation—time integrals may also be useful (e.g., 66, 162) but alone supply less information. The light-sensitive element to be used must be reasonably stable over long periods, and a thermopile—recording radiation directly in energy units—is perhaps the best choice, although infra-red radiation contributes approximately half the response unless eliminated by special filters. Emission photo-electric cells, sensitive only in limited regions of the visible spectrum, have also been used (e.g., 30, 31, 34, 66), but the less stable selenium rectifier cell presents greater difficulties because of the non-linear response and fatigue effects. These instruments are discussed in a valuable recent review of the sources and measurement of radiant energy (762a). Calibration is preferably made by comparison with well tested standards or sub-standards in national institutions, but an approximate reference of value to ecologists is provided by the E_s unit of Aurén, the intensity on a horizontal surface for a solar elevation of 45° with a clear sky. This intensity is, approximately, 80 kilolux or 320 kiloerg/cm^2. sec. of radiation in the spectral region between 400 and 700 mμ utilised in photosynthesis (28, 34, 656); it corresponds to an intensity of total radiation of approximately 1.0 cal./cm^2. min. (or 1 langley/min.) (38, 39, 40, 384, 620). Other sources of data and references on solar radiation include 21, 148, 614. Continuous recording of underwater intensities from submerged photocells has been rarely attempted (356, 584, 750, 359, fig. 25).

Several measures of "transparency", related to underwater light penetration but strongly influenced by scattering, include the depth at which a white disc (Secchi disc) just ceases to be visible (733) and the percentage transmission of light through a tube containing a water sample. Various designs of transparency meter, suitable for use in situ in lake and sea water have been described

(29, 289, 304, 478, 480, 582, 586, 602, 749) and others are designed for laboratory use.

Measurements of transparency are often useful in characterizing a water, and the meters can serve to detect stratification of optical properties more readily than is possible with the normal underwater photometer (cf. 700, 721). Some good examples obtained from use of the transparency meter in lakes are described in 572, 582, 749. Such measurements cannot normally give reliable quantitative information about the vertical gradient of light intensity in nature (see, however, 304 for a modification of the transparency meter). Scattering meters for underwater use are described in 477, 478, 480, 592. Secchi disc readings have been occasionally used to deduce vertical extinction coefficients (e.g., 148, 283, 312, 319, 543, 770) and euphotic zone depths (cf. 702, fig. 1), but in general such calculations are uncertain, particularly when clear and turbid waters are compared (424).

CHEMICAL ENVIRONMENT AND NUTRIENT SUPPLY

The chemical environment which the limnologist may have to explore is a dilute aqueous solution of various ions and molecules, concerning the estimation of which a very extensive specialised literature exists. The bulk of this is outside the scope of this review, which can give only a general outline and refer particularly to some useful recent methods. Valuable general works of reference in this branch of analytical chemistry include 17, 412, 660, 735, and for reviews of chemical methods in marine biology, 49, 240. Many sensitive methods depend on colorimetric estimations, for which 615 gives general advice. Important recent advances have resulted from the introduction of the flame photometer, spectrophotometer, and ion exchange resins; some specific applications are mentioned below. Apart from these, new analytical methods appear in large numbers every year, but the non-specialist is wise to use well-tested methods (17, 615) and enlist the help of an analytical chemist whenever possible. Calibration values given for methods and instruments (including coloured-glass standards, if used) should be checked, together with "blank" errors, by tests on standard or loaded solutions.

If water samples are required from different depths, various water-bottles operated by a messenger (e.g., the Ruttner and

Friedinger samplers) are available. Other samplers have been designed for investigating microstratification (131, 752). In determinations of oxygen and carbon dioxide, contact between the sample and the air must clearly be avoided as far as possible; however, flushing a relatively large quantity of water through the sample container is usually effective. A portable syringe pipette can be used for oxygen (175, 753). Other dangers of contamination or removal by adsorption may result from the use of containers or filters not chemically inert, and from gases, particularly ammonia, or dust in the laboratory.

The chief constituents of interest here may be divided, for convenience, into four groups. First there are properties useful as general characteristics of the water, including electrical conductivity, total salt or ion concentration, alkalinity due to bicarbonate and carbonate (S.B.V. of many Continental authors), pH (which alters with carbon dioxide content, as described below), turbidity and colour. The first three quantities are often closely interrelated, and all of those cited can be readily estimated by standard methods. A useful application of ion-exchange columns to the determination of total cations, and of anions of strong and weak acids, is described in 392, 393. The significance of redox potentials in lake waters and muds, and their measurement, is discussed in 14, 267, 427.

Second, there are the contents of dissolved gases, of which oxygen and carbon dioxide are the most significant. The determination of oxygen for limnological purposes, and methods for eliminating interference by reducing substances, have been recently reviewed (457; 278a also gives useful details). Percentage saturation values for oxygen, and their ready estimation, using nomograms or slide rules, are discussed in 430. Direct determination of carbon dioxide by titration with carbonate is more troublesome, but an indirect calculation from pH and alkalinity can often be applied if free acids, other than carbonic acid, are absent (144, 145, 422 give convenient nomograms). Evidence of some appreciable deviations from the commonly accepted form of interrelation has been given (701) but requires further support.

Much interest has centred on some members of the third category, which contains the ions involved in plant nutrition. These include calcium, potassium, magnesium, nitrate, phosphate, am-

monium, sulphate and iron. Bicarbonate should probably be included as an available source of carbon dioxide for many plants (literature on this debated question is reviewed in 511, pp. 888–891; 512, pp. 1886–1892; 570). Silicon is required by various algae, particularly diatoms (for silicon-sources and conditions of uptake see 297, 298, 299, 300, 361, 362, 363, 377). Mullin and Riley (433) describe a recent method for its analysis. However, the chemistry of silicon in natural waters is not clearly understood (see 123 and 243 for reviews of relevant properties). "Dissolved silica" usually implies that part estimated by the standard molybdate method (see, e.g., 105a, 362). This may be either silicic acid and colloidal aggregates thereof of low molecular weight, or orthosilicates (see 433, p. 165; 105a). A new and useful method for determining ammonium is given in 547. Long-established methods exist for phosphate (Atkins-Dénigès method; see also 95, 499) and nitrate (phenol disulphonic acid; also reduced strychnine and diphenylbenzidine treatments). These two ions have received more attention in relation to plant growth than any others, but a more sensitive method is needed for determining very low phosphate concentrations (< 1 μg. $PO_4 \cdot P$/l.), not uncommon in natural waters. Recent methods of titration with a complexing agent (versenate) have greatly simplified the estimation of calcium and magnesium (252), and ion exchange columns enable sulphate and chloride (and other ions mentioned earlier) to be rapidly determined (392, 393). The flame photometer (references in 589) also provides a rapid method for sodium and potassium, and the spectrograph is used for various trace elements. Study of the latter in relation to plant growth in fresh-waters has been largely neglected.

In a fourth class are dissolved organic substances (reviewed in 689b), whose total concentration often exceeds that of organic matter in the plankton. Noteworthy compounds included are free growth substances, such as thiamin, and especially cobalamins (vitamin B_{12} complex), now known to be required by a number of algae (141, 500, 502). Examples of the microbiological assay of these substances in natural waters, with reference to possible algal requirements, are given in 91, 125, 139, 265, 268, 364, 503, 621a, 689b. Other organic substances, such as "humus" or polypeptides (171), may be active, due to complexing or other properties.

The best practical index of total organic substances is carbon content, determined by dry or wet combustion (65), but the capacity to reduce a hot permanganate solution under certain arbitrary conditions has been widely used as a relative measure. The latter has some disadvantages, and an alternative method, using diammonium hexanitrato-cerate and titration with oxalate, has been proposed (609).

Clearly an investigation of the growth of natural populations in relation to nutrients cannot include an estimation of all types of the latter present; consequently some selection is inevitable. For any natural water it is possible to omit a number of nutrients as unlikely to reach limiting concentrations; common examples are potassium, calcium, magnesium and sulphate. However, the latter is thought to be a limiting nutrient in some African inland waters (55, 159). An obvious yet relatively neglected approach is from a comparison of amounts of elements fixed in the algal crop with those available in the water. It seems to be often forgotten that a doubling of cells by a single division throughout a population will be likely to utilise an amount of a nutrient comparable to that incorporated in all previous growth, so that a limiting concentration may be difficult to define (cf. 298 for silicon). However, complicating effects may arise from the utilisation of material present in the cells in excess of immediate requirements. The relations of some populations of the diatom *Asterionella* (species *A. formosa* and *A. japonica*) to inorganic phosphorus provide good examples (217, 391); others are described in 195 and 215. The latter work is notable in using a radioactive tracer to follow the movements of small quantities of iron (cf. 520 for phosphorus). The available forms of iron in natural waters remain obscure in view of conflicting evidence (see 381); Rodhe (550) has described the application of a method of biological assay. Further discussion of the nutrition of phytoplankton and related unicellular algae can be found in various reviews (169, 170, 240, 270, 271, 314, 316, 380, 381, 389, 435, 503).

Methods have been described for the determination *in situ* of some properties and constituents of natural waters mentioned above; these include dissolved oxygen (16, 176, 308, 398, 457) and electrical conductivity (149). The circulation of elements *in situ*, including uptake by phytoplankton, has been followed by ad-

dition of radioactive tracers, particularly ^{32}P (244, 245 and references therein, 266, 526, 713). Application of nutrients on a larger scale, especially in commercial fertilisation of fish-ponds, is described in a recent review with an extensive bibliography (431).

PHOTOSYNTHESIS

Photosynthesis is well known as a key process in natural economy, and its measurement may aid the resolution of many limnological problems. A standard modern exposition is given in 510, 511, 512, which include much data (mostly of kinetics) of ecological interest; a shorter review is provided in 254. References to laboratory methods of measurement are given in these works and are not considered in the discussion below, which deals with measurements under field conditions. It is unfortunate that few laboratory studies have been made with ecologically important species of algae, or with reference to conditions in natural waters (see, however, 46, 534, 576, 579, 652, 694). Nevertheless, means of applying laboratory data to field conditions are included here, as is also information from " natural experiments " provided by diurnal changes resulting from photosynthesis in open water.

Almost all measurements using aquatic plants in natural water bodies have been based upon determination of oxygen production and consumption in suspended " light " and " dark " bottles. This method derives from pioneer experiments (295) with a terrestrial moss in Oslo fjord, then applied in later experiments with large seaweeds (181), and, with marine plankton algae, by Pütter (507, 508) and especially Gaarder and Gran (179) and Marshall and Orr (408). Essentially the method consists of suspending small bottles (usually paired) containing the plant material at various depths over the euphotic zone, and measuring the production and consumption of oxygen in them by the Winkler estimation. From knowledge of oxygen consumption in darkened bottles, and observed changes of oxygen in " light " (clear) bottles (= apparent photosynthesis), the real or gross photosynthetic changes are calculated. Shading from any support, e.g., a buoy, should obviously be avoided, and a construction of two floats connected by a framework is useful in this respect (376, 408, 654). Special arrangements for supporting the bottles have been described (283, 359, 408, 454, 704). Experiments in freshwaters with a wide variety

of algae, mainly planktonic and either cultured or from natural collections, are described by many authors (e.g., 282 (using marine diatoms), 52, 120, 127, 148, 257, 308, 309, 348, 360, 372, 395, 399, 400, 401, 442, 531, 596, 597, 632, 651, 652, 654, 655, 656, 704, 705, 706, 710, 721, 722). For a similar method for measuring the photosynthesis of epiphytes on the stems of reeds in situ see 24. A modification, in which the measurement of oxygen changes is replaced by that of carbon dioxide changes (deduced from pH changes and the alkalinity: see p. 501) has been used (278, 395, 694, 698, 699, 701, 702). Although this method is often more convenient, the accuracy attainable varies with the alkalinity of the water (cf. 701) and is probably usually less (in our view: but see 701) than that of the normal Winkler estimation of oxygen (about 0.05 mg./l. or 0.0015 m. mol./l.). In comparisons of results based upon oxygen and carbon dioxide, possible deviations of the photosynthetic quotient from unity should be considered (values are discussed in 577; cf. also 456). The limnologist can also find useful information in the later marine studies (15, 111, 117, 258, 283, 409, 482, 532, 533, 557, 623, 625, 629) and work (discussed later) using radioactive carbon (C^{14}).

Despite the frequent use of this field method of measuring photosynthesis, a detailed study of its limitations is lacking and badly needed (see, however, 283, 400, 654). Errors may arise from the use of cells in unstirred suspensions, and from the growth and utilisation of nutrients (particularly carbon dioxide) by the algae, and growth and respiration of bacteria (favoured by the glass surfaces: p. 526) during long exposures. In addition the photosynthesising cells are maintained at a single point in the underwater light gradient as opposed to their freer circulation in nature. For reasons evident from the above, it is best to avoid exposures of more than five hours and to use the shortest exposures and lowest concentrations of plant material compatible with the accuracy of the determinations of photosynthetic changes. Absorption and reflection of visible radiation (utilised in photosynthesis) by the glass walls of bottles is probably of secondary importance—the shape of the bottles does not appear to be critical (283, 400)—but absorption by the glass in the ultra-violet may reduce damaging action from this form of radiation (cf. 203, p. 415; 204). The latter point requires more investigation (see, however, 408, 685) in re-

lation to the partial inhibition of photosynthesis often recorded near the water surface. The object of these experiments with phytoplankton may be the illustration of various special relationships (e.g., between photosynthetic rate and depth or light intensity) or the estimation of the total photosynthetic production beneath unit area of surface. Most detailed investigations in the first category (283, 408, 654) have used cultured material as being more readily standardised and available than natural collections. Comparison of the behaviour of natural and cultured populations of a species (654) has been rarely attempted, although of great interest. In the second type of investigation, of areal productivity, the plankton samples have been commonly taken from the same depths at which they are later exposed, so as to simulate natural conditions more closely; dark bottles at each depth are then also essential. Such an arrangement is necessary if the phytoplankton is markedly stratified, but the results are usually less easily interpreted than those from experiments with homogeneous material (cf. 630, fig. 5).

In many, probably most, natural waters the photosynthetic rates per unit volume are too small for accurate measurement unless exposures of 12 hours or more are used, and such long exposures, as noted above, are best avoided. To overcome this difficulty, a much more sensitive method of measuring photosynthesis was introduced by Steemann Nielsen (630, 631, 634), involving addition of the radioactive isotope C^{14} (as bicarbonate or carbonate) to the medium and its subsequent estimation when fixed in cells after the exposure. Troshin (674) also describes stages in the procedure. Discrimination against this isotope, and effects due to the re-utilization of carbon dioxide from respiration, must be considered (541, 575, 630, 635). Large differences were found for some marine areas, notably the Sargasso Sea, between estimates of phytosynthetic production obtained from determinations of oxygen change made by the Winkler method and from carbon fixation based on the C^{14} method. In an ensuing controversy (reviewed in 577) various explanations of the discrepancy were suggested, including seasonal changes in plankton populations (541), interference in the oxygen changes due to bacterial growth and respiration sensitive to ultra-violet and other radiation (630: but see 685) or antibiotics produced by the algae (633), and relatively high respira-

tion losses by algae when starved of nutrients (575; cf. 636). Results from direct comparisons of the two methods have been used to support different explanations (575, 631, 685). However, discrepant estimates were not found with more densely populated coastal waters (630, 631, 685). The method involving C^{14} has been recently introduced into limnology (349, 454, 551, 552a, 722), but at the time of writing few results are published.

Much work on photosynthesis in natural waters has been directed to the determination of the compensation depth (and in fewer cases the compensation intensity) at which photosynthesis and respiration are equal. These records are mostly of limited value, as the " respiration " has usually included a contribution of unknown magnitude from bacteria and zooplankton organisms present. In a more profitable field, attempts have been made to relate the photosynthetic rates observed in lake or sea waters with the controlling light intensities (283, 399, 400, 401, 651, 654, 656) as opposed to relative fractions of the surface illumination. The latter are generally more limited in value (cf. 71), particularly when measured by the selenium cell without filters, although the " 1% depth "—at which the intensity is 1% of that at the surface—is often taken as approximating the lower limit of the photosynthetic zone. A scale of " optical depth ", based upon the minimum vertical extinction coefficient (p. 498), has been proposed as a more useful measure (655). The relation with intensity may enable an estimate of the variation of photosynthetic rate with depth and time to be obtained for situations not directly covered by experimental data; examples are provided in 148, 399, 651, 652, 655, 657. Data from laboratory experiments may be used here (see also 576). Very limited information can be extracted from direct comparison of photosynthetic rates and photocell readings (e.g., 395, 701), but use of the latter to deduce absolute light intensities is discussed in 292, 359. Attempts to estimate the photosynthetic production beneath unit area from a relatively small number of variables, some of which can be found from laboratory experiments, are described in 535, 576, 630, 631, 653, 655, 656, 701, 702.

The photosynthesis of aquatic macrophytes has also been frequently investigated by determinations of oxygen production or carbon dioxide utilisation in suspended bottles. A modification, in which changes of electrical conductivity were used to measure

photosynthetic changes, is described in 560, 567. There is a considerable literature relating to seaweeds. Limnological examples include 53, 68, 127, 256, 394, 417, 418, 441, 558, 559, 560, 561, 596, 641, 768, 769. With macrophytes, increased difficulties arise in standardizing samples and from limitations imposed by the diffusion of carbon dioxide to relatively massive photosynthetic organs in unstirred media (154, 197, 203).

A relatively neglected source of information on photosynthesis in nature is provided by diurnal changes of the oxygen and carbon dioxide content in open water, caused by photosynthesis in the discontinuous natural illumination. Methods for using such changes in estimating photosynthetic production beneath unit area are discussed in 455, 656, 707, 708, 711.

QUANTITATIVE ESTIMATION OF PLANT MATERIAL

It is generally recognized that there is no one measure of the quantity of living matter suitable for universal use, but that various measures, occasionally very specialised, are of value in limited spheres. The problem of choice is particularly acute in studies of plant growth, and is widely discussed in textbooks of plant physiology. A survey is given below of methods with application in limnology. These include measurement of total weight, of constituents characteristic of plant material that can be separated (e.g., chlorophyll) or estimated in mixtures (e.g., carbon, silicon, nitrogen, protein), of associated optical properties, and estimates from the counting of morphological units (e.g., cell numbers, cell volume).

WEIGHT

The fresh weight of plant material is often the simplest measure of biomass to obtain, and is applicable where rapid rough estimates are required. It is rarely suited for aquatic plants, owing to their very variable water content, and is generally replaced by the " dry weight " obtained by heating a sample at about 105° C. until constant weight is obtained. Estimations of other components (e.g., ash, proteins, carbohydrates, nitrogen content) are commonly related to this (63, 338). A compilation of marine organisms is given in 715, and a similar work for freshwaters would be most valuable (see, however, 747, tables 30–32). Dry weight is a con-

venient measure of a standing crop (338), particularly if a series of estimates can be obtained for a population of similar constituents over a period of time (cf. 425, fig. 1; 452). Great accuracy is usually impracticable for natural samples, particularly of phytoplankton, owing to the difficulty of collection without an admixture of such foreign matter as animals, bacteria, organic remains and inorganic clay or silt. If such matter is neglected, misleading impressions may result, as in the overemphasis of nannoplankton (63). Usually algae vary so much in size and density that they cannot be separated from other suspended matter, although many buoyant planktonic Myxophyceae are exceptions.

Other disadvantages of dry weight include the frequent impossibility of distinguishing between various species in a mixture; difficulties in quantitatively separating a sufficient quantity from a volume of water by processes that do not disrupt the cells (centrifuging and ultra-filtration are discussed under counting methods); and bias caused by heavy cell products of limited distribution (e.g., silica in diatoms). The latter difficulty can often be reduced considerably by obtaining the ash-free dry weight, also called " loss on ignition " or " organic matter ". For these reasons dry weight is usually employed in individual analyses rather than as a method for following the seasonal growth of natural populations.

CELL CONSTITUENTS

Estimation of cell constituents, either elements or organic compounds, may provide a more specific measure of living material than is available from total dry or ash-free weight. Knowledge of constituents may also be needed for comparison with quantities available in the outside medium (e.g., phosphorus: 391), but only the more constant constituents are discussed below.

CARBON is one of the least variable constituents, being usually $53 \pm 5\%$ of the ash-free dry weight (" organic matter ") in plant material. Analyses for small algae include 63, 92, 318, 447, F. J. Mackereth unpubl. The percentage of carbon does vary under exceptional conditions, notably when photosynthesis continues under conditions of nitrogen deficiency. However, values above 60% and under 40% of the ash-free dry weight seem to be so ex-

ceptional that they rarely arise in natural populations. The errors of estimation in most methods of collecting and estimating natural (and often cultured) populations exceed ± 10%, and the population changes under investigation are usually much larger than this. The carbon content of a population is also particularly important in relation to experimental studies of areal productivity (p. 532) estimated from carbon assimilation. However, few analyses have been made; the earlier methods and results are discussed in 343, 344, 345, 723. Additional micro-methods have now been developed (56, 172, 273, 274, 313), and analyses are needed for as wide a range of algae as possible under various environmental conditions. However, use of carbon for routine census of natural populations would require a more rapid, accurate micro-method than is at present available and would not exclude extraneous organic materials.

SILICON is present in appreciable amounts in only a few groups of freshwater plants, of which the diatoms are the most important and best known. There appear to be no analytical data for other silicified algae, such as certain chrysomonads and silicoflagellates, and the analyses for diatoms include few freshwater benthic species. In a number of diatoms, including some important plankton species, the content per cell (of a given size) probably varies but slightly, even when silicon is a limiting nutrient (5, 153, 377). Consequently silicon estimations can be applied to estimating a crop, either by direct analysis of the latter, or from the decrease of dissolved silicon in the water during diatom growth (see p. 525). There are marked exceptions to this constancy of silicon content (76, 299), the cells of some species being able to grow when unsilicified (44, 247, 755, 756)—the data for "*Nitzschia closterium* f. *minutissima*" (758) no longer apply, since this alga is probably not a diatom (see p. 492). However, the variability is probably overemphasized in 299, particularly for freshwater diatoms.

The position for silicon as a cell-wall constituent differs from that of other constituents in that it is the amount per unit surface area of cell which is constant within small and, as yet, not clearly defined limits. It follows that the amount per cell will change during the growth of a population, as diatoms generally decrease in size with each cell division (see below). This may not usually be an important practical difficulty in estimations, since the rate of de-

crease in size is often very small (178, p. 617) and the formation of auxospores in parts of the populations at varying times tends to mask the decrease from cell division. Measurements in a natural population generally show that the distribution of cell size is bi- or tri-modal (42, 130, 600, 738, 740, 741). The amount of silicon per cell varies markedly from species to species (153, tables 2, 3), so that in mixed populations the amount of silicon removed from the water is not referable to the number of cells produced, but it may still be used as a criterion of diatom production as a whole. A total silica budget is necessary, since the concentrations in the inflows may vary and it is not certain that some changes in the silicon concentrations of some freshwaters may not arise from polymerisation (p. 502 and discussion in 381); however, in a year's study of Windermere, no such change was detected (unpublished observations).

With epiphytic diatoms, the silica content of marine *Cladophora* tufts has been used for estimating the production of associated *Grammatophora marina* (5), and general application of the method is suggested for the estimation of diatoms on other substrata, including rocks. There are, however, great practical difficulties, and in the example quoted the situation was unusually fortunate. It is rarely, if ever, possible to remove a diatom crop from rocks or stones without including other siliceous matter. Many freshwater plants, e.g., reeds, contain appreciable quantities of silica, and an algal mat is likely to include particles of silt. Even in the case quoted no analyses were made to check the absence of other siliceous matter in the *Cladophora* tufts after washing, though the results suggest that the amount was negligible.

NITROGEN content, usually determined by a micro-Kjeldahl procedure, is a familiar measure of material in plant physiology and has been used in some studies of plankton periodicity (e.g., 525, fig. 3). It is generally closely related to protein content (a common conversion factor is protein = 6.25 organic N, by weight). Recently direct estimation of protein, using the biuret reaction, has been applied to the estimation of plankton crops (339, 340, 341a, 458, 459). However, the nitrogen and protein content, and also the C/N ratio, of algae are known to vary considerably, particularly when photosynthesis continues in the absence of an available nitrogen source, so that the results may not reflect small changes

in the total crop weight. Moreover, different groups of algae tend to differ in nitrogen content as a fraction of the total dry and ash-free dry weight, Myxophyceae generally showing the highest value, usually about 8% of the dry weight (377, p. 21; 715).

CHLOROPHYLL, with or without other carotenoid pigments, has been used extensively in limnology and oceanography for the estimation of standing crops in nature (e.g., 32, 33, 122, 196, 201, 202, 233, 234, 241, 286, 308, 332, 333, 336, 527, 528, 530, 531, 532, 533, 537, 544, 622, 627, 676, 712) of growth in cultures (534, 550, 642, 644), and for determining photosynthetic rates (146, 198, 199, 201, 399, 577, fig. 2; 552a). Whatever pigment or groups of pigments are used, the method is basically the same: extraction by an organic solvent, such as acetone, and photometric determination of the depth of colour or fluorescence (311) of the solution. The amount can then be found by reference to a standard calibration curve, or nomograph (143), for which commercial chlorophyll preparations are often unsuitable (cf. 185, pp. 741–742; 399, p. 366; 689b, p. 51). This photometric method of estimating plant pigments in general and methods for their estimation have recently been reviewed (217a, 613a). An advantage for estimating algal densities is the rapidity with which estimations can be made; furthermore, all photosynthetic plants contain chlorophyll *a*. In view of the importance of this method, it is unfortunate that it may be open to serious errors (e.g., 73, 184, 185, 186, 406, 676). Most algae have two chlorophylls; one chlorophyll, common in various brown-coloured groups, such as diatoms and dinoflagellates, has been ignored until recently (521). There are, of course, also all the other major photosynthetic pigments, and any or all may vary in kind or amount and ease of extraction, not only from class to class but even from species to species (218, p. 157), so that neither an estimate of chlorophyll nor one of total pigment may give a reasonably accurate picture of the changes in biomass (59, 676). Though chlorophyll decomposes rapidly after death, the residue may still show the typical fluorescence and yield greenish extracts to the solvents used. Thus estimations may include dead plant cells and the excrement of herbivores (151, 207, 218, 341, 689c), and relatively "inactive chlorophyll" has been recorded several times from the hypolimnia of lakes (cf. 201, 332, 399, 689b). Under certain conditions such degradation products may last for a very

long time, appearing in the interglacial and post-glacial deposits of lakes, in oil wells and asphalt, and the same may be true of some other photosynthetic pigments (e.g., 79, 513, 686, 689, 689a, b, c). It is very unlikely that this preservation is ever a cause of error in plankton investigations in the upper layers of lakes or seas, for it seems to be possible only when decomposition occurs under anaerobic conditions leading to the formation of sapropel.

The amount of chlorophyll found will depend on the pigment standard adopted. Use of the Harvey unit, with acetone as a solvent, has been criticised as including carotenoids which may be present in many animals (218). A standard unit based on the absorption spectrum of chlorophyll *a* is now preferred (218, 337, 528, 577). However, carotenoids were found preferable as an index of growth for a blue-green alga (320). The method by which the samples are collected and the organisms concentrated to obtain sufficient pigment for extraction is of vital importance, and in recent years membranes (see p. 546 and 126) have come into use. If the filter used has a pore diameter much above one μ, small algae will be lost, while centrifuging or the use of some kinds of filtering material, particularly if filtration is under pressure, may destroy delicate cells (296, p. 438).

The pigment extraction method is most suitable where single species (e.g., in cultures) or populations composed of related forms predominate, as, for example, the diatom populations which are so commonly predominant in the vernal plankton pulse. This is particularly so if several pigments are estimated, which is most readily done by spectrophotometric measurements at several wavelengths (143, 521, 522). However, it is well known that the amount of chlorophyll *a* and other pigments can vary in relation to environmental conditions such as the intensity and spectral composition of light and nutrient (e.g., N, Mg, Fe) supply. In *Chlorella* the chlorophyll content may vary from 0.03–6% of the dry weight (1, 92), and it is possible that other species may show as much variation (92), although *Chlorella* alone has been investigated thoroughly (for *Scenedesmus,* see 23). Variation induced in the chlorophyll content may not be accompanied by corresponding changes in maximum photosynthetic rates (e.g., 225, 512, chapter 32; 436) so that a ratio connecting the two (assimilation number, "A.Z.") has limitations in limnological (198, 199, 201,

209, 399) and other applications. Almost everyone who has made seasonal observations on natural populations of algae must have noticed how the cells often become pale, particularly in sunny weather, and may have inferred from this that there has been a reduction in the amount of pigment. Variation of colour with depth is also not infrequent (e.g., 407, 505). Indeed, if cells are subjected to ultra-violet light, chlorophyll is destroyed (204 gives examples for phytoplankton). However, the apparent coloration is also affected by starch or oil reserves and by changes in plastid shape. Comparison of the chlorophyll content of natural and cultured populations of a species would be particularly interesting; in some observations on *Asterionella* the content of a natural population appeared much the lower (654).

In general it seems that a far more critical approach to the use of chlorophyll as a measure of production should prevail. In particular, more studies are needed to determine the accuracy of the method under diverse conditions and with a wide range of plants. There seems little doubt that this is a valuable method if its limitations are understood (cf. 531), and the view has been advanced that there is no indication that it is inferior to the other methods used in investigations on plankton (545, see also 151, 218).

COUNTING

Counting has three great advantages over other methods. The first is that the algae are observed each time a count is made so that any changes in the appearance, size, shape or aggregation of the cells are seen. These may provide valuable information, particularly in ecological studies. There are occasions when estimates distinguishing dead or dying cells are valuable, for which there is no other method (fluorescent stains may help here—see p. 547). The second is that estimations can be made of populations whose density is so small that again at present no other method can be used with equal accuracy. Third, counting enables small numbers of specific algae to be distinguished from others and from unwanted debris, although the latter may often limit the sensitivity of the estimation. Even when using cultures with uniform cell suspensions, counting may be the best method if low densities are involved. An alleged disadvantage of counting, frequently cited, is that it must be very time-consuming if sufficiently accurate re-

sults are to be obtained. This is generally not the case (259, 383). A more significant disadvantage is that the morphological units recorded often contain very different quantities of material, particularly when different species are included. Consequently overall estimates of mixed populations in such units as "individuals per litre" may often be misleading, e.g., in graphs of periodicity. Such estimates are, however, common in the literature, and frequently the nature of the "individuals" (e.g., cells, filaments, colonies) is not explained.

Effects arising from the varying size of the "individual" can be reduced by taking its volume or area into account. This can be done crudely by using "weighted numbers" (e.g., 105, 675), or by measuring the area or volume of the species involved under the microscope and expressing total numbers as a volume or area of cells (745). Area is generally the less useful measure for three-dimensional objects (cf., however, 106, pp. 292–293, for *Pediastrum*), and its special utility for phytoplankton in studies of photosynthesis (507, 508) and waterworks filtration problems (460) may be doubted. Cell volume has been more usefully applied in several fields, including the study and comparison of photosynthetic rates (395, 656, 694, 698, 699, 701) and of seasonal changes in plankton populations (130, 155, 260, 370, 565, 695, 698, 747). It deserves more attention than hitherto as a means of combining the selectivity of cell counts with units useful in general (e.g., regional) comparisons. An application in studies of the relative importance of nannoplankton (cf. 27, 130, 552) would be especially welcome. Although in many genera (e.g., *Staurastrum*) cell volume would necessarily be very approximate, even such results may often be of value; plasticine models of algal cells have been used (565) to facilitate computation. Another and distinct measure of volume has often been applied in physiological studies to the overall volume of masses of densely compacted (e.g., centrifuged) cultured material. This measure has also been employed in general limnology (e.g., 11, 326) but is usually unsuitable, as quantities of material are often very small and mixed with unwanted detritus; however, Berardi (58) describes a sensitive instrument for its measurement. Measurements in units of length have been used for filamentous algae and are particularly suitable for those (such as many *Oscillatoria* spp.) with small variations in width and a

cylindrical form. It is then easy to convert these lengths into volume or cell numbers. A square measuring grid in the microscope is helpful (461).

Counts are usually made in special chambers (cells), using either a normal or inverted microscope (378, 383, 445, 678, 679, 680, 681, 682). In the former case a number of chambers have been devised, such as the well-known haemocytometer, the Sedgewick-Rafter cells and variants thereof (106, 206, 327, 603, 747), and the Palmer and Maloney (463) and Petrov-Hausser (130) chambers. Haemocytometers are not very suitable for algae in general (383) but have been found satisfactory for some species in unialgal culture, notably *Chlorella* (471, 490, 520, 760), and some species of the nannoplankton (438). Utermöhl, besides devising the technique utilising an inverted microscope, has investigated most of the other techniques (678–682). With suitable chambers and additions to its basic structure, an inverted microscope can be used for counts under low or high powers of magnification (680, 682). All these methods involve sedimentation of the algae on to the floor of the counting chamber so that it is not necessary to focus up and down through a column of liquid for every field of view. The technique employing the inverted microscope is particularly valuable, as algae can be sedimented from a wide range of water volumes. The more fine detritus is present the less the volume of water from which sedimentation is possible if some of the algae are not to be masked (679). Thus in certain work (656, 657) maximum volumes of 150 ml. were usable for Lake Victoria water but often only two ml. for White Nile water. In practice it is very rare that the turbidity of a water is such that algal counts cannot be made. It would be of help if the counting chamber could be moved mechanically as can be done with some zooplankton counters (e.g., 728); one hand is then free for focussing and the other for recording the count. The smaller chambers are more suitable for the smaller algae, but in some cases at least (e.g., the normal haemocytometer) they will not hold the correct volume of water unless an optically flat coverglass and special pipette are used. Such a coverglass adds so much to the working depth that immersion lenses cannot be used. Even with the best optical conditions it is not certain that all the small algae are seen. Sometimes it is desirable to remove interesting algae from a counting

chamber, and Nielsen (445) describes how this may be done for the sedimentation chambers used with the inverted microscope. The use of membrane filters is discussed on p. 546, but a promising technique for counting appears to be that of Goldberg (summarised in 4), using a membrane ruled into squares. The specimens on the membrane are stained and then cleared so that the organisms can be seen.

In view of the difficulties of counting very small organisms directly, a method commonly used in bacteriology has involved the preparation of dilute cell suspensions and then incubation of samples. Thus a single cell isolated by dilution can be recognised by the growth to which it gives rise. The method raises several difficulties, particularly in the choice of suitable media, and the estimates must be minimal, although useful for checking more direct counting (9, 222, 679). The method was used for soil algae by Bristol-Roach (77, 78); applications to marine nannoplankton are discussed in 9 (cf. also 679, 682) and, with serial dilutions, in 45 and 322. The estimates of crop size from such methods are too small because not all algae will grow in any culture medium yet devised. This is equally true of planktonic bacteria in lakes, which are perhaps even less known than the algae because of over-emphasis on the standard culture techniques of medical and sanitary bacteriology (e.g., see 60, 350, 616).

The statistical significance of much of the data obtained by counting is unknown (for haemocytometers, see 646). Since, in most cases, the sample or portion thereof, in which the organisms are estimated, has been stirred or shaken, they are randomly distributed. They may, however, lose this random distribution in the process of sedimentation and distribution in the counting cell (12, using the method described in 11, 206, 367, 383, 603). The statistical procedures for estimating the probable accuracy of counts of randomly distributed particles can be applied (130, 206, 230, 259, 367, 383). Usually sufficient accuracy can be obtained if about 100 individuals are counted (383); the number should not be less than 15 (259). The method of filling chambers of the Sedgewick-Rafter and Kolkwitz types may lead to errors (206). The aliquots taken from the samples collected are randomised by shaking before being run into the counting chambers, and the process of sub-sampling does not lead to any additional error (383). Thus if all the in-

dividuals in a chamber are counted, upper and lower expectation levels can be determined for any desired level of confidence, usually 95%, from statistical tables (e.g., 161, 472). However, many algal organisms consist of or contain more than one cell, and the number of cells per organism may be very variable and follow diverse distribution patterns. Therefore, similar estimates cannot be applied to the number of cells per unit volume (259, 383), though the less variation there is in this feature, the less the difference from a Poisson distribution. Thus, for *Asterionella,* the errors arising from the variable number of cells per colony are so small, compared to the random errors involved in counting the colonies, that they are rarely important ecologically when one is dealing with cell divisions, that is, changes of 100% (383, see also 206). This is not necessarily the case, however, notably for colonial algae with large numbers of constituent cells (e.g., some Chloro- and Chroococcales). Such "clumped" organisms can be expected to follow the negative binomial distribution, and the degree of contagion can be calculated (67) and a correction factor can be applied (259. We hope we have understood this paper correctly but some parts are far from clear). Unfortunately it will be necessary to calculate this factor for each sample because the distribution pattern of cells per colony or organism varies (206). Usually it is cell number per unit volume which is important in testing comparisons between phytoplankton and environmental factors, but the accuracy needed will vary markedly with the questions posed. This may seem a very obvious consideration but it is often forgotten, so that an unnecessary amount of time and effort is spent in counting. There are cases where quantitative estimates are made on non-random populations. Use of the slide technique (p. 541) for estimating the numbers of benthic algae results in more or less localised growths according to the species concerned, and, as no statistical procedures have been applied to the counts, it is impossible to tell how much greater one estimate of numbers per unit area of slide must be than another for it to represent a significant increase. Another source of error of unknown magnitude is involved in the usual procedure of removing one or, at the most, two slides or groups of slides in a single frame on each occasion of sampling (98, 100). The slide method is undoubtedly of great

value in limnology so that a thorough statistical study of its use for estimating production should be made. Counts of algae living on soft deposits must be very inaccurate (see p. 542), and there is a danger that if the results are expressed numerically, too much importance may be laid upon them. Nevertheless the use of symbols is so subjective that if it is possible to make counts, these are to be preferred.

OPTICAL PROPERTIES

Photometric determination of light absorbed or scattered in passing through unit depth of an algal suspension is of value in investigations on cultured populations (e.g., 106, 229, 272, 550, 618). Monochromatic light should preferably be used. Allowance has to be made for the fact that what is being measured may be affected by variations in the nature and amount of the reserve products, the size or shape of the algae, the pigments or other unknown features, so that a true comparison between one stage of a growth cycle and another, and growth under different nutrient conditions, may be impossible. With the so-called *Nitzschia closterium* f. *minutissima* (= *Phaeodactylum tricornutum*, p. 492), the chief cause of variation in results could be related to the amount of light scattered, the amount absorbed providing a much better relationship with cell numbers, even though the amount of chlorophyll per cell varied (618). Yet, comparisons must be made between cultures in the same " physiological state ", grown in identical lighting conditions and cultured with an adequate supply of iron. The difficulty here is, of course, that the term " physiological state " is not amenable to exact definition (p. 530). Nor is there good agreement between optical density and cell concentration in the post-exponential phases of growth. Finally Spencer (618) emphasizes that his findings may not be applicable to unicellular algae generally.

Using normal *Chlorella* cells and pale ones produced by irradiation, a linear relationship was found between the readings taken with a turbimeter, utilizing the Tyndall scattering effect (335), and the dry weight, irrespective of the pigmentation (135). The method might appear to be rarely of use for natural populations because they are not of sufficient purity, quite apart from the

colour or turbidity of water in which they live. However, the use of measurements *in situ* of selective scattering (cf. p. 500) has been suggested as potentially valuable (540; cf. also 477).

Even with cultures, it is commonly necessary to have cell densities near or above the maximum normally arising in nature. Consequently it may be impossible to determine the growth at the low concentrations of nutrients common in natural waters, particularly in the case of phosphates (618). With large populations and concentrations of nutrients there is a danger that changes in the medium (e.g., pH) may lead to interference through formation of precipitates. These must be removed or allowed for. Sometimes cell aggregates must be broken down in a homogenizer (362). When two or more of these difficulties arise, one may be permitted perhaps to wonder whether counting is not a preferable and simpler procedure. Further, the number of cell generations which can be followed is limited. An optical density permitting accurate photometric determination may be such that the exponential rate of growth of the alga cannot be followed because the growth rate is already limited by the amount of light reaching the cells in the culture. Making allowance for these possible difficulties, the method is of value, particularly by virtue of speed at which a determination can be made. Finally, estimations of large enough growths can be made by eye within $\pm$ 50% accuracy after a little practice in using the material (unpublished observations of the first author). Since a change of 100% in numbers represents only one cell division, this method is of some practical use. Moreover, the eye will often distinguish between turbidities caused by algae and other suspended matter, particularly if a check is made with a hand lens.

OTHER PROPERTIES

Although other reliable properties for estimating growth may exist, they are not evident in past experience. Wet oxidation of algal material by permanganate, with measurement of changes in the latter, has been investigated as a measure (410a, 411, 411a, 672, 712), but suffers from defects evident in similar determinations of carbon content.

A method said to depend upon biological activity has been pro-

posed for estimating plankton populations (6). The reducing enzymes present are determined by measuring the red compound, formazan, produced when 2,3,5-triphenyltetrazolium chloride is reduced. The method does not distinguish between the types of living matter present; indeed, " experiments also suggest that other soluble organic substances in the system resulting from the metabolic activity of plankton and bacteria may play a role in accelerating the reduction of tetrazolium. Others might retard the reduction " (6, p. 172). It is so unclear as to what is being measured that comparisons of crops in time and space cannot yet be made. The value of the method is said to be that it measures " over-all activity ", but what is meant by this phrase? Moreover, it involves pre-treatment of the material, which will affect different organisms to a varied degree, and it seems unlikely that this is a good basis for measurements of the " activity " of plankton. The author does not give any figures from which one can determine to what degree the method permits accurate quantitative estimation of any kind of plankton or any specific activity thereof.

INTERRELATION OF UNITS

In view of the use of different units in various works and in different situations, some knowledge of their interrelation—although only approximate—is clearly of practical value. Unfortunately few comparative studies, including various plant groups, exist in this important field (see, however, 164, 296, 545, table II; and 699). As regards chemical constituents, the necessary data largely concern percentage composition and its variation, and have been briefly discussed in relation to each constituent. " Average composition " of marine plankton is discussed in 164, 318, 577, 715. The position for chlorophyll is particularly important as much work has been based on its relation to some other quantities (especially carbon: see 535, 537, 545, 622). Particular significance is attached to the relation between cell volume and other measures such as dry (or ash-free dry) weight, as reasonably trustworthy conversion factors would enable a very small biomass to be estimated from microscopic observations. Some examples of the relationship with ash-free dry weight are given in 545, fig. II; 609, 699. The relation with total dry weight is likely to be more

variable, particularly if heavy-walled diatoms are considered, but the order of magnitude is probably about 1 mm^3. cell volume = 1 mg. dry weight (565, and unpublished observations).

ESTIMATION OF GROWTH IN NATURAL POPULATIONS

The most obvious way of estimating growth increase in natural populations is the following of changes in their density (standing crop) with time. A large literature exists on such seasonal changes, particularly for phytoplankton, although fully quantitative results, based on frequent sampling and estimation of individual species, are much less common (e.g., 11, 376, 377, 379, 382, 562, 678, 748). Plotting of seasonal growth curves with population density on a linear scale is usual and useful for some purposes, but the operation of many factors (especially if density-independent) can be reliably discerned only if a logarithmic scale is used (e.g., 136, 376, 377, 379, 382, 470, 747, fig. 33), as advocated by Scourfield (601) in 1897. Curves on a cube-root scale (Lohmann's (370) Kugelkurven; for a comparable method, see 90) have been widely used by Continental authors, especially for illustrating depth distributions. Although the mean linear distance between neighbouring cells is also indicated by this method, in our view linear or logarithmic scales are preferable (cf. 259, p. 29). In populations of unattached algae with non-random spatial distribution, population growth may be simulated or obscured by a mechanical redistribution of individuals, and its true determination may then require an elaborate sampling programme. Surface "blooms" of blue-green algae (e.g., 656, fig. 7), diurnal migrations by flagellates (e.g., 678, pp. 204–205; 203, pp. 406–412) and seasonal sedimentation and resuspension of *Melosira* filaments (160, 379, 382, 657) provide good examples. In cases of unequal vertical distribution the estimation of population size under unit area of surface (196, fig. 8; 226, 545, 565, 568) may be useful.

Even when such effects of distribution are absent, the growing natural population is usually subject to various sources of loss (e.g., by grazing and parasitism, and loss to the outflow or deposits) which are usually difficult to estimate quantitatively. Consequently many estimates of reproductive or "turn-over" rates (e.g., 63, 307, 366) are largely guesses, although possibly good ones. Quantitative estimates of some sources of loss (e.g., by

grazing and sinking) are cited later, as are also estimates derived from measurements of photosynthesis. The use of observed population changes to deduce apparent or real rates of increase per unit of population is illustrated in 122, fig. 2; 226, 227, 228, 241, 377, 698. Some remarkably high and widely quoted estimates from 241 (see also 239) appear to result from an incorrect method of calculation. Periods of no net population increase (Gleichgewichtsperioden) were used by Grim (228) to estimate true rates of increase, using data on cell sedimentation.

For certain diatoms whose walls are of constant thickness, it is said that the rate of division, and so production, can be estimated by the reduction in the length or diameter of the cell along the transapical axis with time (129, 130). This could be a very valuable method, but, though statistical analyses and studies with an electron microscope may seem to support this thesis, some of the results in both papers suggest that the method needs re-examination. A limnologist may well be amazed to find that marine *Asterionella japonica* divides 2.9 times per day in the North Sea in the second half of April(130, table 29, p. 60; 38 divisions in 13 days, see p. 99) or that the diatom crop as a whole divides more than once per day (129, p. 17, table 14). Over what depth these increases are taking place is not said. Although the possibility of auxospores arising and the difficulties from the consequent polymodal size distributions generally seen in diatom populations are said to be overcome by the mathematical treatment used, the relationships between size, form and rate of division may be more complex than is here realised (e.g., see 178, 190, 361, 369, 375, 670). For example, the measurements must be made along an axis in which decrease in length is regular, and it remains to be demonstrated that the decrease for cell division is equal to the width of the wall over the area shown in the electron micrographs instead of that in the region of the overlap of the girdle bands.

Grazing can rarely be gauged, for algae are more or less completely destroyed in the animals' digestive tracts, and even if, like diatoms, they can be identified, the rate of ingestion cannot be directly determined in natural populations. Further, algae may pass through their guts unharmed (157, 158, 205b, 684, 691, and unpublished observations of the first author). In laboratory experiments the amount digested and the rate of excretion may differ

more or less markedly from natural conditions (e.g., 80). There is some information on volumes of water filtered by some zooplankton animals; probably the best known is the marine copepod *Calanus finmarchicus* (130, 410). In some cases grazing can be ignored, as the algae are too large to be ingested by the animals concerned (102, p. 242; 379, p. 168; 440; 473, p. 61). Under rare favourable circumstances the effect of grazing can be estimated with some certainty from observations on natural populations (474; see also 20). Computations of rates of removal by grazing exist for various marine areas (e.g., 130, 163, and others mentioned on p. 532); counts of faecal pellets have been used (241). Lastly the distribution of zooplankton in space and time is so irregular that the determination of numbers requires much effort. Parasitism by fungi (102–104) cannot yet be assessed quantitatively, for it is not known how to determine the rates of growth of fungi. All that can be said is that a certain percentage of the algal population present at a given time will die because in almost all cases infected cells do so.

The importance of loss by outflow can be determined from changes in water level if a gauge-discharge relationship is available or if a hydrographic map is made (for methods, see 733). Some idea of this loss is essential if general comparisons are to be made between lakes, for example, in regional studies (cf. 84). Losses by tidal action in estuaries are considered in 315; these areas and rivers present great difficulties because of the need to measure rates of flow. The loss to, or gain from, the deposits is usually impossible to gauge, since there is no accurate method of estimating material in or on their surface layers, and data from traps are not usually reliable (p. 543). Nevertheless in healthy populations of several, perhaps many, plankton algae, it is not unlikely that the loss of cells to the deposits over a considerable period of time is so small that it will not seriously interfere with determinations of growth increase over that period. A far greater source of loss is probably the thermocline (cf. 200), but here more information is needed.

Generally greater difficulties attend the estimation of growth increase of algal populations on substrata (benthos), as will be evident from the survey of sampling methods (p. 539). Examples of such estimates for diatoms are given in 136, 323, and effects of

grazing—probably particularly significant here—are discussed in 81–83, 136.

Since direct methods of estimating growth in nature are so laborious or difficult, primary production is usually assessed indirectly from experiments carried out there or in the laboratory (577, and pp. 504). However, many estimates have been derived from considering the reaction of plant growth upon dissolved constituents of the water. Examples include diurnal changes due to photosynthesis (p. 508) and the uptake of inorganic nitrogen, phosphate and silica. Silica is particularly useful, as it is not utilised by many organisms (e.g., bacteria), and in all but very alkaline lakes re-solution of silica within the lake can be ignored (cf. 300). The method is most valuable for plankton diatoms because, where the benthic diatoms do not appreciably affect the silicon metabolism of the lake as a whole (e.g., in deep, steep-sided glacial lakes), the changes in concentration in the open water commonly reflect the loss from utilisation by the plankton diatoms and the gain from inflows (see, however, p. 511). Lastly mention may be made of the use of changes in the hypolimnia of stratified lakes caused by decomposition of organic matter received from above; notably progressive depletion of oxygen (e.g., 150, 263, 427) and accumulation of carbon dioxide (456, 459) estimated per unit area. However, many studies have probably underestimated the contribution of allochthonous material, such as decaying leaves.

USE OF EXPERIMENTAL, INCLUDING CULTURED, POPULATIONS

The use of experimental populations of algae is considered here as an additional method for analysing the behaviour of natural populations. From this standpoint the advantages gained in greater control of material and environment may be set against the possible introduction of artefacts under ecologically unnatural conditions. Illustrative examples have already been provided in the discussion of photosynthetic behaviour. The dangers of artefacts are often more acute in the study of growth behaviour, the main subject of this section, owing to the additional factors affecting growth and the necessity of longer experimental periods. Consequently the evidence from experiments should be checked wherever possible by observations on algae in nature.

Direct use, as experimental material, of samples from natural populations is unsatisfactory for many purposes, particularly because of the wide alteration which usually occurs during growth in the relative proportions of the species present. This is strikingly illustrated in the pioneer work of Whipple (746), whose tables show how, within a mixture of *Asterionella, Tabellaria, Melosira, Stephanodiscus* and *Synedra,* the last almost invariably became predominant in samples exposed to natural illumination, even when in a small minority originally. It is the small species of *Synedra* and other genera, such as *Chlorella, Ankistrodesmus, Scenedesmus, Nitzschia* and *Navicula,* which are well known to all who cultivate algae as troublesome contaminants. The reasons for this behaviour in samples but not in the original environment are unknown, but, as with bacteria (661), the close proximity of a surface may be important, or these algae may produce substances which inhibit growth of the larger forms (cf. 301). Physiologists have taken advantage of the ease with which they can be cultivated, with the unfortunate consequence that many of the algae of greatest interest to limnologists are not studied.

Again, direct use of natural waters as media in growth experiments has but rarely led to any clearly defined results applicable to natural populations. The causes are generally obscure, but the low concentrations of nutrients and the relatively unbuffered nature of the medium are probably important, particularly as almost all experiments have included undetermined effects from the growth of bacteria. Thus the obvious experimental approach of making known additions of nutrients to natural waters, and estimating the effects upon algal growth in the laboratory (e.g., 159, 489, 598, 599, 644, and various Russian papers reviewed in 354), or in field exposures (p. 528), has (like Huxley's *Bathybius*) not lived up to the promise of its youth. However, it seems to be widely regarded as a reliable routine test.

As a result of difficulties mentioned above, the isolation of individual species in more or less reproducible artificial media assumes considerable importance. The relevant literature on algal cultures is too large to cite here, but general summaries are given in 70, 231, 493, 496. Other recent descriptions of methods for isolating and growing algae include 7, 10, 92, 106, 108, 134, 138, 156, 166, 168, 192, 193, 317, 334, 396, 437, 462, 494, 497, 498,

504, 519, 550, 556, 621, 774. A valuable recent review of the development of artificial media for marine algae (500) contains much information of interest to the limnologist. The use of really "pure" (bacteria-free or axenic) cultures is still in its infancy as regards true plankton algae, whether marine or freshwater (cf. 141, 500). This is primarily due to difficulties of culture and not of obtaining bacteria-free cells. The use of antibiotics has increased as a means of eliminating bacteria (see 156, 504, 617), but mechanical methods have several advantages (cf. 138). Even with unialgal cultures, progress has been slow, particularly for freshwater plankton forms, but some useful media (e.g., No. 10 of Chu, 106, and No. 8 of Rodhe, 550) are now available. For many species soil extract or other complex organic extract is needed and cannot yet be replaced by simpler, chemically defined components. Besides the true growth substances, buffering or chelating properties may be involved, and such artificial pH buffers as Tris(-hydroxy-methyl)-amino-methane, and chelating agents as ethylene-diamine tetra-acetic acid (E.D.T.A.) can often be usefully applied (334a, 500, 501, 730).

In many quantitative studies with algal cultures the population density reached after a given time interval has been used as a comparative measure of growth. This may be valuable if it is the maximum density attainable in the culture, but otherwise is difficult to interpret because factors influencing the lag, exponential and later phases of growth may be involved. In exponentially growing populations it is essential to distinguish between the effects of population size and of relative growth rate upon an observed increase of density. Estimation of relative growth rates (often called "coefficients of growth increase" or "logarithmic growth rates"—standardisation of terms and units would be welcome here), as opposed to true growth rates (strictly the absolute increase in material per unit time, but often misapplied), would repay more attention. The work of Barker (47) on marine dinoflagellates is a model in this respect. Useful discussions of growth measurements in microbiology are given in 255, 421, 690.

It is easy to cite a number of conditions that are usual in culture experiments but rarely or never realised in nature. First, there is the possible effect of the walls of the container in which the plants are grown; the subject is little known and worthy of study. The

close presence of a large area of solid surface may well exert an effect on the algae (cf. p. 526). It may be doubted that the surfaces of substances in common use, such as Pyrex or Quartz-glass (soft glass is best avoided), polyethylene, nylon or other plastics, are both physically and chemically inert, particularly where minute amounts of nutrients are concerned. Goldberg (215), for example, describes the adsorption of iron, added as ferric citrate, which was overcome by coating the glass walls with a polymer of silicon.

Second, the illumination applied to algal cultures is always very different from that experienced by cells in nature. Natural illumination is distinctive in attaining intensities up to about 120 kilolux, far above those normally used in the laboratory, it is experienced by algal cells in an intermittent manner, and is usually associated with ultraviolet radiation. One approach to the problem is the use of cultures, suspended at various depths in natural waters, in measurements of growth (373, 376, 652). Samples of natural populations have been similarly employed in natural or enriched media (179, 187, 219, 221, 223, 227, 264, 372, 527, 538), but suffer from disadvantages discussed earlier (p. 526). The methods of exposure have much in common with those used in corresponding studies of photosynthesis (p. 504), with modifications for the longer exposures necessary; comparisons of results for growth and photosynthesis are given in 179, 652. With cultures care should be taken to restrict measurements to the exponential phase of growth and to avoid effects from cell increase in darkness (376, 652). Even with this method conditions are artificial in that cells maintained, in largely unstirred suspensions, at a constant level in the vertical light gradient, within which they would normally be circulating freely. Experiments involving forced circulation in submerged glass columns would be interesting. The huge " plankton shaft " of Pettersson, Gross and Koczy (481) is another attempt to reproduce conditions in an isolated water column.

Third, most culture experiments have involved relative growth rates and population densities much higher than those likely to occur in nature. The use of low densities, for which cell counts may often be the only practicable means of following growth (p. 514), is therefore to be recommended.

Relatively few laboratory studies with cultures have concerned the temperature and light relations of ecologically important algae (examples for planktonic forms include 41, 46, 47, 74, 75, 180, 237, 240, 353, 376, 575, 576, 579, 598, 652, 654). One limitation, mentioned earlier, is the difficulty of imitating natural illumination, and effects from spectral modifications and angular distribution usually prevent useful comparisons of intensities measured in laboratory and nature. Assessing possible effects of the photosynthetic action spectrum is also difficult (654, 359). A profitable field would be the comparison of photosynthetic behaviour of the same material under artificial illumination and in that of natural waters.

Cultures are being increasingly used to determine the nutritional needs of algae in relation to their growth and occurrence in nature (e.g., 106, 107, 109, 133, 134, 140, 192–195, 205a, 215, 217, 231, 236–238, 240, 269, 376, 377, 391, 411a, 500–503, 550, 574, 719). Though the amounts of certain nutrients needed by algae can be determined in this way, these may be true only for the artificial media and environmental conditions concerned. An example is provided by the apparent promotion of phosphate uptake by an unidentified factor in some lake waters (391, 550). Cultural studies are presumably unequivocal when they show an absolute requirement for an element, ion or molecule. However, a necessary property, especially if of a physical nature, may be shared by a number of substances with a corresponding loss of specificity; possible examples are discussed in 141 and 500.

In view of the difficulties met in comparing the behaviour of natural and cultured populations, some examples of apparent anomalies between them are instructive. For instance, almost all culture media, particularly earlier ones listed by 346, contain higher, often far higher, concentrations of certain nutrients than are apparently available in most natural waters. Chu (106, 107) was among the first to use media with ionic concentrations approximating to those in natural waters. Yet for certain algae (e.g., *Asterionella*) he deduced higher minimum requirements than were available in certain oligotrophic lakes where the algae flourished and which were specifically considered by him (106, 107, 376, 377, 391, 550). This situation applied particularly to phosphate and, in lesser degree, nitrate, so commonly considered

to be two major limiting nutrients for algae in nature. For the phosphorus requirements of *Asterionella* spp. later analyses of algal cells (8, 164, 217, 391) all show a remarkably similar minimum amount per cell. This is so low that even the minute concentrations in many oligotrophic lakes are sufficient for the growth observed, provided that the algal cells can utilise such low concentrations (evidence in 391).

In another example, evidence from culture experiments with certain blue-green algae indicated that a high pH was needed for growth; for two species the optimum was pH 10 (192–194). In nature, although blue-green plankton algae are most abundant in alkaline waters, such high pH values are not a prerequisite nor normal in most waters. Indeed there is evidence that a pH of 10 may be injurious (462, 628, 632). However, it seems not unlikely that the cultures were deficient in available carbon, which is not included by the authors in their list of essential elements, and that a high pH assisted growth by increasing the rate of uptake of carbon dioxide from the air. Similarly another conclusion from the experiments, that inorganic nitrogen is the most likely substance to limit the growth of the species concerned in nature, does not accord with observations on nearby lakes (193, pp. 839–840; 89, p. 44) or others that blooms typically develop when this source (but not organic nitrogen: 468, 469) is near its seasonal minimum. Some later work with cultures (195) is also against the earlier conclusion. We would conclude that the contrast between the availability of nutrients in large (natural) and small (culture) volumes of water, advanced by Gerloff et al. (194, p. 31), is—at least for plankton algae—both implausible and unnecessary.

Several examples of behaviour in natural populations, difficult to explain, have been referred to differences in internal physiological factors or "physiological state", a vague expression best avoided. Such differences are evident in almost any study with algal cultures, as with cells in the lag and stationary phases of growth, but their significance for natural populations has been rarely investigated (see, however, 376, 534, 618, 719). The interpretation of algal reactions to environmental factors in cultures or natural waters by reference to three cardinal points (minima, optima, maxima) has also been common (e.g., 638, 725), but this

approach has severe limitations, particularly for "optima". Interpretation by reference to "limiting factors" has generally been more fruitful (cf. 511, p. 858–860), although often over-rigidly applied.

MATHEMATICAL MODELS OF POPULATION BEHAVIOUR

Mathematical models, purporting to describe behaviour in natural populations, constitute a familiar method of developing and testing theory in other fields, e.g., animal ecology and population genetics. Some applications to the growth of phytoplankton populations, less well known, are reviewed below. The deductive type of reasoning involved here is traditionally distrusted by plant ecologists, and this, together with occasional unjustified and excessive simplification of assumptions and evidence in a mathematical guise, has led to its common neglect. An attempt is made below to show that at least in certain fields of plankton ecology the mathematical model can be a useful tool if not overstrained. Some potential values have been classified (655) as permitting (*i*) the comparative significance of various ecological factors to be more precisely estimated, (*ii*) reduction of the behaviour of natural and experimental populations to a common basis, and (*iii*) calculation of certain general measures (e.g., productivity) of theoretical interest.

A relatively simple yet fundamental example is provided by experimental estimation of photosynthetic production below unit area of surface. The methods available (recently reviewed in 577, 655) depend upon integration of photosynthetic rates with depth. The integration can be made by direct planimetry of depth profiles of photosynthetic rate, by semi-empirical equations based upon previous experience (577, 630, 631, 701, 702), or by a factorial analysis of the depth profiles, leading to a reconstruction of the integral from component factors (535, 649, 655, 722). The proposed solutions of the last class differ considerably in the importance attached to light saturation of photosynthesis. An analogous use of integration with depth has been applied to production in algal mass cultures (92). Once obtained, the photosynthesis-depth integral may require reintegration with respect to time in order to be applied to ecological situations. This process has been discussed in 655, in which a logarithmic scale is proposed for

measuring radiation intensities and radiation-time integrals. This scale was designed to meet certain effects due to light-saturation of photosynthesis which have been also emphasized by Steemann Nielsen (630, 631, 634) but neglected or underestimated in other theoretical models. In general, any such model requires a number of simplifying assumptions (e.g., uniform distribution of the population in the euphotic zone), whose validity must be judged in each case.

The estimates of areal production so derived may be used to calculate the average rate of carbon assimilation per unit of the population. The latter estimate can be converted into units of relative growth rate if the carbon content per unit of population is known and if an estimate (usually very uncertain) of respiration losses can be made. This subject is discussed in 115, 535, 545, 651, 698. If suitable estimates of the relative growth rate based on direct observations are available, an interesting comparison of the observed and calculated values can be made (651, 698). It should be emphasized that all the theoretical procedures mentioned become more uncertain if applied to average properties of mixed populations, in which component species may exhibit different patterns of behaviour.

An interesting and ambitious extension of some of the preceding arguments has been attempted by Riley and various coworkers (535, 537, 545, 546; see also 130, 622). Further corrections were applied to describe the effects of grazing, sinking and nutrient depletion, judged from concentrations of phosphate or phosphate and nitrate. The resulting equations were then used to calculate curves showing the variation of population density with depth or season; in most cases a tolerable agreement was obtained with observed changes (cf. 535, fig. 21; 537, fig. 32; 545, figs. 29–31, 33, 35, 37, 39; 546, fig. 5). However, it may be held that the agreement depends to a considerable degree on non-causal correlations (and some empirical manipulations: cf. 546, pp. 66–67) instead of on success in quantitative analysis of the system concerned. This seems particularly likely when the large areas involved and the necessarily limited primary data are considered. Criticisms of details include the neglect (535) or probable underestimation (545, fig. 11) of light saturation of photosynthesis; the

frequent use of an ill-defined vertical extinction coefficient deduced from Secchi disc readings (cf. p. 500); the estimation of surface photosynthetic rates, using an exposed bath, or suspension near the sea surface, without allowing for possible inhibition effects (common near the water surface); the lack of accurate determinations of algal respiration rates, to which the results are particularly sensitive; the improbability that the complex effects of nutrient depletion (particularly of phosphate: cf. 217, 391) can be expressed by a simple relation; and particularly the likelihood of considerable differences of behaviour between species (illustrated by other work of Riley, 538) whose occurrence varies with season. However, a basic element underlying the treatment, namely, addition of factors expressing rates of change (e.g., from grazing or sinking) expressed on a common scale with relative growth rates, may well be of wide value (see 115, 130, 163, 310, 536, 539, 542). Application to less complex situations with definable density-independent factors is desirable. Simpler equations (e.g., the logistic) describing a complete curve of population growth are suspect, even for relatively uniform cultural populations (cf. 255, 610). In our view their application to algal populations, whether cultural (e.g., 490) or natural (719), is unprofitable.

Several other mathematical treatments deserve mention, although space limitations forbid fuller discussion. A stimulating analysis of growth by marine phytoplankton, with particular reference to the influence of cell size and shape on nutrient absorption and sinking rates, is given in 434. Equations expressing multiple correlations between algal development (usually assessed by chlorophyll) and various environmental factors have been derived by Riley (527, 529, 533, 535). This approach is probably of very limited general value in view of the numerous possible mechanisms for interactions between factors (see, however, discussion in 533). Maucha (413, 414) has given a mathematical treatment of certain photosynthetic behaviour, but at least one basic assumption—that photosynthetic rate is related to light intensity by a sine-curve relation—is probably generally far removed from reality (cf. also 693).

In many contributions mentioned above, the differential and integral Calculus is applied with profit. However, the use of "in-

operable expressions", particularly as a form of shorthand which is not uncommon in general ecology (cf. 287, 397), has been criticised (697).

SAMPLES AND SAMPLING

COLLECTION

PLANKTON. The erratic fluctuations so often seen in graphs depicting rise and fall of phytoplankton populations may suggest that sampling from one or two stations on each occasion is inadequate, and that multiple, mobile sampling is necessary (696). In such cases an integrating sampler, designed to be towed behind a vessel, would resolve, to a great extent, the demand for extra time (259, p. 31 and footnote). This is, no doubt, true of large lakes, which approximate to seas in this respect, and of small or weedy ones, in which water movements are much restricted. However, under more or less isothermal conditions in moderately large bodies of water, free of such obstructions as large weed beds or islands, and which are not very long and narrow, a single sample through only a part of the water column taken in the central regions is likely to be sufficient to calculate the population density of many algae at any one moment with sufficient accuracy (e.g., a sample through the top few metres). Where the populations do vary markedly from place to place, so that several sample stations are necessary, a single sample may be sufficient for any one station (242). Nor are erratic population curves necessarily a sign of inadequate sampling. In all cases, however, preliminary investigation is needed to determine these matters. Probably some elements of the plankton of open lakes of 100 to 1000 hectares can often be studied with adequate precision by a single sample at a central station (524). Clearly the greater the powers of movement of the organism concerned, the less likely it will be distributed at random by turbulent water movements. Some comparative studies on these points would be valuable. The frequency of sampling is most important, as fallacious beliefs can only too easily be caused by collecting at long intervals. Thus many fungal epidemics on plankton algae would not be seen if weekly, or at the least fortnightly, samples were not taken; and to obtain a full picture, sampling often has to be done every three or four days (102). For some aspects, even this frequency may obscure important diurnal changes.

Collection by net is discussed first because it has been used so frequently during the last 70 years. Many types of net have been described (e.g., 114, 234, 235, 326a, 352, 608, 671, 737, 759, discussion in 130). For general reviews, see 130, 717, 733, 747; and for statistical and other tests, see 13, 761, 762. For quantitative work a net is of limited value; some investigators consider it useless (703, 732). However, what appears to be a fundamental relationship between lake morphometry and production has been found from quantitative sampling with nets (515–517; see also 251) and for qualitative purposes they are of great value. The introduction by Hensen (249) of nets which could be used as quantitative instruments nevertheless constitutes a landmark in oceanography, and it should not be forgotten that Hensen knew that small algae would pass through them; indeed, he also used what he calls "Mikromembranfilter" (249, pp. 92–93, Pl. 5, figs. 54, 55; see also p. 14). Twenty years passed, however, before Lohmann (370, 371) showed how large a part of the whole the nannoplankton might be.

There are several obstacles to obtaining accurate estimates of crop from net hauls (summarised in 142). These all apply to the usual net of bolting-silk and some at least to any kind. It is not yet clear whether equally good or better nets can be constructed from artificial fibres, such as nylon (but cf. 736) or metal. Kolkwitz's (328) phosphor-bronze net has the apparent advantage of greater regularity of mesh and less likelihood of damage or alteration with age. Because plankton is often considered to be of two types, that retained by a net (net-plankton) and that passing through (nannoplankton, or if very small, μ- or ultra-plankton), the impression is given that a net will retain all the larger algae in the water filtered. This is not wholly correct, as there are many "large" algae (e.g., *Asterionella formosa:* 377, p. 8, fig. 4), some individuals of which are thin enough to pass through the meshes of a net if oriented rightly. This condition may be favoured, particularly for elongated species, by a flow of water more or less parallel to the long axis of the net. It is more correct to consider net plankton as algae which are partially or wholly retained by the meshes of nets, and nannoplankton as those which pass through unless they are caught up in other algae. The meshwork is likely to be increasingly obstructed by the material collected upon it

(considered by Hensen, 249), reducing the amount of water being filtered over a given distance of towing. Statements that give the impression that there is one set of organisms retained by a net of given mesh and another which passes through (e.g., 701) are, therefore, oversimplified. With the usual bolting cloth of 50–70 μ aperture, the major part of the population which passes through may consist of the same algae as that which is retained. Birge and Juday (63, p. 63) unfortunately rejected Lohmann's (371) original definition of nannoplankton which was based on size, in favour of one depending on the retention or passage of plankton through a net. They also probably overemphasised the importance of nannoplankton, for they collected all net-passing particles, organic or inorganic. For quantitative collections in nature, the net must be towed very gently to reduce displacement of water from the neck. The volume of water passing through can be assessed by incorporating a flow meter in the net or by using a net which can be closed at any desired depth (114, 235, 352, 449, 608, 737). The Clarke-Bumpus measuring mechanism does not operate properly if the net is clogging, and the critical level is said to vary from one instrument to another (442, 767). The view that this sampler is unsatisfactory when nets of fine mesh (e.g., 70 μ) are used (352) is apparently incorrect if the towing velocity is carefully controlled and clogging avoided (147, 767). Lastly the net may shrink in time with use (326). Complete filtration is impossible, for a net of sufficiently fine mesh ($\pm$ 1 μ) is not a practical proposition, and the finer the mesh the more difficult it is to remove algae from it. In a few cases, where only some individuals in a population pass through, it may be possible to apply an approximate correction factor or net "coefficient" (326, 377, 703, 747). This factor, however, not only is more or less variable but also may not be of general application (626). In any case, a correction factor should be determined for each alga. Variability from clogging can be reduced to some extent by filtering small volumes of water, but suitable volumes are often difficult to judge at the time of sampling. Alterations in the size of mesh can be assessed by sampling with some other device at the same time to determine the coefficient of the net (306).

A net, particularly if large, is invaluable for collecting large quantities of plankton and for following the distribution of the

bigger algae in time and space (251), since thousands of litres of water can usually be filtered in a short time. It is often possible to obtain species present in such small numbers that quantitative estimations of their abundance by other methods are impossible. Clearly the absolute absence of a species is impossible to establish, although such categorical statements are often made. Use of the same net in different water bodies can also introduce alien organisms into a sample, as adequate cleaning of fine nets is difficult. The proportional composition of the net-plankton has been much used in lake typology (e.g., 453, 468, 469, 517, 664, 668, 738, 739, 740, 741, 743), but it is as yet uncertain whether the composition of the nannoplankton is so characteristic of the trophic state of the water.

While nets are useful for collecting quantities of algae large enough for chemical analysis and other purposes, collection can be laborious, for the richer the collecting area the sooner the net clogs. Clogging can be overcome by using a sampler with a cylindrical rotating and self-cleaning screen. This method is said to be superior to the use of sand filters, or flocculation or sedimentation techniques and 1–3 Kg. of wet plankton can be obtained (605).

Samples collected by bottles or other containers with closing devices can be used for quantitative sampling of algae and for chemical analysis of the water. They are tedious to use because of the necessity of raising and lowering them for each sample. Many types have been described with diverse opening or closing devices, and in some cases provision for several separate samples to be taken at one time (151a, 288, 326b, 426, 506, 517, 548, 549, 571, 616a, 619, 643, 726, 747). The best known in limnology is that made by Friedinger (see 470). In shallow waters a horizontal sampler may be useful (277). There are some large samplers which take five to ten litres (306, 549). It seems to be almost forgotten that the simple, old fashioned method of lowering a weighted and closed bottle and then pulling out the stopper (e.g., 467, p. 127; 2, pp. 11, 13, 172), is adequate for many purposes in shallow water. Beyond a depth of about 15 m. it becomes impossible to remove the stopper (288). While a pump or a closing sampler must be used for sampling at discrete depths, the lowering of a rubber or plastic hose or other flexible tube, weighted at one end, is a simple, cheap and effective method of sampling a water

column if not too deep (376, 383). The method could probably be adapted for use in relatively deep water. A plastic tube composed of separate lengths has great advantages when working in small bodies of water and among dense weed beds (766).

Use of a pump (e.g., 48, 63, 205, 326, 733) has defects, particularly when the water is stratified, because the tubing must be flushed between samplings and because of the flow system set up around the inlet. It is, however, unlikely that any algae are likely to escape being collected through negative rheotropism, an alleged error in estimating the larger Cladocera by this method which can, however, be overcome. Large volumes of water can be collected quickly, but a check should be made to see that delicate algae are not harmed. The apparatus is expensive and cumbersome. We do not understand the statement that among its disadvantages is " profondeur limite de prospection réduite (75 mètres) " (142, p. 153).

Under ice or elsewhere, when chemical and biological stratification is very sharp over a shallow depth of water, a simple hand operated suction apparatus (379, 412, 732) with short lengths of tubing (as in 766) or a Kolkwitz chamber itself (573) can be used; the latter might well prove especially useful for work on small pools in *Sphagnum* bogs. In very shallow water, which may be sharply thermally stratified or in which there may be great variations in the vertical distribution of the organisms, an apparatus which collects water from very thin horizontal layers of water at short distances apart is clearly needed (cf. 131, 752). Various multiple or fractionating samplers for plankton have been described (331, 355, 754; see also statistical criticism in 128). In large bodies of water or for collecting strongly motile algae, the development of an integrating sampler is likely to be very valuable (259).

The type of containers used for samples affects every aspect of collection and further treatment of water. Clean containers are obviously needed, but in the case of glass the nature of cleanliness may vary according to the use to which it is to be put. New glass containers, even after cleaning, may yield silica (see also 450) and presumably other substances to the water, the amount varying according to the glass used and the temperature and pH of the water. Rinsing with ethylenediamine-tetra-acetic acid is sometimes per-

formed to remove metallic contaminants (272, p. 852). Sterilisation, particularly if under pressure, may also produce a new and more easily soluble surface to the glass. The commonly used chromic-sulphuric cleaning mixture may make the glass harmful to microorganisms. The cause is commonly believed to be chromium (253; see also 595), yet there must be some doubt as to whether this is generally true, for, after the thorough washing which normally follows, the amount of chromium left behind on the glass is very small (294), smaller indeed than the amounts found to be poisonous by Hervey (253). All authors agree, however, that simply rinsing a few times will not remove enough chromium to prevent poisoning. Moreover, tests with Cr^{51} show that after such washing the metal is not easily removed; Pyrex retains more than plate or quartz glass (294). The effect of drastic cleaning may be on the physical chemistry of the glass rather than from traces of poisons from the cleaning mixture. In general it is best to use plastic containers. They are light, not easily broken and available in a wide range of size and shape. Polyethylene (Polythene) is usually favoured and, though inert so far as almost all water-soluble substances, is capable of taking up some (e.g., iodine), and for experimental work with mixed populations it and nylon are less satisfactory than glass because of the increased bacterial growth (unpublished observations). Containers of stainless steel or highly insoluble alloys (e.g., monel metal) are doubtless suitable, but their cost is high and there is need for experiments to determine whether they are insoluble to the extent necssary in some limnological investigations.

Microfiltration (for the use of Kieselguhr, porcelain or plastic coal candles, see 325, 717), and other collecting methods usually carried out after the primary collection of the sample are considered on pp. 544–8.

BENTHOS. Attached algae are notoriously difficult to sample quantitatively. For qualitative purposes most may be transported safely in a damp container, such as a plastic bag or a well stoppered bottle containing as little free water as possible. The latter may be used for quantitative work because such cells as are removed during transportation are easily washed out of a bottle and recovered.

Loosely attached algae, like *Tabellaria* (323), can be removed

by shaking in water. Others (e.g., diatoms) can be scraped off rocks, stones, wood etc. without serious damage, but a good deal of unwanted substratum is included. Even if a special scraper is used (771), the algae cannot be removed wholly unless the surface is smooth or easily removed to a depth which is greater than any illuminated cracks or crevices. Brushing is better, and for some algae on certain types of stream bottom this can be the basis of an accurate quantitative method (136) which could be used also for work on lakes. Many encrusting algae would either be only partially removed by brushing, or would be seriously damaged or destroyed; they are better removed to the laboratory on their substratum if this is possible. Calcareous algae involve special difficulties. Reeds are usually cut with a knife or other cutting device, but, as such methods involve sampling from the water level downwards, the stems are likely to be sampled at different levels each time unless a special cutting and measuring device is used (323). Shaking or squeezing may serve for growths of Bryophytes, notably *Sphagnum*, whose algal population is largely unattached in the water held in the tussocks, though not a few algae live more or less always in the porose cells. In any case such methods are suitable only for qualitative work. In some cases and for some species, the quantitative results can be obtained on material brought in bottles or bags as described. Thomasson (667) favoured letting the algae dry on the substratum (e.g., reed stem, lily leaf, glass slide) in the field because it is then possible to collect large samples without having to cut them up and put them into large numbers of containers. He says that the dried algae stick firmly to the substrate. Obvious disadvantages to the method are that many algae (diatoms excluded) will be unidentifiable, the dried mass is difficult to remove free from the outer tissues of the host plant, and the material will not dry unless the weather is favourable. Nevertheless, the method may be very useful under favourable conditions, for the crop can be conveniently recorded as a dry weight or in terms of carbon, silicon, etc.

All such methods usually sample only a part of the flora or the whole of a particular kind of flora on a suitable substratum. An attempt to overcome this is the use of transparent sheets, such as glass or perspex, which are suspended in the water or placed on the substratum, or even through it in the case of reeds (416).

This method was first used for this purpose some 40 years ago (250) and was previously tried for collecting and examining algae for morphological or physiological work (e.g., 324). Since then it has been applied extensively (82, 96–101, 189, 212, 443, 444, 466, 470, 614a, 667, 772a). In torrential rivers special anchoring devices and holders for the slides are necessary (96, 97, 189).

The degree to which this method gives an accurate picture of the productivity of a habitat is uncertain (443; concerning counting, see p. 518). Glass, particularly the soft glass of microscope slides, is not chemically inert. Some algae are rarely if ever found growing on them, and others are predominantly present as flat discoid thalli rather than upright growths (e.g., *Stigeoclonium* spp., cf. 519). Others equally (e.g., species described in 97) are almost universally present, yet little known from natural substrata; indeed this is a very valuable method for obtaining such algae and following their development (97, 189, 211, 324). However, these facts do not form convincing evidence of any fundamental weakness in the method. Algae such as *Lemanea, Batrachospermum,* certain Myxophyceae, especially encrusting species, and *Hildenbrandia* (212) may be absent for a number of reasons unconnected with the basic principle of the method. Compare, for example, the flora described in 177 from sampling of stones and *Cladophora* with that in 96, 98 obtained by the slide technique. Large algae may be easily torn off smooth surfaces, and some algae may colonize a new one very slowly or grow very slowly. Thus in Windermere huge thalli of *Hildenbrandia* have been found on old-fashioned soft-glass bottles which have probably been in the water more than 20 years (unpublished observations of the first author). As generally practicised, the method is bound to favour the pioneers in colonisation (189), for if the slides are left in too long, the rate of production falls to minimal values because all the available surfaces are colonised (cf. 82). Indeed, the length of time they should be left submerged is an important matter which needs investigation (cf. 443, 772a).

Colonisation on wood, stones or slides has been found to be generally similar, but there were certain differences. The most marked can be related to the fact that new bare surfaces are a rarity in nature. In one case the use of slides gave the impression that conditions were favourable for growth of *Hydrurus foetidus*

when the reverse was the case in the stream as a whole (189). There is some evidence suggesting that these primary colonisers may not be selective as regards the nature of the substrates used. In the sea it has been found that, though certain marine invertebrates vary in their ability to colonise artificial substrata such as glass cloths (fibreglass), algae show no preferences between these and bakelite (51). One method based on the slide technique is believed to be nonselective for diatoms (466), and a comparison of the diatom floras of stones and artificial substrata showed no significant differences (262). It should not be forgotten, however, that many invertebrates graze on attached algae, and if they avoid an artificial surface the algae there will be favoured to an unnatural degree. That they can be selective for natural surfaces, even algal ones, is shown by the work of Picken (484). In view of the simplicity of the method and its frequent use, there is an urgent need for critical examination of it from the aspects outlined above. There is, however, no doubt that this is a very useful method for obtaining and studying little-known algae, and the structure and reproduction of attached algae generally.

No accurate quantitative method of collecting algae living unattached on the deposits has been devised. Soft deposits free of obstructions are best sampled with a Jenkin surface-mud sampler (427), a small, simplified version of which can be operated by hand from a small boat. The Jenkin sampler collects a relatively undisturbed water column, and the tubes can be transported without disturbance if carefully packed and handled. Outside the central regions of lakes it is rare that soft deposits are sufficiently deep and free enough from obstructions for the use of such a sampler. In littoral areas, and shallow bodies of water generally, these unattached algae can be removed by suction (81, 374, 376, 554), using a hand- or foot-operated pump and sucking the surface deposit and water through a funnel. The funnel is passed over the deposit in the manner of a vacuum cleaner, and its mouth is screened to avoid particles (e.g., leaves) which might block the inlet. This method collects neither comparable samples from different types of substrata nor the same ratio of mud to water from any one area on each occasion of sampling.

There are several devices for sampling deposits in depth. The first real advance over samplers which were devised for deposits

on land such as peat (e.g., the Hiller borer), or were generally cumbersome and did not collect undisturbed cores of underwater soils, was the Jenkin core-sampler (284, 285; for earlier methods, see 731). The famous Kullenberg (347, 347a; see also 476 for a possible earlier version) piston core sampler for deep-sea deposits has inspired useful lightweight versions or variants for lakes (368, 555, 687, 776, 777). There is, however, some disturbance of the mud-water interface, and this is claimed to be avoided in a more recent piston sampler (86; see also 555). A method for sampling subsurface deposits at small intervals of depth is described in 648.

Pollen analysis and other techniques used to determine the changes which have taken place in a lake's history are mainly outside our scope, but methods to determine the rate of sedimentation and to date the upper portions of cores have a direct bearing on the problem of assessing plant production. A possible method for relatively indestructible objects, such as diatoms, is the use of traps placed at various depths in the water or on the mud surface. A variety have been described (e.g., 227, 281, 321, 666), and the results have served to estimate the age of parts of cores (475, 677). From the use of such collecting chambers, from growth in water samples suspended at given depths and a knowledge of the standing crop, estimates of the rate of multiplication of diatoms and their rate of sinking have been made (227, 281, and p. 523). All such estimates must be viewed with some suspicion, for any collecting vessel will itself act as a trap, not only for material sinking from above but also for material passing over its mouth in horizontal water movements. In addition, material removed from the bottom deposits may be collected. Probably no method yet devised gives a true picture of the rate at which sediments are built up. In a few cases, recent changes in production (i.e., over the last hundred or so years) have been determined by an examination of the diatoms present, the presence or absence of black bands of sulphides (notably iron sulphide) and records of plankton collected in the surface waters (420, 448, 475, 776). Again such exact dating, particularly when on a yearly basis, should often be viewed with reserve. Profundal animals, notably oligochaetes, often disturb sediments to a greater or lesser degree (see 61, 88, 379, 514, 553, 648, 665). A marked chemical stratification, such as black sulphide rings, may appear at levels which do not corre-

spond in time with the development of intensification of anaerobic conditions in the lower layers of a lake water, for the diffusion of hydrogen sulphide through a core rich enough in iron may result in the formation of Liesegang rings (647, 688).

TREATMENT OF COLLECTED SAMPLES

GENERAL REMARKS. "To my thinking every one . . . should first become fully acquainted with the algae in a living condition" (178, p. xv). This statement applies to several aspects of work besides identification. However, storage during long journeys usually involves some decomposition, so a method for field examinations may be useful. Indeed, there are portable microscopes on the market with which all normal work, including high power magnifications are possible. The most remarkable of them is the microscope of McArthur (386–388), of revolutionary design and first class workmanship. Under three pounds in weight and measuring $4 \times 2\frac{1}{2} \times 2$ inches it is indeed a "pocket" microscope but is claimed "to be capable of any work normally undertaken by a conventional research microscope". Its only disadvantage for field work may seem to be that slides are examined upside down, so that only relatively fine films of water can be permitted between cover-glass and slide without wetting the instrument. This need not be the case, for there is room for the equivalent of a counting chamber. Moreover, it is presumably possible to use a large coverslip as a slide and to examine through this "slide" without exceeding the working distances of many lenses.

As a general rule, no treatment or examination should be carried out in the field, where conditions are often difficult, if it can be done later in the laboratory. The same remarks apply to mobile laboratories (365, 563), although suitably equipped vessels may be essential for some river studies (e.g., 658). Some chemical determinations (e.g., of dissolved oxygen) may require manipulations or estimations in the field, and for these special equipment may be valuable (e.g., 85, 593, 735), particularly if it is easily portable.

PLANKTON. It is often necessary to preserve plankton either for counting or to keep samples for future reference. No killing agent is equally suitable for all purposes, and osmic acid, which is perhaps the best of all, is so expensive that it can be used only with very small volumes of water. The most widely employed pre-

servative is formalin (2–4%), but many delicate algae, notably flagellates, are destroyed by it (e.g., 351), and Myxophyceae with gas vacuoles will not sediment for counting. Lugol's solution—a saturated solution of iodine in a saturated aqueous solution of potassium iodide—preserves such algae though not always in an identifiable form if fresh material or that killed in osmic acid has not been examined first; it also discharges the gas vacuoles of Myxophyceae. Though the authors have not experienced this (see also 130), it is said that some small flagellates (μ-flagellates) are destroyed by Lugol's solution (552).

Plankton must often be concentrated in order to estimate the size of the crop. It may be left to sediment under the action of gravity, be centrifuged or filtered. The first investigations based on sedimentation were not very successful because of the unsatisfactory fixatives employed (e.g., formalin and ethyl alcohol—717, 718). In using Lugol's iodine solution, all algae will sediment so that the method is particularly effective with an inverted microscope, though not in waters rich in detritus (679). Nevertheless, the production of an artificial floc has been an aid for sedimentation, notably aluminium hydroxide on the same principle as it is commonly used as an aid to filtration and clarification in waterworks (33, 45, 637). This floc may be equally serviceable in centrifuging, a method often resorted to (e.g., 45, 63, 219, 222, 305, 306, 637). Addition of $Al_2(SO_4)_3$, combined with reducing the pH to 4.5–5.0, has had success with Myxophyceae (192, 195). Centrifuging generally cannot be applied to live material because some algae (e.g., Myxophyceae) are less dense than water and others, such as flagellates, are very easily destroyed (e.g., 375). It appears, however, that marine flagellates are less easily harmed (45). Equally, the use of a suitable killing agent may protect the cell-structure from damage. Some organisms may adhere to the sides instead of passing to the bottom of a centrifuge tube, but this will be avoided if the tubes are regularly cleaned in chromic-sulphuric acid and washed down after removal of the superatant water. Another source of error is said to be that vortices may be formed when the centrifuge is stopped, but this, too, can be avoided if there is gradual reduction of the speed of rotating (220). Nor will there be any loss of cells when removing the supernatant water in the centrifuging tubes if a tube or pipette

with an upturned end is used (87). Wulff's (765) claim that this method is satisfactory if the tubes are closed with corks and fastened horizontally does not appear to be supported by other workers. A comparison between the clinical electric centrifuge used by Gran (222) and a Foerst centrifuge showed that the former yielded results which were lower by approximately 30% (367). The organisms concerned were not recorded but the speed of the Foerst centrifuge was such (20000 r.p.m.) that delicate algae may well have been more or less completely disintegrated as is true of a Sharples centrifuge (unpublished observations of the first author). It does, however, seem likely that many of the earlier estimations based on centrifuging, in some cases with hand-centrifuges, were too low. The general applicability of the method is, however, still doubtful. Schmidt-Ries (588) and Křiženecky (342), after thorough investigations, came to the conclusion that repeatable, accurate quantitative results cannot be obtained (cf. 624, 679, pp. 482–492; 682, 729). Since other methods are available, Schmidt-Ries considers centrifuging is best used only as a qualitative method, though this is not the conclusion reached in a recent investigation (45). Further work is clearly needed.

Microfiltration (43, 208, 246, 329, 679, 682, 775) has recently come into much greater favour for collecting the smallest nannoplankton algae and bacteria (45, 57, 119, 126, 213, 216, 280, 405, 590, 591). The so-called "molecular" filters composed of incompletely cross-linked high polymer molecules (e.g., cellulose acetate and nitrate) are a great improvement on the old clay or collodion types. A wide range of pore size is available so that organisms of varied range of size can be collected. Even colloidal and other finely divided particulate matter (leptopel) can be collected by the recently devised autofilter (173, 174). Though such matter may be of most interest to those studying filter-feeding animals (296), algae, too, may depend on it in part as a nutrient source (e.g., iron, 215). It is of particular interest that in the sea (464) and very probably in freshwater some of the smallest algae are phagotrophic and ingest such small visible particles, so that utilisation of collodial matter is a possibility.

In order to be able to see the organisms, the membrane must be destroyed, dissolved out or cleared and mounted, and various procedures have been devised (4, 45, 126, 246, 405, 590, 682).

Though it is claimed that microfiltration and subsequent preparation for examination under the microscope do not cause any loss of cells or so great a degree of damage that they are unrecognisable, it does not appear that as yet this is certain. Similarly, the distribution of the algae on the membrane does not seem to have been always tested. Though it has long been known that minute algae abound, there has been no satisfactory method of concentrating the smallest (which may be less than 5 μ in diameter) so that they could be counted, for which immersion lenses are essential.

BENTHOS. Whenever possible, removal of algae from their substrate should be carried out in the laboratory, but the possibilities are limited to those objects, such as small stones, portions, reeds and submerged aquatics and bryophytes, which can be transported in bottles or bags. As no one has yet devised a method of removing rock surfaces in the field in such a way that all the algae are collected in a recognisable form, quantitative work is of limited extent (e.g., 136). Brushing and scraping stones, though satisfactory for diatoms and some Myxophyceae, does not remove many encrusting algae without so much damage that quantitative work is impossible. A technique for stripping all the algae from such surfaces, using collodion (402, 403, 508a), is based on the well-known procedure for fossil material. The algae must be fixed and then stained. The method does not appear to have been called upon widely enough yet to assess its value. Algae epiphytic on some macrophytes may be determined by direct microscopic observations (211, 212) with or without stripping off the epidermal or other outer layers of the organs concerned.

In the case of soft deposits where the cells may be obscured by the particles present, the technique of fluorescent stains may be applicable. So far this method has been used only for soil (662, 663) and marine algae (764), though a similar method has been found to distinguish between dead and live freshwater bacteria and algae (104, 645).

The motile algae which abound on soft deposits are almost invariably positively phototactic, provided the light source is not too intense. They can, therefore, be concentrated by leaving a sample for some hours in relatively weak light in dishes which are blackened except for a small area facing the light (374) or by placing microscope coverglasses on top of some of the deposit and illumi-

nating it from above (375, 554). The former method is particularly for flagellates, the latter for creeping forms such as diatoms, many Myxophyceae and some desmids.

POSTSCRIPT

A large number of methods have been referred to and in conclusion we cannot do better than quote Dr. Richard H. Fleming's (165) remarks concerning oceanography, which apply equally to limnology: "We are living in an age of gadgets. By all means let us take advantage of their help but do not let them become our masters. Our knowledge of the oceans is so fragmentary that the main problem is often to decide *what* to measure, not *how* to measure it. Instruments cannot take the place of brains and can be of real assistance only when we tell them what to do. In the present stage of development of oceanography it is essential that there be full cooperation between the theoretical worker, the field investigator, the analyst and the instrument designer. If such coordination is developed and we maintain a proper distribution of effort between them, rapid progress will be assured".

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ADDRESSES OF SOME INSTITUTES MAINTAINING COLLECTIONS OF CULTURES OF ALGAE

1. L'Algothèque, Laboratoire de Cryptogamie du Muséum, 12 rue de Buffon, Paris V^e, France. (Dr. P. Bourrelly).
2. The National Type Culture Collection of Algae and Protozoa, Cambridge. (Mr. E. A. George).
3. Sammlung von Algenkulturen, Pflanzenphysiologisches Institut, Göttingen, Untere Karspüle, Germany. (Prof. Dr. E. G. Pringsheim).
4. Culture Collection of Algae, Dept. of Botany, Indiana University, Bloomington, Indiana, U.S.A. (Dr. Richard C. Starr).
5. Sammlung von Algenreinkulturen beschriebener Arten, Botanisches Anstalt der Universität, Basel. (Prof. Dr. W. Vischer).