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SYSTEMS ANALYSIS AND SIMULATION IN ECOLOGY

Edited by BERNARD C. PATTEN

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VOLUME I

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Edwin Moul and Murray Buell
AT RUTGERS

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Preface

This is a book of ecology in transition from a "soft" science, *synecology*, to a "hard" science, *systems ecology*, in which the lens of H. T. Odum's "macroscope"[1] on the world of big patterns is the machinery of mathematical modeling, simulation and systems analysis. The book is substantially the creation of young people at a time when youth in America is experimenting with, if not revising and reorganizing, the ethical and moral basis of contemporary civilized life. The systems theme is central in this exploration in its two salient aspects, *change* and *relationship*, and its current pervasiveness in science as well as in society seems no accident as the world presses closer together in the last third of the Twentieth Century.

Soft ecology of the past[2] has identified in nature a hierarchy of organism/environment units, each maintaining structural and functional identity while evolving in the large and fluxing constituents in the small. Such a conception is quintessentially an organismic one, with philosophical overtones that have led recently to an eruption of public concern about the fate and well-being of the planetary "organism" in the face of human extravagance. This book is an enthusiastic and optimistic statement about the fundamental adaptability of the scientific mechanism to newly appreciated truths of existence. It documents, in ecological science, a move away from the explanatory or cognitive criterion of truth, a soft criterion which heuristically lends intellectual points of leverage for seeking understanding, and toward the predictive criterion, a hard one with the potential of leading ultimately to optimal design and control of ecosystems.

[1] Odum, H. T. (1971). "Environment, Power and Society." Wiley (Interscience), New York.

[2] The terminology is that of Rapoport, A. (1970). *Genl. Syst. Yrbk.* **15**, 15.

Systems ecology, in its infancy, is a "bisociation"[3], a hybrid intersection of two branches of science, biology and engineering, previously disconnected. Such a juxtaposition is not new to biology, recalling earlier associations with exact sciences like chemistry and physics that proved so potent in the microscopic concerns about organisms, and indeed, that became the dominant biology of recent years. This new bond comes fortuitously, or perhaps providentially, at a time of winding down of technology in the human appreciative system, with concommitant release from productive work of skilled engineers trained in the hard aspects of systems. Ecologists need only open the door ever so slightly and one can easily forecast a shotgun marriage in only a few years, and an explosive development of the predictive potential. Indeed, it has already begun to happen. Take, as a single example from many indications, the statement last April by Frank C. Rieman, President of SCi (Simulation Councils, Inc.), redirecting the purposes of that entire engineering society:

> . . . SCi has its roots in analog computation in the aerospace industry, from which it grew naturally into the field of hybrid computation. This history dominates the society's image today. The Executive Committee feels that it is now time to change that image. . . . We would like to direct the effort of the Society toward mathematical modeling and specific applications, independent of computational technique, rather than the analog/hybrid hardware orientation we now seem to have. . . . The Executive Committee is recommending that the attention of SCi, as a society, be directed toward solution of problems in the environmental and ecological areas.

This book, written in the language of systems scientists, should help accelerate development of an inevitable kinship between them and ecologists by demonstrating multifariously how ecology can be cast in their terms.

I take particular pleasure in having the work of a number of my students on exhibit here. Students have been the mainspring of my development as a systems ecologist, and they continue to challenge and question the many tentative and half-baked notions that seem to be integral in the learning process. All my students, including those not represented in these pages, deserve special recognition for the unique and significant role they have played and continue to play in this challenging enterprise.

[3] Kestin, J. (1970). *Am. Scient.* **58**, 250.

There are also debts to the past and I discharge, in a small way on the dedication page, the two of profoundest meaning to me. These two men taught and practiced ecology that was of a kind whose kernel should be conserved wherever this field leads from here. It was an ecology of interrelationships that did not fail to look closely and intimately at the players. It was a field ecology, a natural history ecology, but profoundly an ecology of systems.

Throughout this project my wife, Marie, encouraged and prodded and absorbed externalities at home. Thelma Richardson aided in various programming and editorial chores, particularly in the final stages. And Bill Cosgrove, my department chairman, provided an outstanding climate for unencumbered academic pursuits at the University of Georgia. For these assistances, I am grateful. But the book belongs to the authors, and I would like especially to aknowledge and congratulate them all for their roles in bringing it to fruition.

Athens, Georgia
January, 1971

BERNARD C. PATTEN

PART I

INTRODUCTION TO MODELING

A science is known by its methods, and ecology as "the painful elaboration of the obvious" has for a long time followed the questionable path of seeking insights by pushing numbers around. "Quantify and clarify" has been the paradigm of much contemporary study, and the illusion of synecology as a "hard" science has been provided by widespread use and misuse of statistical methods, which have enormous predictive appeal if little explanatory power.

Systems ecology does not lean heavily upon numbers until the latter stages of an investigation. It differs from statistical ecology in its greater emphasis on the explanatory criterion of truth as applied to holistic behavior. It accepts as an operating principle that no complex system can be fully known in all of its interactive details, and accordingly seeks to elucidate global properties that characterize "core" dynamics, the broad set of possibilities from which actual behavior is generated according to environmental inputs. The current method of systems ecology is mathematical modeling, for the dual and distinct purposes of simulation and systems analysis. This section provides an overview of some of the methods and rationales for ecological systems modeling in relation to these purposes.

Chapter 1 is an elementary introduction to the use of analog and digital computers for simulation. The presentation is tutorial, designed to bring the reader with modest mathematical preparation quickly to the point of being able to use modern computing machines effectively. In a sense the treatment is selective and superficial, sparing many details, but it offers the proven advantage of giving a fast return in satisfaction to the new student of simulation. The methods selected, and how they are presented, are the result of a number of years of classroom sifting and sorting. The treatment centers on compartment models and their expression by means of ordinary differential equations.

Analog computation is covered first, as the surest way to captivate a new audience.With a variety of graphic outputs available, and instantaneous turnaround time, there is no better approach to developing a subjective appreciation for what holism is all about in connection with system dynamics. At the turn of a potentiometer dial an individual can alter system inputs, outputs, or internal connections, and observe immediately the behavioral consequences, or lack of them, of his act. Fortran programming, only as much as necessary, is introduced next and, with a presentation of numerical approximation methods, the reader is encouraged by examples and exercises to retrace the same ground on the digital computer that he has just covered with the analog. Thus gaining familiarity with some of the undesirable as well as desirable features of simulation by Fortran, the instruction loop is closed by introducing one of the modern simulation languages, S/360 CSMP. This language essentially makes an analog computer of the digital machine, except for turnaround, and so simple is its use that it could well have been introduced first were it not for the pedagogical advantages of the preceding analog and Fortran struggles. A reader who masters this chapter is well on his way to effective computer use as a basis for his further progress in systems ecology.

Chapter 2 presents a rationale for ecological model-building in the context of a particular system of interest to the author, the pine-mor food web. Stages in model formulation are

divided into five steps, each one being discussed in detail. A Fortran program for the resultant model is presented, with description and analysis of its main features. Then, a distinction between non-dynamic and dynamic state variables is made, and a procedure for eliminating the former (represented by algebraic equations) to obtain a differential equations model for systems analysis (as opposed to simulation) is described. At this point, the mathematics becomes scaled up as Dr. Kowal begins a treatment of the main outlines of linear and non-linear systems analysis. Transient and frequency response are briefly described, followed by a consideration of stability as approached in classical dynamic analysis. The Lyapunov stability theorems are stated, and the methods associated with them outlined and evaluated for their ecological significance. Finally, the subject of system optimization is reviewed in terms of the possibilities for eventual optimal control of ecosystems.

The distinction between simulation and systems analysis, implied by this book's title, should be clearer for the reading of these two chapters. It is further clarified in subsequent sections, particularly in the chapters of Part III—and Part IV (in Vol. II).

1

A Primer for Ecological Modeling and Simulation with Analog and Digital Computers

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Based on a tutorial lecture and workshop series presented September 4–6, 1968 at Columbus, Ohio, August 19–21, 1969 at Burlington, Vermont, and August 24–26, 1970 at Bloomington, Indiana under auspices of the BioInstrumentation Advisory Council, American Institute of Biological Sciences.

University of Georgia, *Contributions in Systems Ecology*, No. 3.

I. Dynamic Modeling of Ecological Systems

A. State of a System

The word *system* is so overused in everyday language that there is a tendency to forget what it means. A *system* is an assemblage of objects united by some form of interaction or interdependence in such a manner as to form an entirety or whole. This is essentially a dictionary definition which can be made slightly less abstract in relation to physical or biological systems: A *system* is a group of physical components connected or related in such a manner as to form and/or act as an entire unit.

The concept of system state is intuitive. The *state* of a system is its mode or condition of being. In systems science, the state usually is given an operational definition in terms of state variables: The *state* of a system is the condition of its state variables. The *state variables* of a system are its component parts or observable attributes, or arbitrary groupings of parts or attributes for particular purposes.

Thus, operationally the definition of a system is a matter of choice, a function of the observer more than of the thing observed. Specification of the state of a system must be in terms of arbitrarily defined state variables.

B. Change of State

Let

$$X(t) = \{x_1(t), x_2(t),..., x_n(t)\}$$

represent the state of a system with n state variables $x_i(t)$, $i = 1, 2,..., n$. Each state variable is a *function* of time t as indicated by the use of functional notation from mathematics: $x_i(t)$. If the variables are understood to be functions of time, it is not necessary to write this *argument* explicitly every time the variable is written. Thus, the *state set* given above can be written equally well as

$$X = \{x_1 , x_2 ,..., x_n\}$$

without any loss of meaning. Later we will be working with *state vectors*

$$\mathbf{x} = (x_1 , x_2 ,..., x_n) \qquad \text{and} \qquad \mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{bmatrix}$$

in which the variables are arrayed in a definite order, unlike sets which merely represent a collection of variables.

If $X(t)$ is the state (set) of a system at time t, then its state after a unit of time has passed can be represented as $X(t + 1)$. If at least one of the n state variables has changed in this time interval, $X(t) \neq X(t + 1)$, the system has undergone a *change of state*, definable as the difference between the old state and the new state. If $x_i(t)$ is the old state of variable i and $x_i(t + 1)$ the new state, then the variable change in the unit time interval can be denoted by $\Delta x_i = x_i(t + 1) - x_i(t)$. More generally, if after a time interval Δt the variable has changed from $x_i(t)$ to $x_i(t + \Delta t)$,

then the *amount of change* which has occurred can be expressed as $\Delta x_i = (x_i(t + \Delta t) - x_i(t))$, and the *rate of change* by

$$\frac{\Delta x_i}{\Delta t} = \frac{x_i(t + \Delta t) - x_i(t)}{\Delta t}.$$

Change, or lack of it, constitutes system behavior. The *behavior* of a system is its mode of acting or, more operationally, a sequence of state changes in time. The sequence may be *discrete* or *continuous*.

C. Deterministic and Stochastic Systems

Consider an abstract system with 16 possible states: A, B,..., P (the letters denote state-variable sets). Suppose the behavior of the system is defined as

$$\begin{array}{c} A\ B\ C\ D\ E\ F\ G\ H\ I\ J\ K\ L\ M\ N\ O\ P \\ \downarrow \\ D\ H\ D\ I\ P\ G\ P\ H\ A\ E\ E\ N\ B\ A\ N\ E \end{array}$$

That is, if the system is in state A it changes to D, if in B to H, and so on. This is a *deterministic* system because prior states determine succeeding ones with unit probability. If, for example, $A \rightarrow D$ with a probability $p = .8$, and to some other states with $p = .2$, the system would be termed *stochastic*. Its behavior is probabilistic.

D. Static and Dynamic Systems

Behavior of the above system can be represented by a "graph" of its sequences of state changes. That is, if the system is in state M, then the subsequent sequence will be $M \rightarrow B \rightarrow H\circlearrowright$. The graph of the entire system behavior is shown in Fig. 1. This *behavior graph* shows at a

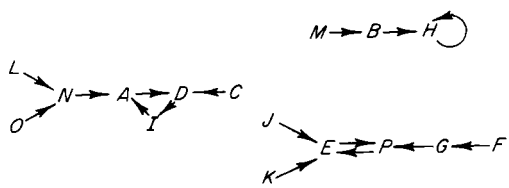


Fig. 1

glance that, depending on the initial state, the system will advance through a sequence of states to one of three sets of states where it will remain. These sets are the self-loop $H\circlearrowright$, and the cycles $E \rightarrow P \rightarrow E \rightarrow \cdots$,

and $A \rightarrow D \rightarrow I \rightarrow A \rightarrow \cdots$. The states contained in these sets, $\{H, A, D, I, E, P\}$, are system *steady states*, and the remaining states, $\{B, C, F, G, J, K, L, M, N, O\}$, are termed *transient states*.

Example 1

Ellison (1954) recognized distinctive vegetation states (communities) in a phytosociological study of the high-mountain Wasatch Plateau in Utah

X_1 = talus vegetation, X_6 = grassland,
X_2 = ephemerals, X_7 = low shrubs,
X_3 = spruce–fir, X_8 = forbs,
X_4 = tall shrubs, X_9 = erosion pavement community,
X_5 = mixed herbs, X_{10} = rock crevice plants.

The natural behavior of this system (succession) is altered if sheep or cattle are grazed, either separately or together. Five classes of grazing influence were distinguished

1 = no grazing,
2 = sheep only,
3 = cattle only,
4 = sheep and cattle simultaneously,
5 = sheep and cattle alternately.

The behavior of this system can be summarized by means of a "transformation matrix"

↓	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
1	X_2	X_3	X_4	X_5	X_5	X_5	X_5	X_5	X_1	X_1
2	—	X_9	—	—	X_6	X_2	—	—	X_{10}	—
3	—	X_9	—	—	X_8	—	—	X_2	X_{10}	—
4	—	—	—	—	X_7	—	X_2	—	—	—
5	—	X_9	—	—	—	—	—	—	X_{10}	—

Dashes indicate only that the particular grazing combination of that row does not act on the system state in whose column a dash appears. The behavior graph of the system is shown in Fig. 2. The bold arrows indicate the sequence of state changes in absence of any grazing; this is the normal successional behavior leading to the climax state X_5 which is indicated

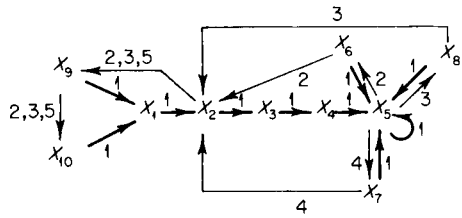


FIG. 2

by a self-loop. Note that any form of grazing disturbance causes the system to retrogress to an earlier state in the developmental sequence.

Systems which do not change are *static* or *constant*; they are represented by the self-loop form of steady state. All other systems are dynamic.

Both static and dynamic systems are important in biology. In fact it gives some concept of the "state" of biological science at the present time to indicate that animals preserved in formalin, dried herbarium specimens, and freeze-dried tissues or cells all are examples of interesting (useful) static systems. Science still largely studies life through death. To study life as living will mean ultimately to develop an orientation to dynamic behavior and change, i.e., a systems orientation. Modeling and computer simulation will become indispensable to serious advances in this effort.

E. MODELS OF SYSTEMS

There is some vagueness about what a *model* actually is, and hence, about what kinds of information can be obtained from models. Many biologists think of models as miniature versions of some real system which will do everything the real system will. This is not only naïve and unrealistic, it is wrong.

Any real system can be looked at from many different points of view, and each one gives a different perspective on the system. All the perspectives do not equal the real system, because it will always be possible to find an additional one. But each view gives some information about the system, and a collection of views permits a system *concept* to be formed. This concept is a function of the observer only. The real system exists very well without it, and irrespective of whether it is "right" or "wrong."

All models, therefore, are abstractions. The degree of abstraction permissible is a value judgement to be made in context of the purpose at hand. The key to effective modeling is to strike a proper balance between realism and abstraction. Technically, a *model* is a "homo-

morphism" (Ashby, 1956) of some real system which it represents. That is, in modeling a *many–one correspondence* exists between the parts and state transformations of the real system and those of the model, with a corresponding sacrifice in behavior alternatives of the latter.

Example 2

Consider the two systems $X = \{X_1, X_2, f_1, f_2\}$ and $Y = \{Y_1, Y_2, Y_3, Y_4, Y_5, g_1, g_2, g_3, g_4\}$. The $X_1, X_2, Y_1, \ldots$, are states, and $f_1, f_2, g_1, \ldots$, are influences such as the five grazing influences of Example 1. Let the behavior of these systems be defined by the following transformation matrices

$\downarrow$	X_1	X_2
f_1	X_1	X_2
f_2	X_2	X_2

,

$\downarrow$	Y_1	Y_2	Y_3	Y_4	Y_5
g_1	Y_2	Y_1	Y_2	Y_3	Y_1
g_2	Y_1	Y_2	Y_3	Y_2	Y_3
g_3	Y_1	Y_2	Y_2	Y_5	Y_4
g_4	Y_2	Y_3	Y_1	Y_5	Y_5

.

The behavior graphs are shown in Fig. 3. There is little in either the transformation tables or the graphs to suggest that system X could serve

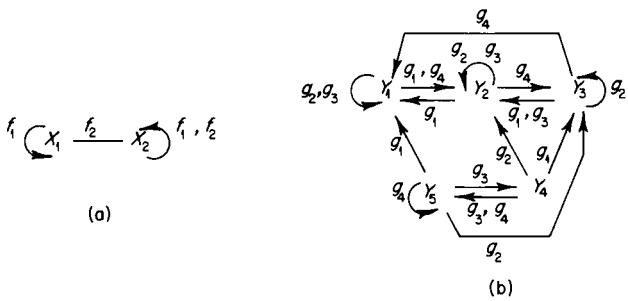


FIG. 3. (a) System X. (b) System Y.

as a model for Y. The two systems in fact appear quite unrelated. However, the following correspondences establish a homomorphism:

Substitute

A for Y_1, Y_2, or Y_3,
B for Y_4 or Y_5,
α for g_3 or g_4,
β for g_1 or g_2.

Then, define the correspondences

$$X_1 \leftrightarrow B, \qquad f_1 \leftrightarrow \alpha,$$
$$X_2 \leftrightarrow A, \qquad f_2 \leftrightarrow \beta.$$

Under these relations, a new transformation table for system Y is

$\downarrow$	A	A	A	B	B
β	A	A	A	A	A
β	A	A	A	A	A
α	A	A	A	B	B
α	A	A	A	B	B

or just

$\downarrow$	A	B
α	A	B
β	A	A

This new matrix becomes, upon interchanging columns, identical to the one given above for system X. The behavior graph is given in Fig. 4 which is identical also under the established correspondences. Thus X is homomorphic to Y and therefore a valid model of Y.

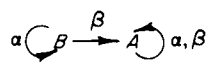


FIG. 4

The above example illustrates the important feature of models that they represent only limited aspects of the behavior of real systems. System X is only a partial representation of Y when Y is viewed in a certain way. This way is established arbitrarily—by the correspondences which define the homomorphism between the two systems. How *usefully* system X represents Y depends upon the needs of the investigator, and utility, not correctness, is the criterion by which models should be judged.

It was stated above, and it is repeated here for emphasis, that the key to effective modeling is the striking of an appropriate balance between realism and abstraction for the purpose at hand. If X is too abstract a representation of Y, then (in effect) another set of correspondences must be sought to establish a more realistic homomorph of the real system. It is well remembered that the only "complete" model of a natural system is the system itself, and to attempt exact one-to-one duplication in another medium, e.g., a computer program, is to fail to recognize the inherent limitations on modeling. More importantly, it betrays a lack of understanding of basic modeling rationale, which would seem a priori to foredoom the effort.

Example 3

King and Paulik (1967) presented three different models of rotifer populations.

a. *Model I.* This model abstracts the life cycle of monogonant rotifers (Class Monogononta: females with paired ovaries, mastax specialized for grinding plankton, detritus, etc. (i.e., ramate), and no secreted tube or lorica), which comprise 90% of known species. The state variables are different stages of the life cycle

X_1 = immature amictic females (2n, diploid),
X_2 = mature amictic females (2n),
X_3 = amictic eggs (2n),
X_4 = mictic females (2n),
X_5 = mictic eggs (n, haploid),
X_6 = resting eggs (2n),
X_7 = males (n).

The behavior graph is shown in Fig. 5. Both parthenogenetic and sexual cycles occur. In the first case mature amictic females (X_2) lay

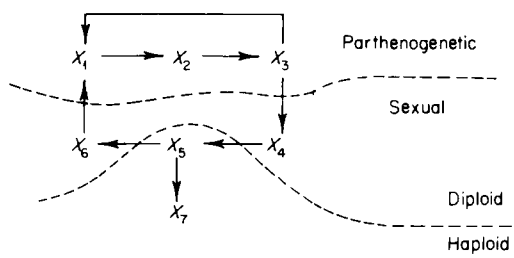


FIG. 5. Model I.

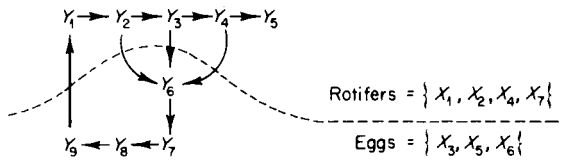
amictic eggs (X_3) which hatch into immature amictic females (X_1). In the bisexual mode the amictic eggs (X_3) hatch to produce mictic females (X_4). Presumably the environment regulates the production of amictic versus mictic females, but whether the influence is exerted on X_1, X_2, or X_3 is not, apparently, known. The mictic female meiotically produces haploid mictic eggs (X_5) that hatch into males (X_7) if unfertilized. If fertilized, the mictic eggs become resting eggs (X_6), and after some time delay these hatch into immature amictic females (X_1).

b. *Model II.* This model is a different view of the same system. The state variables are age categories of animals and eggs

Y_i = population density of rotifers in ith age category ($i = 1, 2, \ldots, 5$),

Y_j = density of eggs in $(j - 5)$th age category ($j = 6, 7, \ldots, 9$).

The behavior graph is shown in Fig. 6a. The sequence of states $Y_6 \rightarrow Y_7 \rightarrow Y_8 \rightarrow Y_9$ serves to lag an egg for the period of time between laying and hatching.



(a)

FIG. 6. (a) Model II.

c. *Model III.* A third concept of the rotifer system is given by the following model. Instead of dividing the life-span of the animal into days, it is divided into reproductive periods. The state variables are reproductive periods

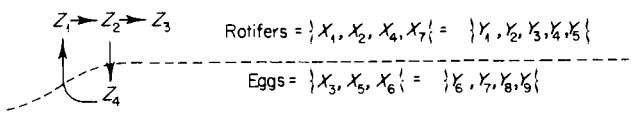
Z_1 = immature rotifers,

Z_2 = mature rotifers,

Z_3 = postreproductive animals,

Z_4 = eggs.

This model is more practical for field studies because of difficulties in distinguishing X_2 and X_4, and X_3, X_5 and X_6 in model I, and of aging animals and eggs in model II. The behavior graph is given in Fig. 6b.



(b)

FIG. 6. (b) Model III.

These three models each give a different concept of rotifer populations and, because of the way they are structured, have different data requirements for implementation and yield different forms of information about rotifers. The animals themselves never differ, only the models.

F. Population Growth: Exponential

None of the models of Example 3 is yet complete enough to permit quantitative study of its dynamic behavior. Working toward this end, consider the traditional models of population growth.

Let density $N(t)$ of a plant or animal population be the only characteristic of that system of interest. The state of the system is then defined by the single state variable $N(t)$, a function of time. If the birth and death rates, b and d, are constant (do not change as a function of the argument time), then the *rate of change* of population size dN/dt is given by the difference between population gains and losses

$$dN/dt = \mathrm{b}N - \mathrm{d}N = (\mathrm{b} - \mathrm{d})N = rN.$$

The difference between birth and death *rate constants* r is termed the "biotic potential," "specific growth rate," or "intrinsic rate of natural increase" of the population.

This is a *differential equation* because it contains a derivative of the state variable. Dynamic systems frequently are modeled by means of differential equations. An *analytical solution* of a differential equation is an algebraic equation, free of derivatives of the dependent (state) variable with respect to the independent variable(s), which relates values of the independent variable to those of the dependent variable. With an analytical solution, it is possible to substitute values of the independent variable and calculate corresponding values of the state variable.

Example 4

The analytical solution of the population growth equation,

$$dN(t)/dt = rN(t),$$

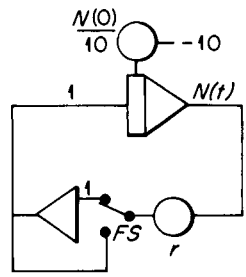
is

$$N(t) = N(0)\, e^{rt}.$$

Knowing the initial population density $N(0)$ the density at any time $t \geqslant 0$ can be computed.

In analog computation, a program for obtaining the solution is shown in Fig. 7a. In digital computation, a Fortran segment for obtaining the same solution is

```
      REAL N
10    DN = DT * (R * N)
      N = N + DN
      GO TO 10
```



(a)

FIG. 7. (a) Analog computer program for solving population growth equation.

An analytical solution is obtained in the following manner:

(1) Begin with the differential equation

$$dN/dt = rN.$$

(2) Separate the variables

$$dN/N = r\,dt.$$

Then N appears on the left-hand side and everything else on the right.

(3) Integrate both sides

$$\int dN/N = \int r\,dt$$

$$\ln N + C_1 = rt + C_2\,.$$

Since differentiation and integration are inverse operations, the derivative is integrated away. Let C_1 and C_2 be arbitrary constants of integration; they can be combined into a single constant, $C = C_2 - C_1$

$$\ln N = rt + C.$$

(4) Exponentiate both sides

$$e^{\ln N} = e^{rt+C}$$

$$N = e^{rt} \cdot e^{C} = C'e^{rt},$$

where $C' = e^{C}$.

(5) Evaluate C' at $t = 0$

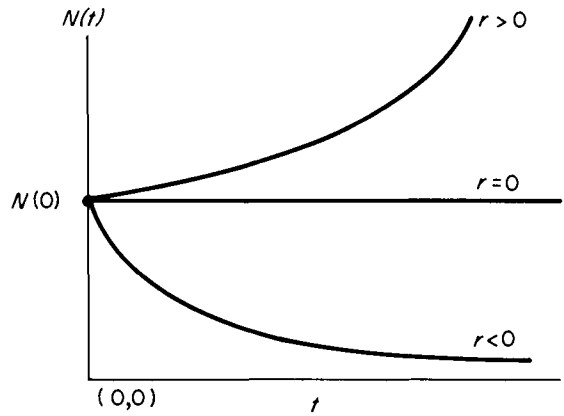
$$N(0) = C'e^{r\cdot 0} = C'.$$

(6) Substituting

$$N(t) = N(0)\, e^{rt},$$

the desired result.

A graph of this solution for three possible cases is shown in Fig. 7b. (1) If the birth rate exceeds the death rate ($r > 0$), the population grows exponentially at a rate determined by the value of r. The system never



(b)

FIG. 7. (b) Three cases of exponential growth equation solutions.

has a steady state when $r > 0$ since the population continues to grow as t gets larger. (2) If birth and death rates are equal ($r = 0$), $N(t) = N(0)$ always, and the population is in perpetual equilibrium, with a behavior graph which is a self-loop. (3) Finally, if the death rate is greater ($r < 0$), then the population declines exponentially to zero size as $t \to \infty$ in the limit. The steady state of $N(t) = 0$ is never actually reached; it is said to be approached asymptotically.

The remainder of this chapter will not be concerned with analytical solutions of differential equations, but rather with development of programs, such as the two illustrated in the above example, which permit obtaining solutions by analog and digital computers.

G. POPULATION GROWTH: LOGISTIC

Populations in nature do not, of course, grow without bound. As populations get large, they become either self-inhibited or environment-limited—internally or externally controlled. Early stages of growth may

be exponential, but increased density leads to greater and greater departure from the exponential growth form, producing the well-known s-shaped curve of growth shown in Fig. 8. This sigmoid pattern is accounted for by, among others, the logistic model, which can be

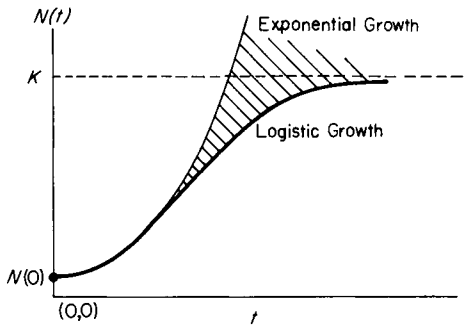


FIG. 8

formulated in terms of either self-inhibition by the population, or in terms of environmental limitation.

The first form is

$$dN/dt = (r - cN)N,$$

which displays the growth rate (the terms in parentheses) as a decreasing function of population size. The constant c represents reduction of the growth rate per unit of N. The product cN is the total reduction, often termed "environmental resistance." The logistic differential equation is *nonlinear* because the state variable N appears raised to a power higher than one. The exponential equation was *linear*.

The environmental–resistance aspect of this theory is brought out explicity by defining a parameter K, the maximum supportable population density in a given environment. In Fig. 8, K is the asymptote of the sigmoid curve and is termed the "carrying capacity" of the environment. Letting $c = r/K$, the logistic equation can be rewritten in the following forms

$$\frac{dN}{dt} = \left(r - \left(\frac{r}{K}\right)N\right)N = rN\left(1 - \frac{N}{K}\right) = rN\left(\frac{K - N}{K}\right).$$

These forms display the product rN from the exponential model diminished by the expressions within parentheses.

Note in the figure that logistic population behavior involves only dynamic states, technically, since the steady state $N = K$ is approached only in the limit as $t \to \infty$.

II. Elements of Analog Computation

A. Introduction

Analog computers essentially are single purpose devices: they solve differential equations. Consequently, they can be used to simulate and analyze the behavior of models which are expressed as systems of differential equations. There is only one independent variable available—time—and one dependent variable—voltage. Different computers have different reference voltages, usually 10 V or 100 V. This chapter will assume a 10-V machine, so that all the behavior of a simulated system must take place within the voltage range $-10 \leqslant E \leqslant 10$. For ecological systems this becomes in practice $0 \leqslant E \leqslant 10$ since negative quantities generally are inappropriate.

The computer consists of a set of basic components which can be interconnected so that they are governed by the same differential equations as those which represent the model of the real system. These components are capable of (1) summation, (2) integration, (3) multiplication, and (4) arbitrary function generation.

B. Operational Amplifiers

High gain, operational amplifiers are the basic functional units in modern, electronic analog computers. A *linear amplifier* is a device which augments a signal by a factor μ termed the *open-loop gain.* Gains can be of magnitudes 10^8 or higher. A common *reference level* or *ground* (0–25 μV) exists between the amplifier input and output. All voltages are measured relative to this reference level (see Fig. 9). The symbol for a high-gain linear amplifier is, as shown, a triangle with a curved back representing the input side. Note that a characteristic of the amplifier is that on output it reverses the polarity of the input signal.

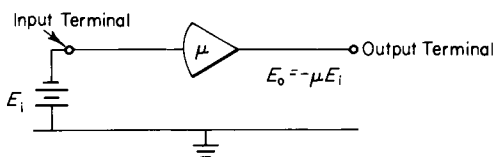


Fig. 9

C. Closed-Loop Gain

If input and feedback impedances, Z_i and Z_f, respectively, are introduced into the circuit of a high-gain amplifier, the configuration shown

in Fig. 10 results. Here E_g is the voltage at the amplifier grid; I_i is the input current, I_f the feedback current, and I_g the grid current, $I_i + I_f$.

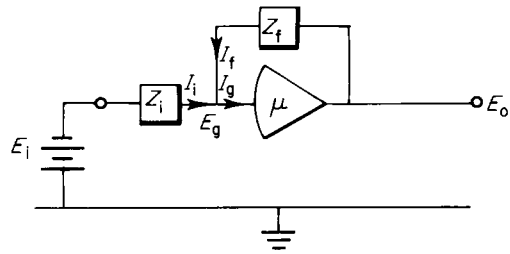


FIG. 10

Fundamental Gain Theorem

The gain of an amplifier containing an input and a feedback impedance is approximately equal to the ratio of the feedback impedance to the input impedance.

Proof:

(1) The open-loop gain is $E_0 = -\mu E_g$.

(2) From Kirchhoff's first law (the algebraic sum of currents flowing into any point in a circuit is zero) the grid current is zero

$$I_g = I_i + I_f = 0.$$

(3) From Ohm's law,

$$I_i = \frac{E_i - E_g}{Z_i} \quad \text{and} \quad I_f = \frac{E_o - E_g}{Z_f},$$

which, substituted into the previous result, gives

$$\frac{E_i - E_g}{Z_i} + \frac{E_o - E_g}{Z_f} = 0$$

$$\frac{E_i}{Z_i} + \frac{E_o}{Z_f} - E_g\left(\frac{1}{Z_i} + \frac{1}{Z_f}\right) = 0.$$

(4) Substitute $E_g = (1/\mu)E_o$

$$\frac{E_i}{Z_i} + \frac{E_o}{Z_f} + \frac{1}{\mu}E_o\left(\frac{1}{Z_i} + \frac{1}{Z_f}\right) = 0.$$

(5) Since μ (open-loop gain) is very large, the third term virtually vanishes, leaving

$$E_0 \doteq -\left(\frac{Z_f}{Z_1}\right) E_1 ,$$

the desired result.

For multiple inputs it can be shown in the same manner that

$$E_0 \doteq -\left(\frac{Z_f}{Z_1} E_1 + \frac{Z_f}{Z_2} E_2 + \cdots + \frac{Z_f}{Z_n} E_n\right).$$

These results lead to the definition of the *closed-loop gains* of a linear amplifier as the ratios of the feedback impedance to the input impedance associated with each input voltage. Note that the output voltage of an amplifier with input and feedback impedances is dependent only upon the closed-loop gains, and not on the intrinsic open-loop gain of the amplifier itself. The open-loop gain is so large that small input voltages (a few microvolts) could produce several volts of output. Also electronic noise could distort considerably the output signal. Noise-free, undistorted gains of 1 to 20 are achieved by introducing the negative feedback loop, and this feedback essentially trades quantity of gain for quality (accuracy and stability). The term *feedback* signifies that a portion of the ouput voltage is returned to the input. It is "negative" because the returned voltage is opposite in polarity to the input voltage.

D. The Summing Amplifier

When both input and feedback impedances are resistances R, the resulting device—a *summer*—is capable of adding voltages. A general schematic for a summing amplifier is given in Fig. 11. In analog computer programs, this same unit is represented by the symbol shown in Fig. 12, where the G's are closed-loop gains. The output voltage is thus $E_0 = -(G_1E_1 + G_2E_2 + \cdots + G_nE_n)$.

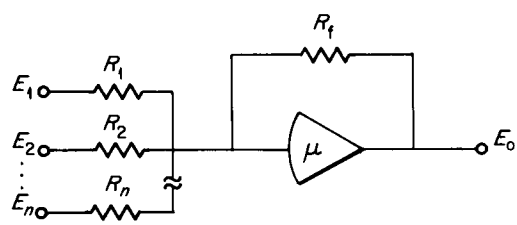


FIG. 11

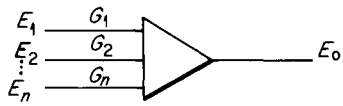
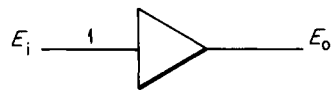


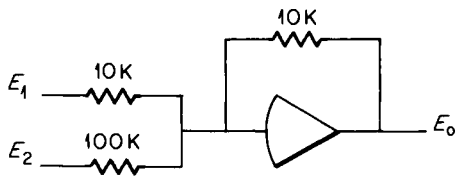
FIG. 12

If there is a single input signal with a gain of one, the unit is called an *inverter* because its only function is to change polarity: $E_0 = -E_i$. The symbol for an inverter is given in Fig. 13a.



(a)

FIG. 13. (a) Inverter.



(b)

FIG. 13. (b)

Exercise 1

(1) The circuit in Fig. 13b shows a high gain amplifier with two input resistances R_1 and R_2 of 10,000 Ω and 100,000 Ω, and a feedback resistance R_f of 10,000 Ω.

(a) Draw an analog computer symbol to represent this circuit.

(b) Write an expression for the output voltage.

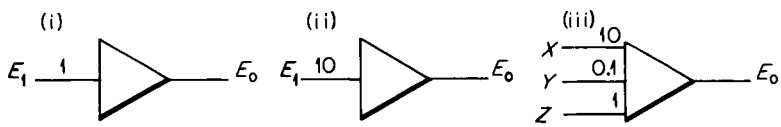


FIG. 14

(2) (a) Draw schematic circuits with appropriate combinations of resistances to represent the summers given in Fig. 14.

(b) Write expressions for the output voltages in each case.

E. The Integrating Amplifier

When the feedback impedance is a capacitance C, and the input impedance still a resistance, the amplifier unit becomes an integrator. The configuration in Fig. 15 is represented by the symbol shown in Fig. 16, where $E_0 = E(0) - \int_0^t (G_1E_1 + G_2E_2 + \cdots + G_nE_n)\,dt$. Note that

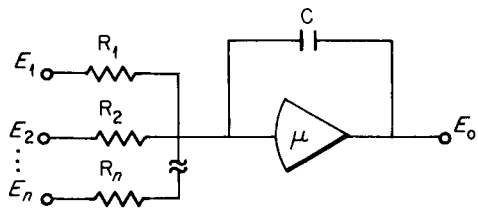


FIG. 15

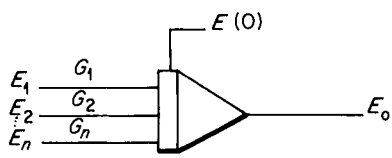


FIG. 16

the unit sums as well as integrates. The term $E(0)$ represents *initial condition* voltage on the integrator at $t = 0$. Each of the gains G_i is given by the relation

$$G_i = 1/R_iC$$

because $Z_f = 1/C$.

Considering the single input case, we have as in the proof of the fundamental gain theorem

$$I_g = I_1 + I_f = 0$$

$$\frac{E_i}{R_i} + I_f = 0.$$

The capacitance is $C = Q/E_0$ coulombs per volt, or farads, so that $Q = CE_0$. The feedback current is

$$I_f = \frac{dQ}{dt} = \frac{d}{dt}(CE_0) = C\frac{dE_0}{dt}.$$

Therefore, the expression for the grid current becomes

$$\frac{E_i}{R_i} + C\frac{dE_0}{dt} = 0.$$

Solving for E_0

$$\frac{dE_0}{dt} = -\frac{1}{R_iC}E_i$$

$$dE_0 = -\frac{1}{R_iC}E_i\,dt$$

$$\int_{E(0)}^{E_0} dE_0 = -\int_0^t \frac{1}{R_iC}E_i\,dt$$

$$E_0 - E(0) = -\int_0^t \frac{1}{R_iC}E_i\,dt$$

and finally

$$E_0 = E(0) - \int_0^t \frac{1}{R_iC}E_i\,dt.$$

In the case of multiple inputs, this expression becomes

$$E_0 = E(0) - \int_0^t \sum_{i=1}^{n} \frac{1}{R_iC}E_i\,dt.$$

Exercise 2

(1) A microfarad (μf) is 10^{-6} farads (coulombs per volt), a kilohm (kΩ) is 10^3 Ω, and a megohm (MΩ) is 10^6 Ω. What integrator gains are represented by the following RC combinations?

(a) $R = 1$ MΩ, $C = 10$ μf

(b) $R = 10$ kΩ, $C = 1$ μf

(c) $R = 1$ kΩ, $C = 1$ μf

(d) $R = 100$ kΩ, $C = 10$ μf

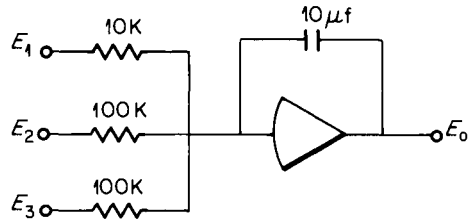


FIG. 17

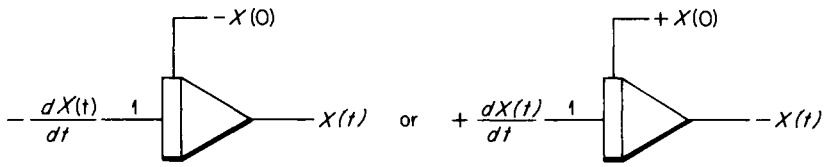


FIG. 18

(2) Draw an analog computer symbol to represent the circuit in Fig. 17, and write an expression for the output voltage.

(3) Because integration is the inverse operation of differentiation, integrators can be used to obtain state variables from their derivatives (see Fig. 18). In fact, this is the most common usage of the integrator in analog computation and the basis for solving differential equations. Draw appropriate integrators or combinations of integrators to solve the following differential equations:

(a) $dx/dt = y + 10z$,
(b) $\dot{x} = -0.1x + 10y + z$,
(c) $\dot{z} = 10x + y + 100z$,
(d) $\ddot{w} + 10\dot{w} = u + 10v + 0.1w$.

(The dot notation refers to time derivatives: $\dot{x} = dx/dt$, $\ddot{x} = d^2x/dt^2$, etc.)

F. POTENTIOMETERS

The potentiometer is a variable resistance by means of which it is possible to multiply voltages or voltage differences by constants k which lie in the interval $0 \leqslant k \leqslant 1$. A schematic for grounded "pots" is shown in Fig. 19. This configuration permits multiplication of a voltage by a constant and its corresponding analog computer symbol is given in Fig. 20(a).

Potentiometers also can be used to divide voltages by constants. Consider the configuration of a high-gain amplifier shown in Fig. 20b.

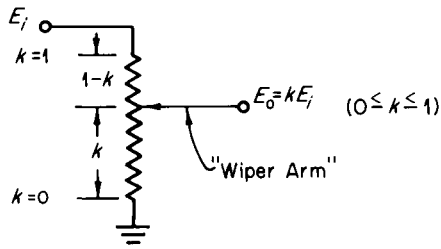


FIG. 19

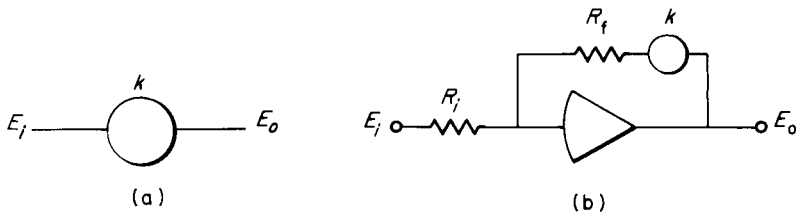


FIG. 20. (a) Multiplication of voltage by a constant. (b) Division of voltage by a constant.

The output voltage from the pot is kE_0. Summing the input and feedback currents at the grid, we obtain as before

$$I_1 + I_f = I_g = 0$$
$$\frac{E_i}{R_i} + \frac{kE_0}{R_f} = 0,$$

and solving for E_0

$$E_0 = -\left(\frac{R_f}{R_i}\right)\frac{E_i}{k}$$

For multiple inputs,

$$E_0 = -\sum_{i=1}^{n}\left(\frac{R_f}{R_i}\right)\frac{E_i}{k}.$$

The analog computer symbol for the above circuit is shown in Fig. 21.

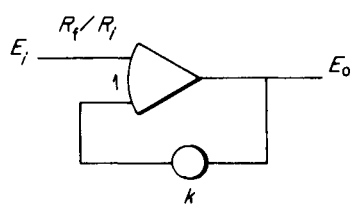


FIG. 21

Exercise 3

(1) Write expressions for the output voltages E_o of each of the following circuits:

(a) Fig. 22
(b) Fig. 23
(c) Fig. 24
(d) Fig. 25
(e) Fig. 26
(f) Fig. 27
(g) Fig. 28
(h) Fig. 29
(i) Fig. 30
(j) Fig. 31
(k) Fig. 32
(l) Fig. 33

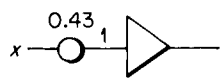


FIG. 22

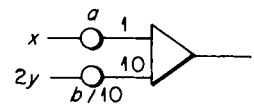


FIG. 23

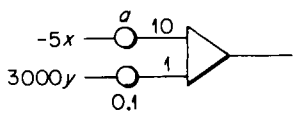


FIG. 24

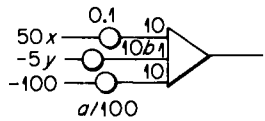


FIG. 25

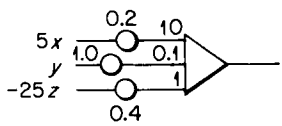


FIG. 26

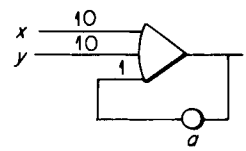


FIG. 27

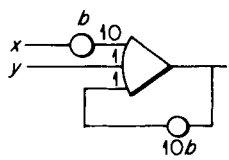


FIG. 28

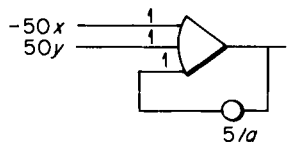


FIG. 29

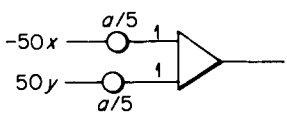


FIG. 30

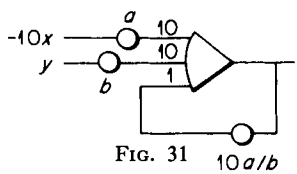


FIG. 31

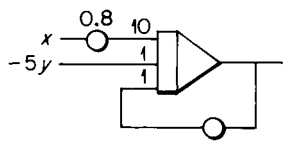


FIG. 32

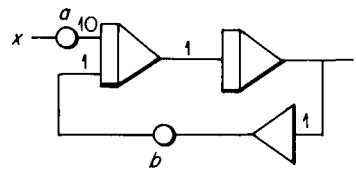


FIG. 33

(2) Draw simplest possible analog computer programs to solve or represent the following equations for the state variable $x(t)$, given $+x$, $+y$, and $+z$ as available voltages.

(a) $\dot{x} = y + 10z$,

(b) $\dot{x} = -(y + 10z + ax)$,

(c) $\dot{x} = ay - bz - cx$,

(d) $x = az - by$,

(e) $\dot{x} + ax = 0$,

(f) $\ddot{x} + ax = 0$.

G. THE MULTIPLIER

Multipliers are components of the analog computer which permit multiplication (or division) of two variable voltages. This is a nonlinear operation and, consequently, the multiplier makes it possible for analog computers to solve nonlinear differential equations.

The multiplier circuitry is designed to implement the identity

$$xy = \tfrac{1}{4}[(x + y)^2 - (x - y)^2].$$

For this reason these devices frequently are referred to as "quarter-square" multipliers.

The symbol for a multiplier is given in Fig. 34, or more succinctly in Fig. 35. Note that although it is desired to obtain the product

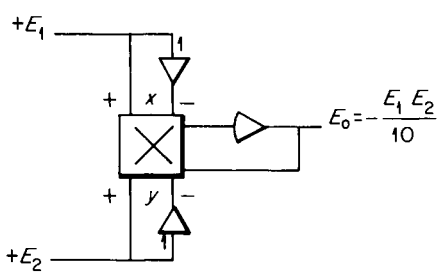


FIG. 34

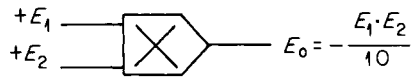


FIG. 35

$+E_1 \cdot E_2$, $-E_1 \cdot E_2/10$ is actually generated. This is due to the internal circuitry of the multiplier and the usual sign-inverting property of the amplifier. The sign inversion can be avoided by interchanging the $+X$ and $-Y$ inputs, or the $+Y$ and $-Y$ inputs. The lost gain of 10 must be picked up elsewhere in the circuit.

The configuration for division, E_1/E_2, is given in Fig. 36, and the simplified symbol is shown in Fig. 37. The additional gain of 10 which is picked up must be reduced at some other point in the circuit.

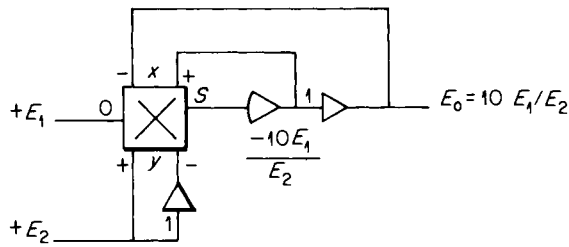


FIG. 36

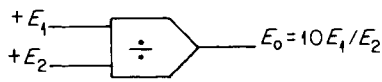


FIG. 37

H. OTHER COMPONENTS

Diode function generators (DFG's) are used to generate arbitrary functions which are approximated by a number of straight line segments. The segments may be for fixed or variable time intervals, depending upon the particular unit which is being used. Some DFG's in common use are x^2, LOG, SIN–COS, and VDFG (variable). The VDFG is particularly useful in making it possible to approximate experimental data of any curve form for use in system simulation without writing equations to describe the curves.

Function switches are single-pole, double-throw, mechanical binary switches which permit different program segments to be switched in or out manually. Their symbol is given in Fig. 38.

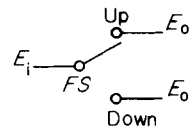


FIG. 38

Comparators are program-actuated switches which operate two sets of contacts, permitting computed problem voltages to determine connections or conditions applying in a patched circuit. As the name implies, the comparator accepts two input voltages, compares their sum to zero, and positions two switches up or down depending on whether the sum is greater than or less than zero.

Altogether, these components make it possible to obtain exact solutions to differential equations, and to simulate with considerable flexibility the time behavior of dynamic systems.

Exercise 4

With reference voltages of $+10$ and -10 available, write analog computer programs to solve the following differential equations:

(1) "ramp" function $\dot{x} = k$,

(2) sine-cosine generator $\ddot{x} = -\omega^2 x$,

(3) exponential population growth $\dot{N} = rN$,

(4) logistic population growth $\dot{N} = rN(1 - N/K)$.

III. Population and Ecosystem Models

A. Coupled Systems

In Section I.A a system was defined to consist of a group of components interconnected in such a way as to form a conceptual or functional entity. We wish now to extend this system concept further. A *control system* is an arrangement of physical components connected or related in such a manner as to command, direct, or regulate itself or another system. By this definition, populations which grow either exponentially or logistically are control systems: Their current states are determined by previous states, and they are examples of *state-determined* systems.

State-determinancy is the loosest possible concept of control since few systems lack this quality. To develop a stronger meaning, concepts of *coupling* and *feedback* are needed. An *input* to a system is a stimulus, excitation or force (a *signal*) applied from an external energy or informa-

tion source. A system *output*, on the other hand, is the response or behavior which results from applying an input. Two systems are said to be *coupled*, *joined*, or *connected*, etc. in interaction, if communication (energy, matter, or "information" transfer) can take place such that one can influence the other.

Coupling of systems, subsystems, or system components means connecting an output from one so that it becomes an input to another

B. Ecological Coupling: Population Competition

The Lotka–Volterra theory of competitive interaction between two logistic populations is a good example of coupled ecological systems. The state set is $\{N_1(t), N_2(t)\}$, the population sizes as functions of time. The "rules" of coupling are expressed as interaction coefficients, α and β, in the system equations

$$dN_1/dt = r_1N_1[1 - (1/K_1)\,N_1 - (\alpha/K_1)\,N_2]$$

$$dN_2/dt = r_2N_2[1 - (1/K_2)\,N_2 - (\beta/K_2)\,N_1],$$

where $(1/K_1)$ and $(1/K_2)$ are self-inhibition coefficients, as in the logistic formula

$$dN/dt = rN[1 - (1/K)\,N].$$

Since $(1/K_1)$ is the self-inhibition of population 1 by one individual of itself, total self-inhibition is the second term in brackets, $(1/K_1)N_1$. Similarly, $(1/K_2)$ is the unit self-inhibition of population 2, and $(1/K_2)N_2$ the total. Also, (α/K_1) is the inhibition of species 1 by one individual of species 2, and total inhibition by the competitor is $(\alpha/K_1)N_2$; (β/K_2) is the unit inhibition of population 2 by 1, with $(\beta/K_2)N_1$ the total inhibition. Since both total self-inhibition and total competitive inhibition depend on the population sizes, these are said to be density-dependent attributes of the populations; in systems terms they are state-determined attributes.

It may not be obvious from the Lotka–Volterra equations that the only manner of coupling between the two populations is through the competition coefficients α and β. However, this feature of the system shows to good advantage in the analog computer program illustrated in Fig. 39. The upper part of the diagram represents the equation for species 1 and the lower part that for species 2. Note that the only connections between upper and lower halves are through potentiometers representing (α/K_1) and (β/K_2).

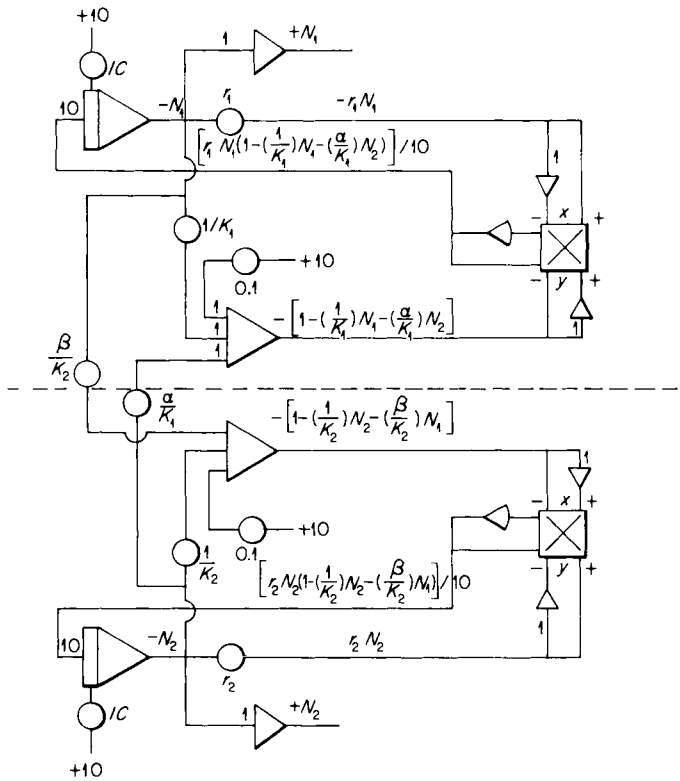


FIG. 39

C. FEEDBACK

Control systems are classified into two general categories, open-loop and closed-loop. The distinction is determined by the mechanism of *control action*—how the system is activated to produce an output. An *open-loop* control system is one in which the control action is independent of the output. A *closed-loop* control system is one in which the control action is dependent on the output. Closed-loop control systems more commonly are referred to as *feedback* control systems. Feedback is that property of a closed-loop system which permits the output representing some controlled system variable to regulate specific inputs. *Feedback* can be defined as the coupling of system output to input in such a way that the input is related to and controlled by the output. Feedback is *positive* if increased output results in increased input, as in the case of exponentially growing populations. Control is achieved through *negative feedback*, in which output and input are inversely related. The logistic

population model incorporates both positive and negative feedback, respectively, in the two components of population change rate, rN and $-N^2/K$.

D. Block Diagrams

A *block diagram* is a pictorial way of representing cause-and-effect relations between inputs and outputs of a physical system. The simplest form of block diagram is a single "block" with one input and one output as in Fig. 40. The interior of the rectangle usually represents either (1) some system component (state variable) or (2) some mathematical operation (e.g., transfer function) to be performed on the input to yield the output (see Fig. 41). Convention (1) will be used in this chapter exclusively.

It was noted in Section I.E that definition of a system is arbitrary. Once it is made, however, what is part of the system and what is external to it becomes fixed. Input signals to the system which originate in energy or information sources outside the system will be termed *forcings*. Such systems are *forced dynamic systems*, in contrast to *unforced*, as in Figs.

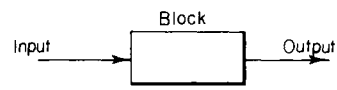


Fig. 40

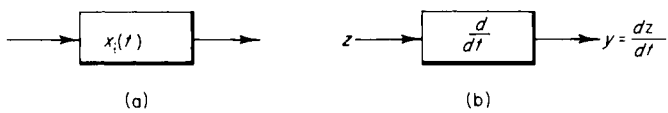


Fig. 41. (a) System component. (b) Mathematical operator.

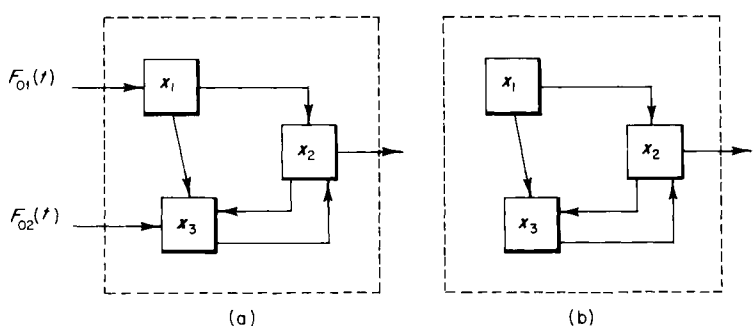


Fig. 42. Systems of definition: (a) forced, (b) unforced.

42a and b, respectively. In these diagrams, $\mathbf{x}$ represents the state vector, the notation $x_i(\mathbf{x}, t)$ signifies that state variable i may be a function both of the system state and of time, and $F_{0j}(t)$ signifies a forcing on the jth block, a function of time only.

E. Signal-Flow Graphs

A *signal-flow graph* is another pictorial device used to display transmission of signals through a system. Consider the algebraic equation

$$x_j = A_{ij}x_i \, .$$

The corresponding signal-flow graph is given in Fig. 43. The variables x_i and x_j are represented by a small dot called a *node*, and the *transmission*

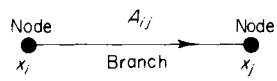


Fig. 43

(signal-flow) *function* A_{ij} is depicted by a line with an arrow, called a *branch* or *arc*. In representing systems by signal-flow graphs, every state variable is designated by a node, and every transmission function by a branch. Branches are always unidirectional, the arrow signifying the direction of signal flow. Outputting nodes are *source* or *donor* nodes while nodes which receive inputs are called *terminal* or *receptor* nodes. A *path* is an uninterrupted, unidirectional sequence of branches along which no node is passed more than once.

Signal-flow graphs and block diagrams are used extensively in control theory and operations research, with many mathematically sophisticated variations. Signal-flow graphs are formal models of systems, with well-developed algebras and other mathematical theories (such as transfer function and network flow theories) which make them powerful tools when implemented by computers. In biology and ecology, the particular kind of graphic system representation most used has been the compartment model. This form of model incorporates aspects of both block diagrams and signal-flow graphs.

F. Compartment Models

In *compartment models*, state variables of a system are denoted by blocks, and signal flows between these "compartments" by unidirectional branches. There is little difference between this and a block diagram.

The real difference lies in the mathematical system description implied by the diagram: In compartment models relations between the state variables are expressed as a system of differential equations. For example, a compartment model of the forced system block-diagrammed in Section III.D is given in Fig. 44. The system equations are based on an

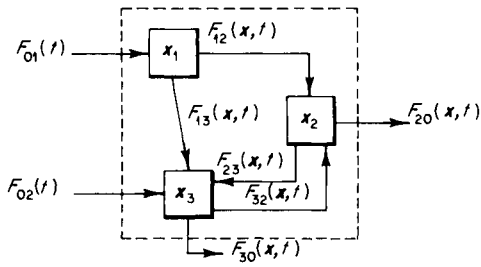


FIG. 44

income-and-loss rationale dictated by the *conservation principle.* All energy or substance transmitted must be accounted for

$$dx_1/dt = F_{01} - F_{12} - F_{13}$$
$$dx_2/dt = F_{12} + F_{32} - F_{20} - F_{23}$$
$$dx_3/dt = F_{03} + F_{13} + F_{23} - F_{30} - F_{32}.$$

The system behavior is obtained by solving the equations simultaneously. Note how intrasystem coupling is represented by shared variables, i.e., F_{12} in the first and second equations, F_{13} in the first and third, and F_{23} and F_{32} in the second and third.

G. Definition of Flows in Compartment Models

The compartment model is particularly well suited to ecology because abstract "signal" flows readily can be converted to energy or material transfers between compartments. These are, in principle at least, measurable, although with differing degrees of difficulty for different ecological systems. Having quantified a flow empirically, it then must be given a mathematical representation to be of use in a compartment model.

An elementary unit of a compartmentalized ecological system is shown in Fig. 45, where $F_{ij}(\mathbf{x}, t)$ is the *flux* of energy or matter from compartment i to j, and $x_i(\mathbf{x}, t)$ and $x_j(\mathbf{x}, t)$ are concentrations in the

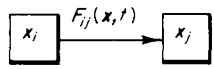


FIG. 45

donor and recipient compartments, respectively. If the concentration units are, e.g., kilocalories per square meter or milligrams per liter, then corresponding flux units might be, e.g., kilocalories per square meter per year and milligrams per liter per day.

The *flux* or *flow* over a branch in a compartment model is the amount of energy or material delivered to the terminal compartment in a unit interval of time. This usage will be in contradistinction to the rate of flow. The *rate* of transfer, or *flow rate*, is the fractional quantity of some function of source or terminal materials delivered over a branch per unit time. The distinction between flux and rate is made best in terms of units. If a flux F_{ij} is in kilocalories per square meter per year, then the corresponding rate of flow ϕ_{ij} is expressed per year. Similarly, if F_{ij} is in milligrams per liter per day, then ϕ_{ij} is given per day.

A hierarchy of useful mathematical expressions for flows in ecological compartment models and their corresponding rationales is:

(1) $F_{ij} = k$ (constant). Flow from compartment i to j does not change with time or system state.

(2) $F_{ij} = \phi_{ij}x_i$. Flow to j is proportional to the content of i. The donor compartment only is controlling.

(3) $F_{ij} = \phi_{ij}x_j$. Flow is regulated by the receiving compartment only, as in the case of herbivores or detritivores when plants (detritus) are in abundant supply.

These first three functions represent linear flows; those which follow denote nonlinear flows:

(4) $F_{ij} = \phi_{ij}x_ix_j$. Flow is regulated jointly by both source and terminal compartments.

(5) $F_{ij} = \phi_{ij}x_i(1 - \alpha_{ij}x_j)$. The flow has two components: a positive, linear one regulated by the donor compartment and a negative, nonlinear one controlled by interaction of both compartments.

(6) $F_{ij} = \phi_{ij}x_j(1 - \alpha_{ij}x_i)$. A positive, linear component is controlled by the terminal compartment and a negative, nonlinear one by inter-

compartmental interaction. The constant α_{ij} corresponds here and in the above flow to the coupling coefficients, (α/K_1) and (β/K_2), in the Lotka–Volterra model of population competition (Section III.B).

(7) $F_{ij} = \phi_{ij}x_j(1 - \beta_{ij}x_j)$. The flow is regulated by a positive feedback, linear term and a negative feedback, nonlinear term. This latter is the same "self-inhibition" rationale which appears in the logistic model of population growth (Section I.G) and also in the Lotka–Volterra equations.

(8) $F_{ij} = \phi_{ij}x_j(1 - \alpha_{ij}x_i - \beta_{ij}x_j)$. This flow corresponds to the full Lotka–Volterra system, with two negative feedback loops to represent both interactive $(-\alpha_{ij}x_ix_j)$ and intrinsic $(-\beta_{ij}x_j^2)$ flow control by the terminal compartment.

These flow expressions comprise a significant, though by no means exhaustive, set for description of energy and material transmissions in compartment models of ecological systems.

Example 5

In Section I.E three models of rotifer populations were described as examples of different ways to view a given real system (Example 3). A compartmental representation of model I viewed as an energy-transferring system is shown in Fig. 46. Here a number of forcings

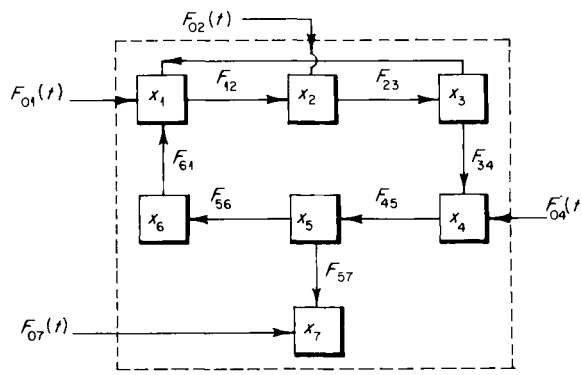


FIG. 46

F_{0j} have been introduced to all the nonegg compartments to allow energy to enter the system (e.g., by feeding). Acceptable units for the state variables would be, e.g., numbers per liter or milligrams per liter, and the corresponding fluxes might be in numbers per liter per day or milligrams per liter per day. In every case, an appropriate transmission function would be the linear flow $F_{ij} = \phi_{ij}x_i$ because creation of units

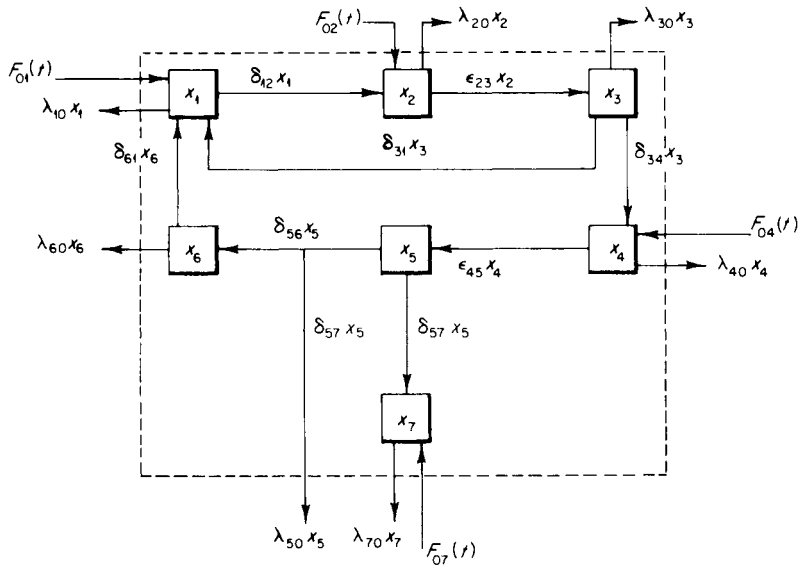


FIG. 47

in the terminal compartments depends only on concentrations of units in donor compartments.

The foregoing model is not very complete because it ignores the conservation law: production of amictic eggs (x_3) by mature amictic females (x_2), for example, is not the only source of (energy) loss from x_2. The model can be improved by adding transmission branches to represent predation, natural mortality, and other losses (see Fig. 47). In this completed diagram, all the nonforcing flows are defined mathematically. The rate notations aid in recalling the different biological processes: λ is the losses due to mortality, predation, emigration, etc.; δ is the developmental maturation; ϵ is the egg production; ϕ is the fertilization. The differential equations for this system are

$$\begin{aligned}
\dot{x}_1 &= F_{01} + \delta_{31}x_3 + \delta_{61}x_6 - \delta_{12}x_1 - \lambda_{10}x_1 , \\
\dot{x}_2 &= F_{02} + \delta_{12}x_1 - \epsilon_{23}x_2 - \lambda_{20}x_2 , \\
\dot{x}_3 &= \epsilon_{23}x_2 - \delta_{31}x_3 - \delta_{34}x_3 - \lambda_{30}x_3 , \\
\dot{x}_4 &= F_{04} + \delta_{34}x_3 - \epsilon_{45}x_4 - \lambda_{40}x_4 , \\
\dot{x}_5 &= \epsilon_{45}x_4 + \phi_{75}x_7 - \delta_{56}x_5 - \delta_{57}x_5 - \lambda_{50}x_5 , \\
\dot{x}_6 &= \delta_{56}x_5 - \delta_{61}x_6 - \lambda_{60}x_6 , \\
\dot{x}_7 &= F_{07} + \delta_{57}x_5 - \phi_{75}x_7 - \lambda_{70}x_7 .
\end{aligned}$$

An analog computer program to solve these equations is shown in Fig. 48.

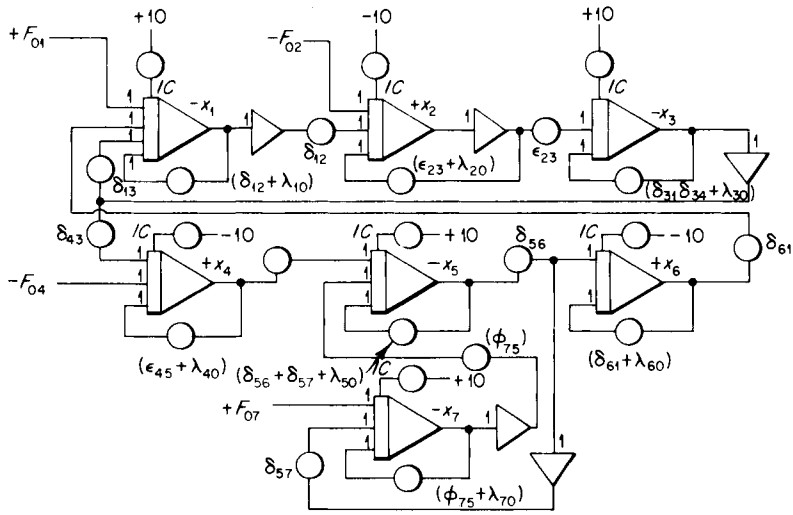


FIG. 48

Exercise 5

For the model II and III rotifer systems of Example 3:

(1) Prepare compartment models in block diagram form.

(2) Write system differential equations.

(3) Prepare analog computer programs that represent each of the systems.

H. A Model Food Chain: Silver Springs, Florida

Odum (1957) abstracted the details of energy flow in the Silver Springs ecosystem into Fig. 49. The data obtained in this study are sufficient to implement compartment models for the system.

The state variables, in kilocalories per square meter, are

$$x_1(\mathbf{x}, t) = \text{producers}, \qquad x_4(\mathbf{x}, t) = \text{top carnivores},$$
$$x_2(\mathbf{x}, t) = \text{herbivores}, \qquad x_5(\mathbf{x}, t) = \text{decomposers}.$$
$$x_3(\mathbf{x}, t) = \text{carnivores},$$

The caloric contents of these compartments (annual averages) can be taken as initial conditions

$$x_1(\mathbf{x}, 0) = 3421.26, \qquad x_4(\mathbf{x}, 0) = 8.87,$$
$$x_2(\mathbf{x}, 0) = 213.44, \qquad x_5(\mathbf{x}, 0) = 24.38.$$
$$x_3(\mathbf{x}, 0) = 62.06,$$

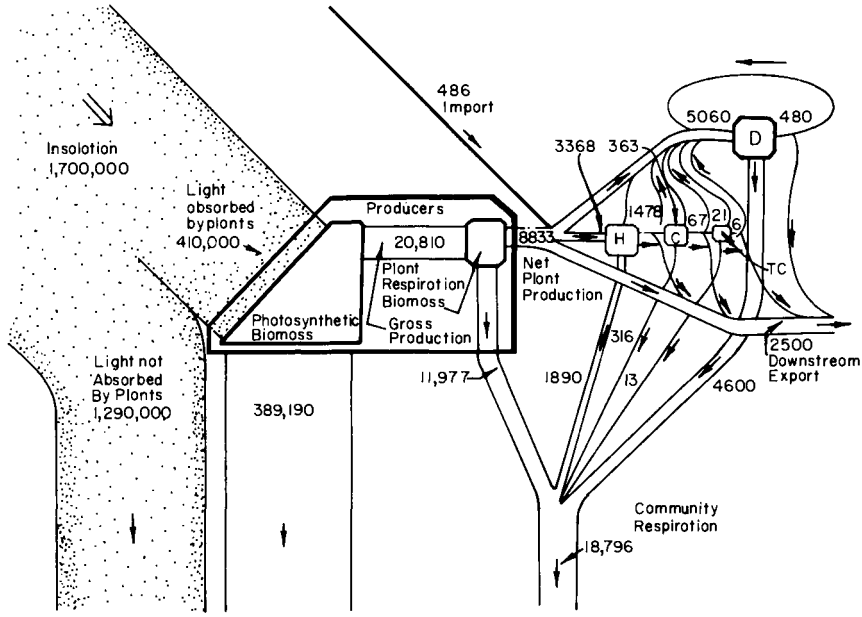


FIG. 49. Values are given in kilocalories per square meter per year. Reproduced from H. T. Odum (1957). *Ecol. Mono.* **27**, 61. Reprinted by permission of Duke University Press, Durham, North Carolina.

Two of the state variables are forced—primary producers by photosynthesis, and herbivores by bread added to the spring daily to make animals conspicuous for tourists. The values of these inputs, in kilocalories per square meter per year, are

$$F_{01}(t) = 20{,}810 \quad \text{and} \quad F_{02}(t) = 486.$$

The measured values of energy fluxes within the system, also in kilocalories per square meter per year are shown in Table I. A compartmental diagram of this system is shown in Fig. 50.

TABLE I

SILVER SPRINGS NONFORCING ENERGY FLOWS

Feeding	Mortality	Respiration	Export
$F_{12} = 2874$	$F_{15} = 3455$	$F_{10} = 11974$	$F'_{10} = 2498$
$F_{23} = 382$	$F_{25} = 1095$	$F_{20} = 1891$	
$F_{34} = 21$	$F_{35} = 46$	$F_{30} = 317$	
	$F_{45} = 6$	$F_{40} = 13$	
		$F_{50} = 4598$	

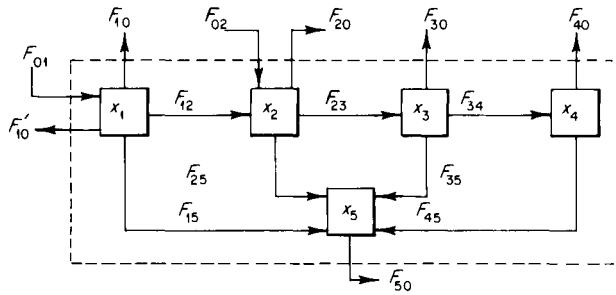


FIG. 50

Two models will be examined for purposes of illustration:(1) a linear system in which all flows are functions of the source compartment only ($F_{ij} = \phi_{ij}x_i$), and (2) a nonlinear system in which all nonfeeding flows are linear as in the first model, but feeding transfers are functions of both donor and recipient compartments ($F_{ij} = \phi'_{ij}x_ix_j$). Using τ to represent trophic level feeding rates, ρ for respiration, μ for natural mortality, and λ for losses downstream, system equations for the first model are

$$\dot{x}_1 = F_{01} - \tau_{12}x_1 - \mu_{15}x_1 - \lambda_{10}x_1 - \rho_{10}x_1 ,$$
$$\dot{x}_2 = F_{02} + \tau_{12}x_1 - \tau_{23}x_2 - \mu_{25}x_2 - \rho_{20}x_2 ,$$
$$\dot{x}_3 = \tau_{23}x_2 - \tau_{34}x_3 - \mu_{35}x_3 - \rho_{30}x_3 ,$$
$$\dot{x}_4 = \tau_{34}x_3 - \mu_{45}x_4 - \rho_{40}x_4 ,$$
$$\dot{x}_5 = \mu_{15}x_1 + \mu_{25}x_2 + \mu_{35}x_3 + \mu_{45}x_4 - \rho_{50}x_5 .$$

The nonlinear system equations are

$$\dot{x}_1 = F_{01} - \tau'_{12}x_2x_1 - \mu_{15}x_1 - \lambda_{10}x_1 - \rho_{10}x_1 ,$$
$$\dot{x}_2 = F_{02} + \tau'_{12}x_2x_1 - \tau'_{23}x_3x_2 - \mu_{25}x_2 - \rho_{20}x_2 ,$$
$$\dot{x}_3 = \tau'_{23}x_3x_2 - \tau'_{34}x_4x_3 - \mu_{35}x_3 - \rho_{30}x_3 ,$$
$$\dot{x}_4 = \tau'_{34}x_4x_3 - \mu_{45}x_4 - \rho_{40}x_4 ,$$
$$\dot{x}_5 = \mu_{15}x_1 + \mu_{25}x_2 + \mu_{35}x_3 + \mu_{45}x_4 - \rho_{50}x_5 .$$

I. SOLUTION COMPONENTS OF DIFFERENTIAL EQUATIONS

In Section I.D *transient* and *steady-state* system behavior were distinguished, and in Section III.D the distinction between *forced* and

unforced behavior was introduced. These classes of system response have their nominal counterparts in the solution components of differential equations.

The solution of a differential equation can be divided into two parts, a free response and a forced response. The sum of these two responses constitues the *total response* or *total solution*. The *free* or *unforced response* of a differential equation is the solution when the input forcing is identically zero. Differential equations which are unforced are termed *homogeneous* differential equations. The *forced response* of a differential equation is the solution when the initial conditions are identically zero.

The total solution can also be partitioned into transient and steady state solutions. The *transient response* of a differential equation is that part of the total response which approaches zero as time approaches infinity. The *steady-state* response is that part of the total solution which does not approach zero as time approaches infinity.

IV. Analog Computer Programming

A. Voltage Scaling

In Section II.A it was stated that only two variables are available on the analog computer: an independent variable, time, and a dependent variable, voltage. It was indicated also that all behavior of systems to be simulated by an analog computer must be compressed into the voltage range (e.g., 0–10 V) of the particular machine being used.

For the Silver Springs system (Section III.H), producers contain almost 4×10^3 kcal m^{-2} of energy while top carnivores have less than 1×10^1. If 4×10^3 were equated to 10 V, then the top carnivores would be represented only by around .0025 V and their behavior would not be discernible. To avoid this problem, each state variable is scaled independently so that its behavior can be observed conveniently within the full voltage range available. This is done through a process termed *voltage scaling* by equating an estimated maximum value of each compartment to 10 V, determining voltage scale factors, doing the same for forcing functions, and then rewriting the system equations in terms of voltage-scaled computer variables and forcings.

Example 6

Determine voltage-scaled system equations for the Silver Springs linear model.

(1) Set up tables to determine computer variables and computer forcings as shown in Table II.

TABLE II

PROCEDURE FOR DETERMINING VOLTAGE-SCALED COMPUTER VARIABLES AND FORCINGS

State variables, x_j (kcal m^{-2})	Estimated maxima (kcal m^{-2})	Scale factors, α_j (V/(kcal m^{-2}))	Computer variables, $[\alpha_j x_j]$ (V)
x_1	5×10^3	$10/(5 \times 10^3) = 2 \times 10^{-3}$	$[2 \times 10^{-3} x_1]$
x_2	5×10^2	$10/(5 \times 10^2) = 2 \times 10^{-2}$	$[2 \times 10^{-2} x_2]$
x_3	2×10^2	$10/(2 \times 10^2) = 5 \times 10^{-2}$	$[5 \times 10^{-2} x_3]$
x_4	2×10^1	$10/(2 \times 10^1) = 5 \times 10^{-1}$	$[5 \times 10^{-1} x_4]$
x_5	5×10^1	$10/(5 \times 10^1) = 2 \times 10^{-1}$	$[2 \times 10^{-1} x_5]$
Forcing functions, F_{0j} (kcal m^{-2} yr^{-1})	Estimated maxima (kcal m^{-2} yr^{-1})	Scale factors, σ_j (V yr^{-1}/(kcal m^{-2} yr^{-1}))	Computer forcings, $[\sigma_j F_j]$ (V yr^{-1})
F_{01}	2.5×10^4	$10/(2.5 \times 10^4) = 4 \times 10^{-4}$	$[4 \times 10^{-4} F_{01}]$
F_{02}	5×10^2	$10/(5 \times 10^2) = 2 \times 10^{-2}$	$[2 \times 10^{-2} F_{02}]$

(2) Rewrite the system equations in terms of the voltage-scaled computer variables and forcings. This means converting equations in which every term on the left- and right-hand sides has units of kilocalories per square meter per year

$$\dot{x}_j = F_{0j} + \sum_{i=1}^{n} \phi_{ij} x_i - \sum_{i=1}^{n} \phi_{ji} x_j ,$$

to equations whose terms have the units volts per year

$$[\alpha_j \dot{x}_j] = \frac{\alpha_j [\sigma_j F_{0j}]}{\sigma_j} + \sum_{i=1}^{n} \frac{\alpha_j \phi_{ij} [\alpha_i x_i]}{\alpha_i} - \sum_{i=1}^{n} \frac{\alpha_j \phi_{ji} [\alpha_j x_j]}{\alpha_j}$$

$$= \frac{\alpha_j}{\sigma_j} [\sigma_j F_{0j}] + \sum_{i=1}^{n} \frac{\alpha_j}{\alpha_i} \phi_{ij} [\alpha_i x_i] - \sum_{i=1}^{n} \phi_{ji} [\alpha_j x_j].$$

The ratios α_j/σ_j and α_j/α_i turn out to be gains on integrators, the ϕ_{ij} are rate constants which are set on potentiometers, and the terms in brackets, $[\sigma_j F_{0j}]$, $[\alpha_i x_i]$, and $[\alpha_j x_j]$, are computer forcings and variables. It is the

latter which will appear as outputs from integrators. The unscaled linear system of Section III.H becomes

$$
\begin{aligned}
[2 \times 10^{-3}\dot{x}_1] &= 5[4 \times 10^{-4}F_{01}] - (\tau_{12} + \mu_{15} + \lambda_{10} + \rho_{10})[2 \times 10^{-3}x_1] \\
&= 5[4 \times 10^{-4}F_{01}] + (a_{11})[2 \times 10^{-3}x_1]
\end{aligned}
$$

$$
\begin{aligned}
[2 \times 10^{-2}\dot{x}_2] &= [2 \times 10^{-2}F_{02}] + 10(\tau_{12})[2 \times 10^{-3}x_1] \\
&\quad - (\tau_{23} + \mu_{25} + \rho_{20})[2 \times 10^{-2}x_2] \\
&= [2 \times 10^{-2}F_{02}] + 10(\tau_{12})[2 \times 10^{-3}x_1] + (a_{22})[2 \times 10^{-2}x_2]
\end{aligned}
$$

$$
\begin{aligned}
[5 \times 10^{-2}\dot{x}_3] &= 2.5(\tau_{23})[2 \times 10^{-2}x_2] - (\tau_{34} + \mu_{35} + \rho_{30})[5 \times 10^{-2}x_3] \\
&= 2.5(\tau_{23})[2 \times 10^{-2}x_2] + (a_{33})[5 \times 10^{-2}x_3]
\end{aligned}
$$

$$
\begin{aligned}
[5 \times 10^{-1}\dot{x}_4] &= 10(\tau_{34})[5 \times 10^{-2}x_3] - (\mu_{45} + \rho_{40})[5 \times 10^{-1}x_4] \\
&= 10(\tau_{34})[5 \times 10^{-2}x_3] + (a_{44})[5 \times 10^{-1}x_4]
\end{aligned}
$$

$$
\begin{aligned}
[2 \times 10^{-1}\dot{x}_5] &= 100(\mu_{15})[2 \times 10^{-3}x_1] + 10(\mu_{25})[2 \times 10^{-2}x_2] + 4(\mu_{35}) \\
&\quad \times [5 \times 10^{-2}x_3] + 0.4(\mu_{45})[5 \times 10^{-1}x_4] - (\rho_{50})[2 \times 10^{-1}x_5] \\
&= 100(\mu_{15})[2 \times 10^{-3}x_1] + 10(\mu_{25})[2 \times 10^{-2}x_2] + 4(\mu_{35}) \\
&\quad \times [5 \times 10^{-2}x_3] + 0.4(\mu_{45})[5 \times 10^{-1}x_4] + (a_{55})[2 \times 10^{-1}x_5]
\end{aligned}
$$

In these equations the numbers without parentheses represent gains on integrators, the expressions within parentheses are rate constants, and the bracketed expressions are computer variables or forcings. Note that, for reasons to be explained later, the negative of the sums of loss coefficients for each compartment have been combined into a single loss-rate constant (a_{jj}). These coefficients represent negatives of the *turnover rates* of each compartment. The equations comprise a system of voltage-scaled differential equations for the Silver Springs linear model.

B. Time Scaling

The terms of the voltage-scaled equations in Example 6 have the units volts per year. This means that to simulate a year of Silver Springs behavior would take a year on the machine, and to simulate 10 or 100 years would take that long. This difficulty is averted by *time scaling*—introducing a time-scale factor into the system equations. The scale factor is

$$\beta = \frac{\text{computer time}}{\text{real time}},$$

where "computer time " is in seconds and "real time" is the unit of time in which the system has been measured. For the Silver Springs models, real time is years because the original data were reported in years. So β is in seconds per year, expressing how many seconds of computer time correspond to a year of Silver Springs' operation.

To convert each system equation in volts per year

$$[\alpha_j \dot{x}_j] = \frac{\alpha_j}{\sigma_j}[\sigma_j F_{0j}] + \sum_{i=1}^{n} \frac{\alpha_j}{\alpha_i} \phi_{ij}[\alpha_i x_i] - \sum_{i=1}^{n} \phi_{ji}[\alpha_j x_j]$$

to a corresponding equation in volts per second, it is necessary only to divide each term by β (i.e., volts per year/seconds per year = volts per second)

$$\beta^{-1}[\alpha_j \dot{x}_j] = \frac{\alpha_j/\sigma_j}{\beta}[\sigma_j F_{0j}] + \sum_{i=1}^{n} \frac{\alpha_j}{\alpha_i} \frac{\phi_{ij}}{\beta}[\alpha_i x_i] - \sum_{i=1}^{n} \frac{\phi_{ji}}{\beta}[\alpha_j x_j].$$

As indicated, this means dividing pot settings by β for all nonforcing inputs to each integrator, and also dividing gains for the forcing inputs by the value of β.

When a system of equations is voltage-scaled and time-scaled, and numerical values are available for its rate parameters, it is ready for conversion to an operational analog computer program. The step yet remaining for Silver Springs is to calculate rates.

C. Determination of Rate Parameters

Average annual flows were measured for the Silver Springs system (Section III.H). In the linear model these take the mathematical form $F_{ij} = \phi_{ij} x_i$, and in the nonlinear model they have the form $F_{ij} = \phi'_{ij} x_i x_j$. The values of x_i and x_j also are known as annual averages, and thus the rate constant component of each flow can be determined from the relations

$$\phi_{ij} = F_{ij}/x_i \quad \text{(per year)}$$

and

$$\phi'_{ij} = F_{ij}/x_i x_j \qquad \text{(square meters per year per kilocalorie)}$$

The ϕ_{ij} values for Silver Springs are shown in Table III. In the nonlinear model, $\tau'_{13} = .0039$, $\tau'_{23} = .0272$, and $\tau'_{34} = .0382$.

TABLE III

RATE CONSTANTS FOR THE SILVER SPRINGS LINEAR SYSTEM

Feeding	Mortality	Respiration	Export	Summed loss rates
$\tau_{12} = .84$	$\mu_{15} = 1.01$	$\rho_{10} = 3.50$	$\lambda_{10} = .73$	$a_{11} = -6.08$
$\tau_{23} = 1.79$	$\mu_{25} = 5.13$	$\rho_{20} = 8.86$		$a_{22} = -15.78$
$\tau_{34} = .339$	$\mu_{35} = .74$	$\rho_{30} = 5.10$		$a_{33} = -6.179$
	$\mu_{45} = .676$	$\rho_{40} = 1.466$		$a_{44} = -2.142$
		$\rho_{50} = 188.6$		$a_{55} = -188.6$

D. ANALOG PROGRAM FOR SILVER SPRINGS LINEAR MODEL

Substituting the rate constant values into the scaled equations of Example 6, the following final system equations are obtained.

$$[2 \times 10^{-3}\dot{x}_1] = 5[(4 \times 10^{-4})(2.0810 \times 10^{4})] - 6.08[2 \times 10^{-3}x_1]$$
$$= 10(.4162)[10] - 10(.608)[2 \times 10^{-3}x_1]$$

$$[2 \times 10^{-2}\dot{x}_2] = [(2 \times 10^{-2})(4.86 \times 10^{2})] + 10(.84)[2 \times 10^{-3}x_1]$$
$$- 15.78[2 \times 10^{-2}x_2]$$
$$= (.972)[10] + 10(.84)[2 \times 10^{-3}x_1] - 100(.1578)[2 \times 10^{-2}x_2]$$

$$[5 \times 10^{-2}\dot{x}_3] = 2.5(1.79)[2 \times 10^{-2}x_2] - 6.179[5 \times 10^{-2}x_3]$$
$$= 10(.4475)[2 \times 10^{-2}x_2] - 10(.6179)[5 \times 10^{-2}x_3]$$

$$[5 \times 10^{-1}\dot{x}_4] = 10(.339)[5 \times 10^{-2}x_3] - 2.142[5 \times 10^{-1}x_4]$$
$$= 10(.339)[5 \times 10^{-2}x_3] - 10(.2142)[5 \times 10^{-1}x_4]$$

$$[2 \times 10^{-1}\dot{x}_5] = 100(1.01)[2 \times 10^{-3}x_1] + 10(5.13)[2 \times 10^{-2}x_2] + 4(.74)$$
$$\times [5 \times 10^{-2}x_3] + 0.4(.676)[5 \times 10^{-1}x_4] - 188.6[2 \times 10^{-1}x_5]$$
$$= 10^{3}(.101)[2 \times 10^{-3}x_1] + 100(.513)[2 \times 10^{-2}x_2] + 10(.296)$$
$$\times [5 \times 10^{-2}x_3] + (.2704)[5 \times 10^{-1}x_4] - 10^{3}(.1886)[2 \times 10^{-1}x_5]$$

The voltage-scaled variables (or reference voltages in the case of forcings) are in brackets, pot settings in parentheses, and integrator gains unenclosed in the final form of each equation.

A program to represent this system is given in Fig. 51.

Exercise 6

(1) Prepare a scaled analog computer program for the Silver Springs linear system in which rate constants retain their identities by being

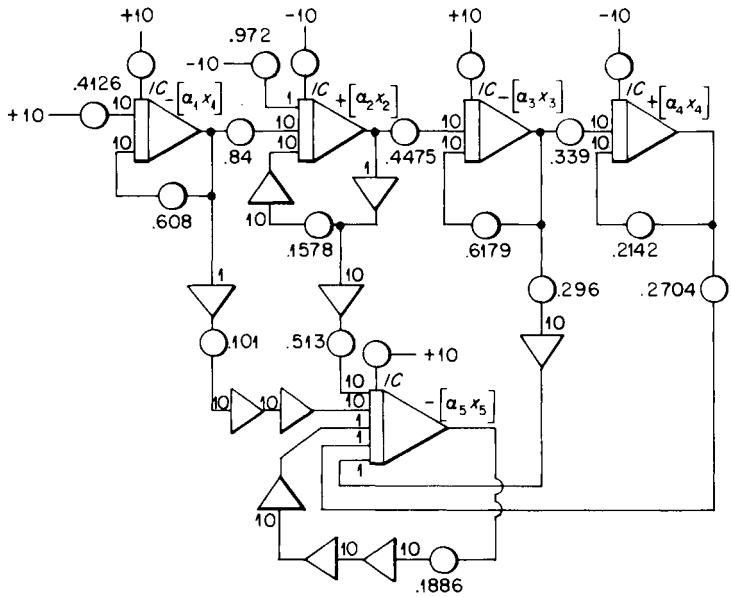


FIG. 51

represented individually on separate potentiometers. Contrast the virtues and limitations of this type of program with those of the program above.

(2) Prepare a scaled analog computer program for the Silver Springs nonlinear model.

V. Introduction to Digital Computers

A. Comparison of Digital and Analog Computers

There is very little similarity between analog and digital computers, either in principles of operation or in suitability for different tasks. The analog computer is essentially a one-purpose machine (solving differential equations), although in the hands of an expert its versatility can be made to appear impressive. The digital computer, as its name implies, processes numerical information. It is best suited for implementing discrete data and producing numerical output, whereas the analog computer deals with continuous signals both on input and output. Since most of the quantitative data of science, business, industry, and government is numerical, it is no surprise that digital computers have found a wider range of applicability in human enterprises than analog devices.

In using analog computers for dynamic systems modeling, one trades numerical accuracy for immediacy: The solution of an entire system of equations is virtually instantaneous, and simulation experiments with changing parameters take as long as reaching out and turning a potentiometer dial. The operator is coupled very closely to the machine, and hence to his model, and this leads to great insight about behavior of dynamic systems.

With digital computers this intimacy and short turnaround time are sacrificed in favor of numerical accuracy and a greater variety and size of mathematical models, particularly algebraic and statistical, which can be handled. The digital computer is largely a production machine; it grinds out numbers impersonally and, by the intricate programming languages through which access is afforded, imposes this by-the-numbers rigidity on its users.

An analog machine, once-programmed, is "played" more like a musical instrument, perhaps, and is capable of translating quickly subjective insights of an investigator into electronic realities. The cartoon in Fig. 52 overstates the difference. Efforts to gain the best

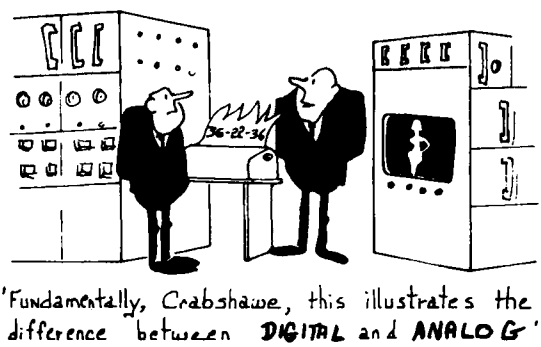


FIG. 52. Reproduced by permission of Analog Computer Educational User's Group.

advantages of both types of computers take the form of development of "hybrid" computers in the analog field and programming languages for continuous system simulation in the digital field.

B. FUNCTIONAL UNITS OF DIGITAL COMPUTERS

It may not always be possible to associate particular physical components in a modern digital computer installation with specific functions, but basically there are always five functions represented: input, memory,

arithmetic–logic, control, and output, as shown in the block diagram of Fig. 53.

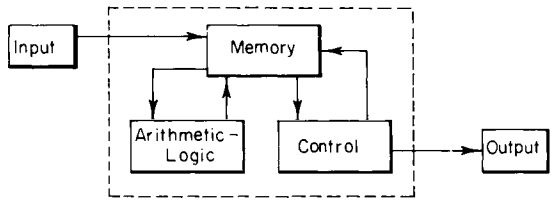


FIG. 53

The *input unit* permits information to be entered into memory by means of codes acceptable to the computer. This coded information may be on cards, paper tape, magnetic tape, or paper imprinted with special characters (such as those commonly used on bank checks). In scientific applications IBM (or Hollerith) cards and magnetic tape are used most frequently.

An *IBM card* consists of 12 rows and 80 columns. A combination of punches in each column represents a specific alphabetic, numeric, or special character (see Fig. 54). Cards are punched on a *keypunch*, and

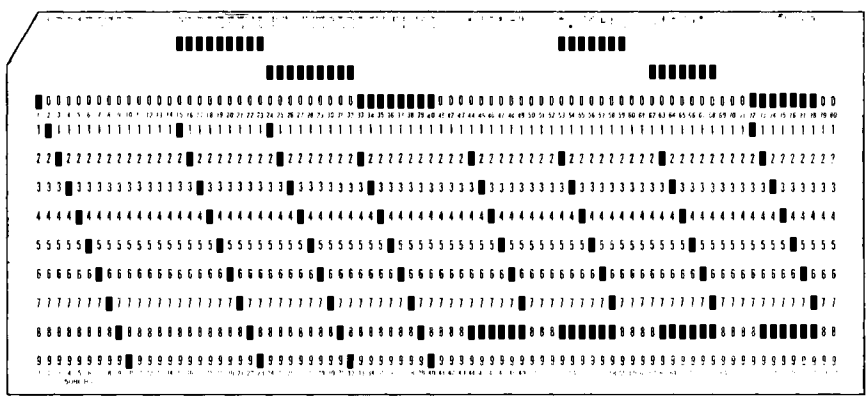


FIG. 54

read into memory by a *card reader*. Cards may be "read" photoelectrically, or by brushes which make an electrical contact when they drop through a hole. *Magnetic tape* is a plastic ribbon coated with a metallic oxide which will accept and hold magnetism permanently. On 7-track tape there are seven lengthwise rows (channels) and many crosswise columns forming positions which can be magnetized or not

according to a code. Characters can be entered with great density serially along the length of the tape. Densities vary from about 200–1500/in., and data can be read in at rates of about 340,000 characters/sec.

Memory is accomplished by either *drum*, *disk* or *core* storage units. These are composed of *binary cells* capable of being magnetized or not, and thereby representing the binary digits 0 and 1. Such one-*bit* cells are used together to represent larger binary numbers. A consecutive number of binary cells is a *byte*. All information used by the machine is binary-coded, e.g.,

Character	*6-Cell binary code*
0	0 0 0 0 0 0
1	0 0 0 0 0 1
2	0 0 0 0 1 0
3	0 0 0 0 1 1
4	0 0 0 1 0 0
8	0 0 1 0 0 0
A	0 1 0 0 0 1
Z	1 1 1 0 0 1
*	1 0 1 1 0 0

Characters stored in cells in memory are manipulated in groups of consecutive cells, called *words*. Different computers manipulate different word lengths. Each word location is identified by a number which can be used as an address to retrieve the word stored there. Some machines have fixed word lengths, others have variable word lengths. The *capacity* of a computer's memory refers to how much information can be stored. A "32K" capacity means that a computer can store 32,000 words.

The *arithmetic–logic* performs arithmetic operations (addition, subtraction, multiplication, and division) and simple numerical and logical operations on words brought over from memory.

The *control unit* is the functional part of a computing system. One instruction at a time is taken from the program stored in memory, interpreted, and then executed. What the instruction means and how it is carried out is implicit in the control unit's circuitry. The operations occur in two basic machine cycles called the *instruction cycle* (I-time) and the *execution cycle* (E-time). During I-time the control unit receives the next instruction in the stored program and prepares it for execution. The instruction is performed during E-time. In receiving, interpreting,

and executing instructions, the control unit coordinates the operations of input, memory, arithmetic–logic, and output portions of the computer.

The *output* serves to present results to the user, either on cards, paper or magnetic tape, paper, or by cathode ray display, etc. The most common method is a print-out on large sheets of paper, performed very rapidly (1100 lines/min) by a *printer*.

C. Elements of Programming

The physical machinery that comprises the functional units of a digital computer—the *hardware*—is of little direct concern to the user. Modern computer facilities generally are operated on a closed-shop basis in which jobs are submitted, run, and results returned without the individual user ever entering the computer room. The user is concerned more directly with programs and programming systems, collectively referred to as *software*.

A *computer program* is a set of instructions coded in such a way that the machine can perform each one in an indicated order. The basic code that a machine can accept, interpret, and execute is called *machine language*. This differs for different computers, but in general consists of long strings of decimal or binary numbers. These are too tedious and detailed for people to handle readily and, consequently, other languages are used in programming which are converted to machine language within the computer. These other languages basically are of two kinds—those for assembly systems and those for translating systems. An *assembly system language* is a symbolic language which is machine-oriented; it is used to specify how hardware components are to be used. A *translating system language* is more human-oriented, and bears a greater relation to the language in which a problem is normally written than to machine language.

A translating system consists of (1) a processing program called a *compiler*, and (2) a language. The programmer writes instructions in accordance with rules of the language; these are then read into the computer where the compiler converts them to machine language. Examples of modern translating systems are Algol, Cobol, and Fortran. In science, probably 90% of existing programs are written in Fortran, so this is a good language to learn.

D. Fortran IV: Introduction

Fortran IV is the version of this language currently in use with IBM equipment, such as 7090/7094 and 360 systems. Like other translating systems it consists of two phases—compilation and execution.

For *compilation*, the compiler program in machine language is entered into memory through an input unit. A *source program*, written in Fortran IV and keypunched on cards, is entered into memory through a card reader. The compiler translates each card from the *source deck* into machine language instructions. Depending upon what operations are to be performed, a number of *subprograms* will be called from the compiler. These are determined by *monitor control cards* included with the source deck and also by statements within the source program. The machine language program produced by translation of the source program is called an *object program*. This can be stored in memory, or outputted as an *object deck* or printed *listing* as the source program. Generally, a listing becomes the primary documentation of a program.

During *execution* the object program takes command of the machine. It calls for data from a *data deck* entered into memory, usually with the source program, and processes these in accordance with instructions of the original source program. Results are furnished through an appropriate output unit.

A schematic representation of a typical entire process of compiling and executing a Fortran program is shown in Fig. 55. In some systems the object deck is by-passed completely.

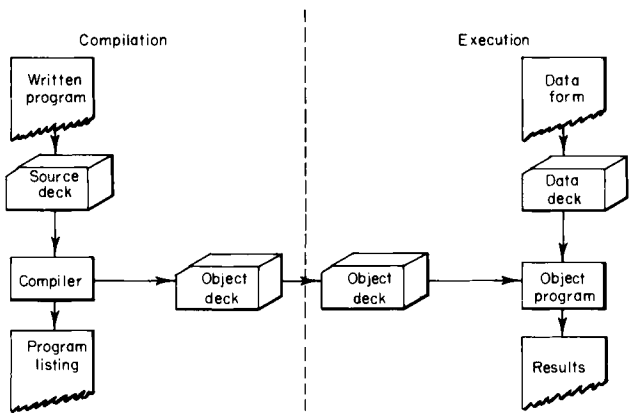


FIG. 55

A typical card input package consists of the source deck followed by the data deck, and appropriate control cards as in Fig. 56. The *job-control cards* identify the user and an account number to which the job is to be charged, and they also determine what subprograms are to be called for entry into the object program. The *data-control card* signals that the

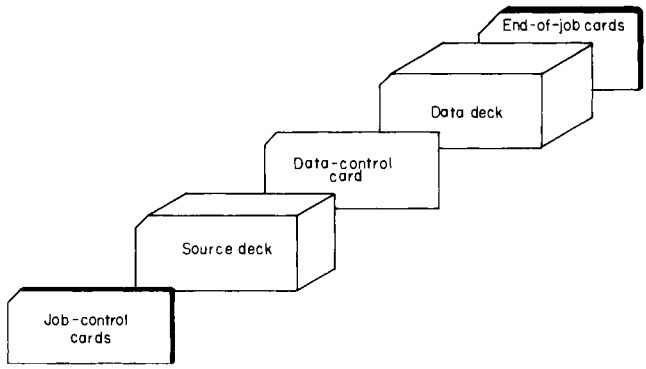


FIG. 56

data deck follows, and the *end-of-job cards* specify the end of the data deck and termination of the job. The control cards are specific for each type of computer, and sometimes there may be local variations introduced at different installations.

VI. Digital Computer Programming with Fortran IV

A. FORTRAN STATEMENTS

A Fortran IV program consists of five kinds of *statements*: (1) input and output, (2) assignment, (3) control, (4) specification, and (5) subprogram. The first three kinds are termed "executable." The compiler translates them into equivalent machine language during I-time and they are executed during E-time. *Input* and *output* statements direct the flow of information between memory and an input or output unit. *Assignment* statements direct arithmetic and logical computations. *Control* statements determine the order in which statements are executed.

Specification and subprogram statements are "non-executable," being descriptive in nature. *Specification* statements indicate to the compiler types of variables used in the program, arrangements of input and output data, and storage allocations. *Subprogram* statements permit subprograms to be identified and used in a main program.

In Fortran IV there are available 53 source program statements, but no compiler uses all of them. The IBM-7090 uses 45, and the 360 (H level) uses 47.

When data cards are punched, use of the 80 columns of an IBM card is as stated by specification statements in the source program. However, in punching the source deck itself there are restrictions on how statements are to be entered.

COLUMNS	CONTENT
1–5	The first five columns are for statement numbers, which may be omitted except when they are needed. A C punched in column 1 signifies that card to be a *comment card*. These are strictly for clarification or other purposes of the programmer. Comment cards are not processed by the Fortran compiler.
6	This column is reserved for *continuation cards*, necessary when a statement exceeds a card's capacity. On continuation cards, columns 1–5 are blank, column 6 contains any character except 0 or blank (typically numbers 1–9 are used sequentially), and the remaining columns are as for other cards.
7–72	The statement begins in column 7 and may extend through 72.
73–80	These columns are not processed by the compiler. They are left blank or may contain sequence numbers which can be used to preserve the order of cards in the deck.

Unless control statements specify otherwise, executable statements are performed in the same order as that in which the cards on which they are keypunched enter the computer.

B. CONSTANTS AND VARIABLES

Two kinds of *constants* are used in Fortran. An *integer* is a whole number, positive, zero, or negative. A *real number* is denoted by a decimal point. The numbers 3.1416, −.314, 3.0, 2., and 0. are real, while 3, 2, −2, and 0 are integers. Within the computer real numbers are represented in *floating point form*: some fraction between 0.1 and 1.0 and a power of 10. The following are floating point representations of the numbers 3.1416 and 0.0031416: 0.31416×10^{1} and 0.31416×10^{-2}.

There also are two kinds of Fortran *variables*. *Integer variables* take on integral values, and are named by 1 to 6 letters or digits, the first of which is I, J, K, L, M, or N. *Real variables* assume real values, and they also are named by 1 to 6 letters or digits, the first of which is *not* I, J, K, L, M, or N. The compiler uses the first letter of the variable name to determine if it is real or integer. Special characters are not permitted in constants or variables.

C. Operations and Expressions

Five *arithmetic operations* are provided in Fortran, each represented by a distinct character:

Addition	+
Subtraction	−
Multiplication	*
Division	/
Exponentiation	**

An *expression* is a rule for computing a numerical value. For example,

$$\frac{a \cdot b}{c + d} - a^2$$

is represented by the Fortran expression

```
(A * B)/(C + D) - A ** 2
```

The following rules must be obeyed in writing such expressions:

(1) Two operation symbols must never be adjacent. Thus `A** -B` is not valid, but `A ** (-B)` is.

(2) Parentheses are used for grouping as in ordinary mathematical notation. In complex expressions there must always be the same number of left parentheses as right parentheses: `(A * (B - C ** 2)) * (X + B)`. Parentheses cause inner operations to be performed first; `(X + B)` must be computed before its product with `(A * (B - C ** 2))` can be obtained.

(3) If the *order of operations* is not completely specified by parentheses, the order is: exponentiation first, multiplication and division next, and addition and subtraction last. Thus, the expression `X * Y + U/V - W ** A` is equivalent to `(X * Y) + (U/V) - (W ** A)`.

(4) In a sequence of multiplications and divisions, or additions and subtractions, where the order of operations is unspecified by parentheses, the evaluation is left-to-right. Thus `X/Y * Z` means $(x/y) \cdot z$ and not $x/(y \cdot z)$; also, `A - B + C` means $(a - b) + c$ rather than $a - (b + c)$.

(5) *Mixed-mode* expressions are forbidden technically (actually they are allowable on most modern Fortran compilers). That is, integer and real quantities cannot be mixed, except that a real quantity can be raised to an integer power: `A + I * J`, `EMU/IBIS`, and `K ** A` are incorrect, but `EX ** IJAY` and `WHY ** AIJAY` are both correct.

The mixed-mode restriction comes about because it is possible in Fortran to perform two kinds of arithmetic, integer and real. *Integer arithmetic* is calculated in the integer mode. In integer division, fractional parts of the quotient are ignored; the quotient is *rounded down* or *truncated* to the next lowest whole number. Thus, $5/3 = 1$, $(7 * 2)/3 = 4$, and $7 * (2/3) = 0$. *Real arithmetic* also has its problems. For example, the sum 1./3. + 1./3. + 1./3. to eight digits is .33333333 + .33333333 + .33333333, or .99999999. If a program were written to compare this result with 1.00000000, the result would be "not equal." Yet clearly, $1/3 + 1/3 + 1/3 = 1$ in ordinary arithmetic.

D. Mathematical Functions

Fortran functions include the following:

Mathematical function	*Fortan name*
Exponential	EXP
Natural logarithm	ALOG
Common logarithm	ALOG10
Sine (radians)	SIN
Cosine (radians)	COS
Square root	SQRT
Absolute value	ABS

These are *external functions* normally supplied with the Fortran IV compiler. To use them they are followed by a constant, variable, or an expression in parentheses, called the *argument* of the function; the function of the named argument is computed, e.g., e^{at} is EXP (A * T), sin ωt is SIN (OMEGA * T), and $\sqrt{b^2 - 4ac}$ is SQRT (B ** 2 — 4. * A * C). Note that all variables and constants of the arguments are real. There also are functions for *complex* and *double precision* variables, neither of which will be discussed here.

E. Arithmetic Assignment Statements

Computation of a new value of a variable is accomplished with an *arithmetic assignment statement*. The general form is

$$a = b$$

where a is a variable name, written without a sign, and b is any expression. This type of statement is an order to compute the value of the expression

on the right and assign that value to the variable on the left. Thus, in

```
Y = A + B * X
```

A + B * X is calculated and the value given to Y. If Y had a previous value, it is lost since the variable Y is allocated a specific position in memory. The result of the following two Fortran statements in the given sequence in a program

```
Y = 25. * .043 + 2.
Y = 0.
```

is to assign a value of 3.075 to Y and then assign a value of 0.0. The first value is lost when the second statement is executed.

Note that the "=" sign has a different meaning in Fortran than in mathematics, and statements like

```
X = X + 1.
```

are not only valid, but they also are very useful.

Exercise 7

(1) Write the following as Fortran real constants:

(a) 784	(d) −0.0000784
(b) 7.84	(e) 10^9
(c) 7.84×10^{-3}	(f) -7.84×10^9

(2) Which of the following are unacceptable integer constants ?

(a) −256	(d) 256,000,000,000
(b) +256.	(e) 256000000000.
(c) 2,560	(f) 256000000000

(3) Indicate integer, real, and unacceptable variables in the following list:

MAX	POPSIZ	XSQ
AMAX	X1	X ** 2
EMU	N1	A
ROTIFER	SILSPR	IA

(4) Write real-mode Fortran expressions for each of the following mathematical expressions:

(a) $x + y^2$

(b) $(x + y)^2$

(c) $x + \frac{y}{z}$

(d) $\frac{x + y}{z}$

(e) $1 + x + \frac{x^2}{2} + \frac{x^3}{3}$

(f) $\frac{a + b}{c - 3}(3c + 2)$

(g) $\frac{a}{n - 1}(4n^2 + 1)$

(h) $\frac{1}{a^2}\left(\frac{r}{10}\right)a$

(i) $a + x[b + x(c + dx)]$

(j) $\tan\frac{x}{2}$

(k) $(1 - e^{-at})$

(l) $1 + \sin\theta\,(\cos 2\phi)^2$

(5) Write arithmetic assignment statements to compute values of the following variables:

(a) $a = \pi r^2$

(b) $-y = k\sin(\omega t)$

(c) $j = qp/t$ (What is the value of j if $q = 5$, $p = 20$, and $t = 3$?)

(d) $x = -b + \sqrt{b^2 - 4ac}$

(e) $\dot{N} = rN$

(f) $\dot{N} = rn\left(\frac{K - N}{K}\right)$

(g) $F_{ij} = \phi'_{ij}x_i x_j$

(h) $\dot{x}_2 = F_{02} + \tau_{12}x_1 - \tau_{23}x_2 - \mu_{25}x_2 - \rho_{20}x_2$

(i) $y = \frac{1}{2}\log\frac{1 + \sin x}{1 - \sin x}$

F. Input and Output

In this section FORMAT, READ, WRITE, STOP, and END statements of the Fortran IV language are discussed.

The *FORMAT statement* is a nonexecutable specification statement which defines how input data will appear in the data deck or other input media, and what the arrangement of results will be on output media.

In other words, the FORMAT statement specifies input and output *data fields*, and it is always used in conjunction with a READ or WRITE statement. The form of the FORMAT statement is

$$n \text{ FORMAT } (s_1 , s_2 ,..., s_m)$$

where n is the statement number and $s_1 , s_2 ,..., s_m$ are any number of field specifications. Each field specification describes the kind and arrangement of one data field:

Specification	*Type of field*
I*w*	Integer
F*w.d*	Real without exponent
E*w.d*	Real with exponent

where I, F, and E denote the type of field, w the width of the field (number of characters), and d the number of digits to the right of the decimal point (not including any part of the exponent).

Example 7

Consider a card with the following data punched in columns 1–28 (the notation ⓝ will be used to signify n blanks):

①−3570②28656−0.095①8.76*E*①02⑤②

It is impossible to judge what the data are without field specifications. The following FORMAT statement provides the necessary information:

③13①FORMAT①(I6, I7, F6.3, E9.2)

The first field (I6) contains an integer constant (−3570), the second (I7) another integer constant (28656), the third (F6.3) a real constant with three digits to the right of the decimal (−0.095), and the last field (E9.2) contains a real number expressed as an exponent, with two digits to the right of the decimal (8.76×10^2). The blank space after the E is reserved for a + or − sign. The remaining 52 spaces of the data card are unspecified in the FORMAT statement and therefore unused.

The *READ statement* is used to read input data into the computer's memory, and the *WRITE statement* is used to transfer results to an output medium.

The general form is

READ (i, n) variables

WRITE (i, n) variables

where i is the number code of an input or output device, n is the number of the corresponding FORMAT statement, and "variables" is an ordered sequence of variable names separated by commas. A card-reader input unit usually is designated by $i = 5$, a printer for output by $i = 6$, and a card punch for output by $i = 7$. Magnetic tapes, disks, etc., for both input and output are designated generally by numbers 0, 1,..., 4.

Example 8

To solve the exponential growth equation

$$N(t) = N(0)\, e^{rt},$$

values of the birth- and death-rate parameters and the independent variable t must be read in as data and the computed value of $N(t)$ printed out. Assume that b and d are to be entered in an F10.0 field specification, $N(0)$ in an I8 field, and t in an F6.3 field, and that r is to be printed out in an E12.4 field, and $N(t)$ in an I10 field. A program segment to accomplish this is would be

```
      READ (5, 20) B, D, NZERO, T
20    FORMAT (2F10.0, I8, F6.3)
      R = B — D
      ENZERO = NZERO
      NT = ENZERO * EXP(R * T)
      WRITE (6, 30) R, NT
30    FORMAT (1H①, E12.4, I10)
```

In this program b, d, r, and t are real variables; $N(0)$ and $N(t)$ are integer variables because they represent numbers of individuals, for which there can be no fractions. In computing $N(t)$, however, this variable must be real to avoid NZERO * EXP(R * T), a mixed-mode expression. Conversion to a real variable is accomplished by the assignment statement ENZERO = NZERO. Note that $N(t)$ is automatically computed

as an integer variable, however, in the statement NT = ENZERO * EXP(R * T).

In the first FORMAT statement the notation 2F10.0 means that there are two adjacent F10.0 field specifications. This convention, also valid with I and E specifications, saves writing each field specification explicitly when there are a number of identical fields in sequence. The second FORMAT statement contains the notation 1H① which advances the paper in the printer one line. Other common printer controls are 1H0 for advancing two lines, and 1H1 for advancing to a new page.

The *STOP statement* terminates execution of the object program and returns control to the monitor. The *END statement* signifies the end of a source program, and must be the last card of every Fortran IV source deck. These statements are written as

```
STOP
```

```
END
```

Exercise 8

(1) The logistic model of population growth is, from Section I.G,

$$\dot{N} = (r - cN)N.$$

Write a Fortran IV program which (1) receives data on population birth rate, death rate, the environmental resistance parameter c, and population size; (2) computes the rate of change of the population at the specified size; (3) computes the carrying capacity of the environment; and (4) prints the results.

G. Transfer of Control

Sometimes it is necessary to execute statements in a different order from that in which they appear in the program. This so-called *branching* is accomplished by statements described in this section: GO TO, logical IF, arithmetic IF, and computed GO TO.

The *GO TO statement* directs a one-way branch. It takes the form

```
GO TO n
```

where n is the number of another executable statement in the program.

Statement *n* thereupon is executed next, no matter where it appears in the program.

The *logical* IF *statement* provides a two-way branch in the Fortran IV language. Its form is

```
IF (e) S
```

where *e* is any expression involving one of the relational operators described below and S is any statement except another logical IF or a DO statement (described later in Section VI.J). The six *relational operators* are:

Relational operator	*Meaning*
.LT.	Less than
.LE.	Less than or equal to
.EQ.	Equal to
.NE.	Not equal to
.GE.	Greater than or equal to
.GT.	Greater than

The periods are part of the notation. If the logical expression *e* is true, statement S is executed; otherwise S is not executed and the program moves in normal sequence to the next statement.

Example 9

Suppose a linear relation between y and x varies with the value of x

$$y = a + bx \quad \text{if} \quad x < p,$$
$$y = c + dx \quad \text{if} \quad x \geqslant p.$$

A program sequence which would select the proper equation for a particular computation would be

```
IF (X.LT.P) Y = A + B * X
IF (X.GE.P) Y = C + D * X
```

The usefulness of the logical IF is extended considerably by using relational expressions in combination with *logical operators*:

Logical operator	*Meaning*
.AND.	And
.OR.	Inclusive or (*a* or *b* or both)
.NOT.	Not

For example, it is possible to write

```
IF (X.LT.P.AND.P.NE.Q) GO TO 137
```

or equivalently:

```
IF (.NOT.(X.GE.P).AND.P.NE.Q) GO TO 137
```

A three-way branch is provided by the *arithmetic IF statement.* The form is

```
IF (e) n1 , n2 , n3
```

where e is any expression and n_1 , n_2 , and n_3 are statement numbers. If $e < 0$, n_1 is executed; if $e = 0$, n_2 is executed; and if $e > 0$, n_3 is executed.

Finally, multiple branching is made possible by the *computed GO TO statement.* This statement has the form

```
GO TO (n1 , n2 ,..., nm), i
```

where n_1 , n_2 ,..., n_m are statement numbers, and i is an integer variable such that $i = 1, 2,..., m$. If the value of the variable i is 1, then control is transferred to statement n_1; if the value is 2, then the program branches to statement n_2 , and so forth. For example, in

```
GO TO (7, 14, 3, 72, 100), KAPPA
```

if KAPPA = 4 from elsewhere in the program the next statement to be executed will be that numbered 72.

Example 10

Suppose it is desired to write a Fortran IV program to (1) accept a biotic potential r and an initial population size $N(0)$; (2) solve the exponential growth differential equation (Section I.F) sequentially over a specified time interval, $0 \leqslant t \leqslant t_{\max}$; and (3) print the results for each computation time so that, in effect, the print-out will be a discrete, numerical representation of the system's dynamic behavior.

Such a program is

```
C       NZERO = INITIAL POPULATION SIZE, R = BIOTIC
C       POTENTIAL, TMAX = COMPUTATION TIME, DT = TIME
C       INTERVAL BETWEEN COMPUTATIONS.
C       READ IN DATA.
        READ (5, 100) NZERO, R, TMAX, DT
  100 FORMAT (I10, 3F10.4)
C       INITIALIZE TIME (T).
        T = 0.
C       PRINT INITIAL CONDITIONS.
        WRITE (6,101) T, NZERO
C       INITIALIZE POPULATION SIZE (EN).
        EN = NZERO
C       COMPUTE DIFFERENTIAL OF POPULATION SIZE.
   20 DN = DT * (R * EN)
C       COMPUTE NEW POPULATION SIZE.
        EN = EN + DN
C       CONVERT EN TO INTEGER VARIABLE.
        N = EN + .5
C       INCREMENT TIME.
        T = T + DT
        PRINT RESULTS
        WRITE (6, 101) T, N
  101 FORMAT (1H(1), F10.0, I10)
C       REPEAT COMPUTATION FOR NEXT TIME INTERVAL.
        IF (T.LT.TMAX) GO TO 20
        STOP
        END
```

Exercise 9

(1) Write a Fortran IV program to solve the coupled system of differential equations which represents Lotka–Volterra population interaction (Section III.B). The program should be able to receive input data for r_1, r_2, K_1, K_2, α, β, and the initial population sizes $N_1(0)$ and $N_2(0)$, and should print out system behavior, $N_1(t)$ and $N_2(t)$, as a function of time. (This program essentially corresponds to the analog computer program for the same system given in Fig. 39.)

H. FLOWCHARTS

A great aid in digital computer programming is the flowchart, which essentially is a special block-diagram representation of the program logic. Flowcharts help the programmer keep track of where he is in developing the program, and they serve also as a visual documentation of the completed program. The symbols shown in Fig. 57 typically are used.

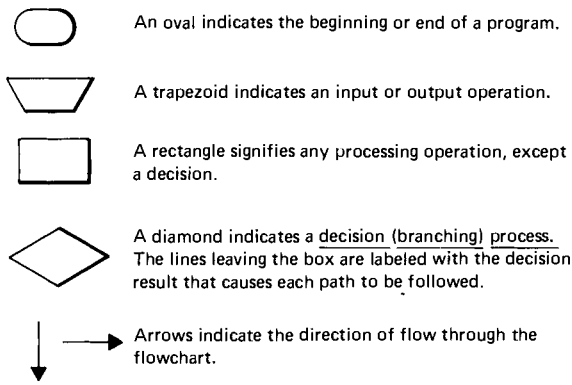


FIG. 57

Example 11

A flowchart for the program of Example 10 is given in Fig. 58.

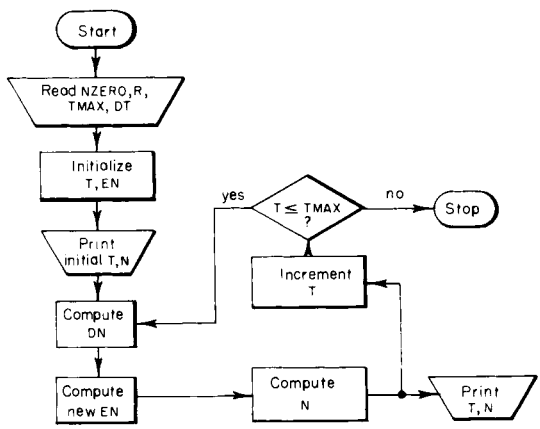


FIG. 58

Exercise 10

(1) Prepare a flowchart for the program written in Exercise 9.

I. Subscripted Variables

Use of *subscripted variables* makes it possible to denote many variables with one variable name. The set of variables is termed the *variable array*, and the individual members of the array are called *elements*. In Fortran, subscripted variables can have one, two, or three subscripts, representing 1-, 2- or 3-dimensional arrays. The state sets and vectors of Section I.B are examples of 1-dimensional arrays, and the combined loss coefficients a_{jj} of the scaled system equations in Example 6 are elements of a 2-dimensional array which will be formed later in order to represent the Silver Springs system in vector-matrix notation.

One-dimensional array elements such as x_1, x_2,..., x_n are written in Fortran subscript notation as X(1), X(2), ..., X(n), or X(I), where I = 1, 2,..., n is an integer variable. Similarly, the elements of the matrix

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \end{bmatrix}$$

are written A(1, 1), A(1, 2), etc., or using integer variables, A(I, J), where I = 1, 2 and J = 1, 2, 3.

When subscripted variables are used in a program, (1) which variables are subscripted, (2) how many subscripts for each variable, and (3) the maximum size of each subscript are items of information that must be supplied to the compiler. This is done with a *DIMENSION statement*, which must appear before the first occurrence of the dimensioned variable in the program. The form of the dimension statement is

```
DIMENSION V, V, V,...
```

where the v's stand for variable names followed by parentheses enclosing one, two, or three unsigned integer constants which denote the maximum size of each subscript. For example, a one-dimensional array X with eight elements, a 2×3 two-dimensional array Y, and a $3 \times 5 \times 4$ three-dimensional array Z would be indicated by the following statement:

```
DIMENSION X(8), Y(2, 3), Z(3, 5, 4)
```

The compiler then assigns eight memory locations to variable X, six (2×3) to Y, and 60 ($3 \times 5 \times 4$) to Z. The DIMENSION statement is non-

executable since its only function in the program is to provide information to the compiler; it does not generate any instructions in the object program.

When subscripted variables appear in READ statements, as

```
READ (5, 25) X, Y, Z
```

where X, Y, and Z are the subscripted variables X(8), Y(2, 3), and Z(3, 5, 4), the elements of each array are entered in column order, i.e., in such a manner that the first subscript varies most rapidly and the last least rapidly. For Y, the sequence of entering elements would be Y(1, 1), Y(2, 1), Y(1, 2), Y(2, 2), Y(1, 3), Y(2, 3). Of course, array elements can be read in any order by specifying the elements in explicit form in the READ statement, for example,

```
DIMENSION Y(2, 3)
READ (5, 35) Y(1, 1), Y(1, 2), Y(1, 3), Y(2, 1), Y(2, 2), Y(2, 3)
```

Note that in the DIMENSION statement "Y(2, 3)" refers to a 2×3 variable array, whereas in the READ statement "Y(2, 3)" specifies the element in the second row, third column of the same array.

Example 12

The differential equations of Example 5 representing the model I rotifer system can be written as follows by combining loss coefficients:

$$\begin{aligned}
\dot{x}_1 &= F_{01} + \delta_{31}x_3 + \delta_{61}x_6 + (a_{11})\,x_1\,,\\
\dot{x}_2 &= F_{02} + \delta_{12}x_1 + (a_{22})\,x_2\,,\\
\dot{x}_3 &= \epsilon_{23}x_2 + (a_{33})\,x_3\,,\\
\dot{x}_4 &= F_{04} + \delta_{34}x_3 + (a_{44})\,x_4\,,\\
\dot{x}_5 &= \epsilon_{45}x_4 + (a_{55})\,x_5\,,\\
\dot{x}_6 &= \delta_{56}x_5 + (a_{66})\,x_6\,,\\
\dot{x}_7 &= F_{07} + \delta_{57}x_5 + (a_{77})\,x_7\,.
\end{aligned}$$

In vector–matrix notation, this system is written more succinctly as

$$\dot{\mathbf{x}} = \mathbf{f} + A\mathbf{x},$$

where:

$$\dot{\mathbf{x}} = \begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \\ \dot{x}_4 \\ \dot{x}_5 \\ \dot{x}_6 \\ \dot{x}_7 \end{bmatrix}, \qquad \mathbf{f} = \begin{bmatrix} F_{01} \\ F_{02} \\ 0 \\ F_{04} \\ 0 \\ 0 \\ F_{07} \end{bmatrix}, \qquad \mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \\ x_7 \end{bmatrix}$$

and

$$A = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} & a_{16} & a_{17} \\ a_{21} & a_{22} & a_{23} & a_{24} & a_{25} & a_{26} & a_{27} \\ a_{31} & a_{32} & a_{33} & a_{34} & a_{35} & a_{36} & a_{37} \\ a_{41} & a_{42} & a_{43} & a_{44} & a_{45} & a_{46} & a_{47} \\ a_{51} & a_{52} & a_{53} & a_{54} & a_{55} & a_{56} & a_{57} \\ a_{61} & a_{62} & a_{63} & a_{64} & a_{65} & a_{66} & a_{67} \\ a_{71} & a_{72} & a_{73} & a_{74} & a_{75} & a_{76} & a_{77} \end{bmatrix} = \begin{bmatrix} a_{11} & 0 & \delta_{31} & 0 & 0 & \delta_{61} & 0 \\ \delta_{12} & a_{22} & 0 & 0 & 0 & 0 & 0 \\ 0 & \epsilon_{23} & a_{33} & 0 & 0 & 0 & 0 \\ 0 & 0 & \delta_{34} & a_{44} & 0 & 0 & 0 \\ 0 & 0 & 0 & \epsilon_{45} & a_{55} & 0 & \epsilon_{75} \\ 0 & 0 & 0 & 0 & \delta_{56} & a_{66} & 0 \\ 0 & 0 & 0 & 0 & \delta_{57} & 0 & a_{77} \end{bmatrix}.$$

In the coefficient matrix A note that the subscripts of the coefficients are the reverse of those of the corresponding matrix-element names: $a_{13} = \delta_{31}$, $a_{16} = \delta_{61}$, $a_{21} = \delta_{12}$, etc. This is due to the naming convention for signal flows from source to terminal compartments established in Section III.E.

A Fortran IV program to solve this system, comparable to the analog computer program of Example 5, is

```
C       DIMENSION THE VARIABLES.
        DIMENSION X(7), F(7), A(7, 7), DX(7)
C       READ F, A, AND INITIAL X, ALSO TMAX (COMPUTATION TIME)
C       AND DT (COMPUTATION TIME INTERVAL).
        READ (5, 10) X, F, A, TMAX, DT
   10 FORMAT (7F10.3/ 7F6.2/ 7E10.2/ 7E10.2/ 7E10.2/ 7E10.2/
     1    7E10.2/ 7E10.2/ 7E10.2/ 2F10.4)
C       COMPUTE SOLUTIONS OF SYSTEM EQUATIONS.
        T = 0.
C       PRINT INITIAL CONDITIONS.
        WRITE (6, 13) T, X
   14 I = 1
   12 SUM = 0.
        J = 1
```

```
   11 SUM = A(I, J) * X(J) + SUM
      J = J + 1
      IF (J.LE.7) GO TO 11
      DX(I) = DT * (F(I) + SUM)
      X(I) = X(I) + DX(I)
      I = I + 1
      IF (I.LE.7) GO TO 12
C     INCREMENT TIME.
      T = T + DT
C     PRINT SOLUTIONS.
      WRITE (6, 13) T, X
   13 FORMAT (1H①, F5.3, 7F10.3)
      IF (T.LT.TMAX) GO TO 14
      STOP
      END
```

Note, in format statement 10, that additional cards are indicated by /. The use of subscripted variables in this program facilitates greatly the bookkeeping requirements of solving this many equations simultaneously. With very large systems, the advantages of dimensioning become particularly significant.

Exercise 11

(1) Write a Fortran IV program to solve the model III rotifer system of differential equations formulated for Exercise 5. Prepare a flowchart, and use subscripted variables.

J. The DO Statement

As with dimensioning of variables, the so-called DO *loop* permits very complex computations to be performed rather easily. This feature of Fortran is one that contributes, probably more than any other, to the power and versatility of the language. The DO *statement* can be written in either of two forms

DO n $i = m_1 , m_2 , m_3$

DO n $i = m_1 , m_2$

The first form states "Do (i.e., execute) down *through* statement n from $i = m_1$ *through* $i = m_2$ in i-increments of m_3." It means to execute all statements within the *range* of the loop for every value of i specified by m_1, m_2, and m_3. The action is that the program cycles through the loop repeatedly for each value of i, executing each of the indicated statements each time. In the second form of the DO statement, $m_3 = 1$ is implied by convention.

Certain rules must be adhered to in using the DO statement: (1) The first statement following the DO statement must be executable (i.e., DIMENSION and FORMAT statements are prohibited). (2) Other DO statements are permitted within the range of a DO; in fact, DO statements can be *nested* sometimes with great complexity. An *inner* DO *loop* must terminate before an *outer* one which contains it, or both can terminate with the same statement. (3) The last statement (numbered n) cannot be a GO TO, arithmetic IF, STOP, or another DO, nor a logical IF which contains any of these. (4) No statement within the DO loop may alter or redefine the index i of the loop, or its range or increment (m_1, m_2, and m_3). (5) Control should not be transferred to a statement within the range of a DO, except from the range of an inner loop into that of an outer loop.

Rule (3) prohibits the last statement of a DO loop from transferring control. This can be achieved, however, by use of the statement

```
CONTINUE
```

The *CONTINUE statement* is a dummy statement used frequently to terminate DO loops. It causes no action when the object program is executed, and merely provides an innocuous executable statement to which the number n can be attached.

Example 13

A Fortran IV program, employing DO statements, which solves the 7-compartment, model I rotifer system of Example 12 is

```
      DIMENSION X(7), F(7), A(7, 7), DX(7)
      READ (5, 10) X, F, A, TMAX, DT
   10 FORMAT (7F10.3/ 7F6.2/ 7E10.2/ 7E10.2/ 7E10.2/
     1     7E10.2/ 7E10.2/ 7E10.2/ 7E10.2/ 2F10.4)
      T = 0.
      WRITE (6, 13) T, X
   13 FORMAT (1H①, F5.3, 7F10.3)
```

```
C       OUTER DO WITH INDEX I FOLLOWS.
   14   DO 100 I = 1, 7
        SUM = 0.
C       INNER DO WITH INDEX J FOLLOWS.
        DO 101 J = 1, 7
  101   SUM = A(I, J) * X(J) + SUM
        DX(I) = DT * (F(I) + SUM)
  100   X(I) = X(I) + DX(I)
        T = T + DT
        WRITE (6, 13) T, X
        IF (T.LT.TMAX) GO TO 14
        STOP
        END
```

In this program, exit from both DO loops is automatic and the CONTINUE statement is not needed to obtain a transfer of control.

2. *Exercise* 12

(1) Prepare Fortran IV programs employing DO statements and subscripted variables to solve the system differential equations of:

(a) Lotka–Volterra population competition (Section III.B); compare this program with that of Exercise 9.

(b) The model III rotifer system based on equations developed in Exercise 5; compare with the program produced for Exercise 4.

K. Digital and Analog Computers: Summary Comments

If there is a philosophy emergent in the preceding notes on the uses of modern computing systems in ecological modeling, it is perhaps related to how much Fortran has been left out. This has had to be a succinct and cursory treatment, and many important topics such as FUNCTION and SUBROUTINE *subprograms*, *type statements* for other than real and integer variables and constants, and useful *field specifications* such as A (alphameric) and H (Hollerith) have gone undiscussed. The same is true of analog computer technique as an expert would view it. (These notes are intended only to be introductory in nature, and the interested reader will want to consult standard references and users' manuals, a sampling of which is provided in Appendix B). Still, within the framework of these notes is a sufficient treatment of programming elements to permit ecological models of no small significance (systems of coupled differential equations) to be implemented effectively for simulation or systems analysis studies on both digital and analog computers.

The philosophy here is identical to one we all subscribe to in our use of the automobile and scores of other mechanical and electrical devices in our daily lives. It is to learn enough to become a user, not an expert. If we are apprehensive about a particular machine, such as a car or airplane, we avoid its use, but the alternative is to move more slowly and inconveniently. As some machines serve to make our personal lives both more facile and effective, computers hold the potential for accomplishing the same in our scientific lives. A small investment of time and effort puts us, as ecologists, within communicating reach of the technical specialist. Is there really a sensible alternative?

VII. Digital Simulation

A. Introduction

Many of the chapters in this book are concerned with simulation—mimicking or reproducing the time behavior of dynamic systems—using digital computers to solve differential or difference equations. In the former case where the models are continuous, this means using a machine which operates in discrete, finite time-steps to approximate systems whose state transformations occur in infinitesimal increments of time. Thus, the subject of *numerical approximation* is relevant, and in this section we consider it briefly along with discussions of special- versus general-purpose programs, and the topic of simulation languages.

B. A Special-Purpose Program: SILVER SPRINGS

In Examples 10, 12, and 13 differential equations were solved numerically by the "brute force" technique of computing differentials over small intervals of time and adding these to the state-variable values at the beginning of each interval. This method is straightforward and effective so long as the time intervals between calculations are very small. The special-purpose program of this section, SILVER SPRINGS, implements this method for both the linear and nonlinear models of Section III.H as options, and provides for multiple runs. A flowchart of the program appears in Fig. 59, and Table IV is a listing.

In Table IV the first statement after statement 104 is a type statement. It overrides the naming convention and makes LAMD10 and the MU-variables, normally integers, real throughout the program. In the next statement NCASE is an integer variable specifying the number of cases (experiments) in a particular computer run; x01, x02,..., x05 are initial values of the compartments. In statement 20, JFLAG is a variable

TABLE IV

PROGRAM SILVER SPRINGS LISTING

```
C       PROGRAM SILVER SPRINGS
C       LINEAR OR NONLINEAR FEEDING TRANSFERS, LINEAR NON-FEEDING LOSSES
C       FIVE COMPARTMENTS, THE FIRST AND SECOND FORCED
C       COMPARTMENTS-- X0=ENVIRONMENT,X1=PRODUCERS,X2=HERBIVORES,
C         X3=CARNIVORES,X4=TOP CARNIVORES,X5=DECOMPOSERS
C       FORCINGS-- F01=PHOTOSYNTHESIS, F02=BREAD INPUT
C       FLOW RATE CONSTANTS-- TAUIJ=FEEDING, RHOIO=RESPIRATION,
C         LAMDIO=LOSS DOWNSTREAM, MUI5=MORTALITY
     99 FORMAT(1H1)
    100 FORMAT(6OH      T          X1          X2          X3          X4          X5
       1     )
    101 FORMAT(6F10.4)
    102 FORMAT(I1,F3.0,9F8.0)
    103 FORMAT(8F10.0/5F10.0)
    104 FORMAT(I2,5F10.0)
        REAL LAMD10,MU15,MU25,MU35,MU45
        READ(5,104) NCASE,X01,X02,X03,X04,X05
        T=0.
        TC=0.
        I=0
      8 DO 10 I=1,NCASE
C       ENTER JFLAG (0 OR 1), NUMBER OF YEARS FOR COMPUTATION (Y),COMPUTATION
C         INTERVAL (DT), PRINTING INTERVAL (PRNT), INITIAL CONDITIONS(KCAL/M**2),
C         AND CONSTANT FORCINGS (KCAL/M**2*Y)
     20 READ(5,102) JFLAG,Y,DT,PRNT,X1,X2,X3,X4,X5,F01,F02
C       ENTER RATE CONSTANTS
     21 READ(5,103) TAU12,TAU23,TAU34,RHO10,RHO20,RHO30,RHO40,
       1RHO50,LAMD10,MU15,MU25,MU35,MU45
C       COMPUTE NONLINEAR COEFFICIENTS
        TTAU12=TAU12/X02
        TTAU23=TAU23/X03
        TTAU34=TAU34/X04
        WRITE(6,99)
        WRITE(6,100)
        WRITE(6,101)T,X1,X2,X3,X4,X5
        MAXT=Y/DT+.5
        DO 9 J=1,MAXT
        RJ=J
        T=DT*RJ
C       COMPUTE COMPARTMENT DIFFERENTIALS
        IF(JFLAG.EQ.1)GO TO 50
        DX1=DT*(F01-X1*(RHO10+LAMD10+MU15+TAU12))
        DX2=DT*(F02+TAU12*X1-X2*(RHO20+MU25+TAU23))
        DX3=DT*(TAU23*X2-X3*(RHO30+MU35+TAU34))
        DX4=DT*(TAU34*X3-X4*(RHO40+MU45))
        DX5=DT*(MU15*X1+MU25*X2+MU35*X3+MU45*X4-RHO50*X5)
        GO TO 60
     50 DX1 =DT*(F01-X1*(RHO10+LAMD10+MU15+TTAU12*X2))
        DX2=DT*(F02+TTAU12*X1*X2-X2*(RHO20+MU25+TTAU23*X3))
        DX3=DT*(TTAU23*X2*X3-X3*(RHO30+MU35+TTAU34*X4))
        DX4=DT*(TTAU34*X3*X4-X4*(RHO40+MU45))
        DX5=DT*(MU15*X1+MU25*X2+MU35*X3+MU45*X4-RHO50*X5)
C       COMPUTE SOLUTIONS
     60 X1=X1+DX1
        X2=X2+DX2
        X3=X3+DX3
        X4=X4+DX4
        X5=X5+DX5
        TC=TC+1.
C       PRINT RESULTS ONLY AFTER EVERY 'DELT' COMPUTATIONS
        DELT=PRNT/DT
        IF(TC.LT.DELT)GO TO 9
      1 WRITE(6,101) T,X1,X2,X3,X4,X5
        TC=0.
      9 CONTINUE
        T=0.
     10 CONTINUE
        STOP
        END
```

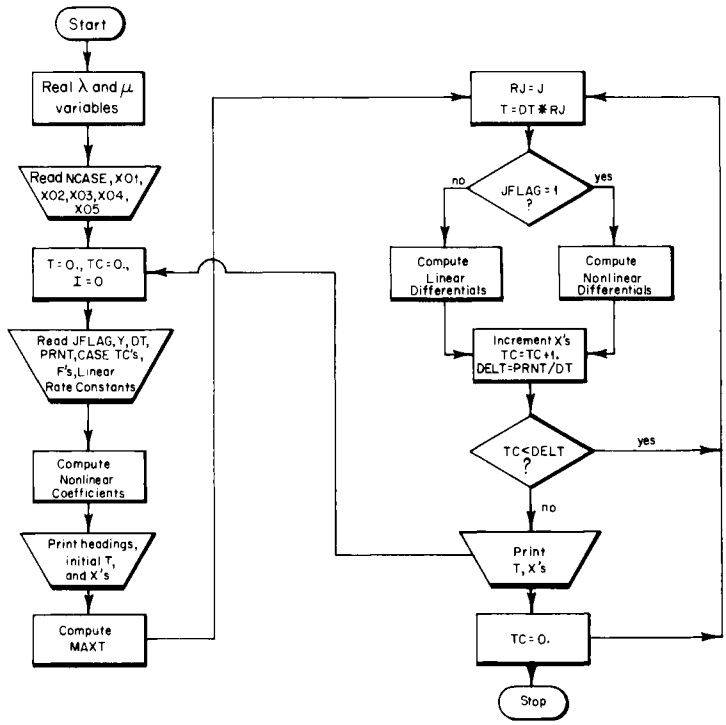


FIG. 59

that directs for each case whether the linear or nonlinear model is to be used; Y is a real variable denoting the number of years for which the solution is to be computed, e.g., Y = 10 yr; DT is the computation time interval, e.g., DT = .001 yr. This means that in $0. \leqslant Y \leqslant 10.$ yr, MAXT = 10^4 calculations of each state variable will be performed. The variable PRNT (printing interval) specifies which of these will be printed on output. For PRNT = 0.1 yr, there will be 10 lines of output per year, or 100 lines for a 10-yr total period (plus one line for initial values). FORMAT statement 99 is a special carriage control statement which instructs the printer to start a new page for each new case. FORMAT statement 100 specifies column headings and their positions on the printout.

There are two DO loops in the program. Statement 8 is an outer DO with index I = 1,NCASE. The program loops through the sequence of statements through statement 10 as many times as there are cases. The inner loop, DO 9 J = 1, MAXT, specifies the number of iterative computations of each state variable to be performed. MAXT is an integer variable computed by the program from input data provided for Y and DT; the

statement MAXT = Y/DT + .5 adjusts for rounding error in conversion from real to integer variables by adding 0.5 to each result before it is rounded down. In the inner DO loop, it is necessary to "float" the index J, i.e., to convert it to a real variable, RJ, to avoid mixed mode in the statement T = DT * RJ. In order to print the results, a variable DELT = PRNT/DT is defined which specifies the printing interval in terms of number of computations (every 100 computations in the present cases). After every computation a counter TC is advanced one unit. When TC = DELT the results are printed (statement 1), the counter is reset, TC = 0., and the program cycles again through the inner loop. When J = MAXT, and after statement 1 is executed a final time, control is transferred to the outer loop and a new case is begun. Exit from the outer loop occurs automatically after the computations for I = NCASE, and the program terminates.

Three types of data cards are required for this program as shown in the Type 1, 2, and 3 tabulations below. Each type of card is repeated NCASE times, one set for each case.

TYPE 1
Case Control, and Initial Conditions for Computing Nonlinear Rate Constants

Column:	1–2	3–12	13–22	23–32	33–42	43–52
Format:	I2	F10.0	F10.0	F10.0	F10.0	F10.0
Input:	NCASE	X01	X02	X03	X04	X05

TYPE 2
Linear or Nonlinear Decision Card, Initial States and Forcings[a]

Column:	1	2–4	5–12	13–20	21–28	29–36	37–44	45–52	53–60	61–68	69–76
Format:	I1	F3.0	F8.0	F8.0	F8.0	F8.0	F8.0	F8.0	F8.0	F8.0	F8.0
Input:	JFLAG	Y	DT	PRNT	X1	X2	X3	X4	X5	F01	F02

[a] JFLAG (linear–nonlinear control flag) is 0 for linear model and 1 for nonlinear model.

TYPE 3
Linear Rate Constants[a]

Column:	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80
Format:	F10.0	F10.0	F10.0	F10.0	F10.0	F10.0	F10.0	F10.0
Input:	TAU12	TAU23	TAU34	RHO10	RHO20	RHO30	RHO40	RHO50

Column:	1–10	11–20	21–30	31–40	41–50
Format:	F10.0	F10.0	F10.0	F10.0	F10.0
Input:	LAMD10	MU15	MU25	MU35	MU45

[a] Nonlinear rate constants are computed in the nonlinear portion of the program.

Table V presents sample output from the program: 2.5 yr of the free response of the linear model.

TABLE V

FREE RESPONSE OF SILVER SPRINGS LINEAR SYSTEM BY PROGRAM SILVER SPRINGS (EULER METHOD)

T	X1	X2	X3	X4	X5
0.0	3421.2598	213.4400	62.0600	8.8700	24.3800
0.1000	1859.2056	144.1214	57.0822	9.0002	14.5704
0.2000	1010.3384	84.0527	45.3400	8.8315	8.1602
0.3000	549.0391	46.8446	32.7007	8.3109	4.5144
0.4000	298.3557	25.6943	22.1805	7.5339	2.4891
0.5000	162.1333	14.0113	14.4410	6.6292	1.3729
0.6000	88.1074	7.6240	9.1354	5.7023	0.7592
0.7000	47.8796	4.1451	5.6579	4.8224	0.4217
0.8000	26.0187	2.2529	3.4479	4.0272	0.2358
0.9000	14.1390	1.2244	2.0745	3.3321	0.1331
1.0000	7.6835	0.6654	1.2354	2.7381	0.0761
1.1000	4.1754	0.3616	0.7295	2.2388	0.0443
1.2000	2.2690	0.1965	0.4277	1.8238	0.0264
1.3000	1.2330	0.1068	0.2493	1.4818	0.0162
1.4000	0.6700	0.0580	0.1445	1.2016	0.0103
1.5000	0.3641	0.0315	0.0834	0.9730	0.0068
1.6000	0.1979	0.0171	0.0479	0.7872	0.0046
1.7000	0.1075	0.0093	0.0275	0.6364	0.0033
1.8000	0.0584	0.0051	0.0157	0.5142	0.0024
1.9000	0.0318	0.0027	0.0089	0.4153	0.0018
2.0000	0.0173	0.0015	0.0051	0.3354	0.0014
2.1000	0.0094	0.0008	0.0029	0.2708	0.0011
2.2000	0.0051	0.0004	0.0016	0.2186	0.0008
2.3000	0.0028	0.0002	0.0009	0.1764	0.0007
2.4000	0.0015	0.0001	0.0005	0.1424	0.0005
2.5000	0.0008	0.0001	0.0003	0.1149	0.0004

C. NUMERICAL METHODS FOR SOLVING DIFFERENTIAL EQUATIONS

The material of this section, except that on the matrix exponential method, is drawn largely from Benyon (1968) and IBM Application Program Manual H20-0367-3. Benyon's article, in particular, should be consulted for further details and entries into the literature.

1. *Euler (Rectangular) Method*

The technique employed in Examples 10, 12, 13, and in program SILVER SPRINGS preceding is the Euler or rectangular method. Consider the system of differential equations

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, t)$$

any one of which at an arbitrary time n can be represented as

$$\dot{x}_n = f(\mathbf{x}_n, t_n).$$

A solution in the interval (t_n, t_{n+1}) is depicted graphically in Fig. 60. The objective of numerical approximation is to estimate this solution,

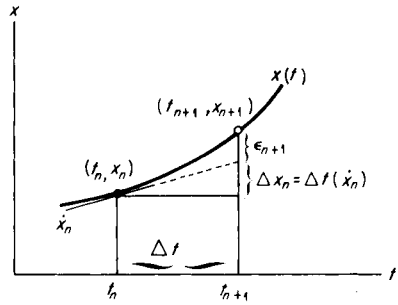


FIG. 60

i.e., to determine a new value of x, x_{n+1}, after some time interval of choice, $\Delta t = t_{n+1} - t_n$, given an initial value x_n and the amount Δx_n that it changes in the interval. That is,

$$x_{n+1} = x_n + \Delta x_n$$

is to be approximated because the only information available is x_n and its *instantaneous* rate of change $\dot{x}_n = f(\mathbf{x}_n, t_n)$. The approximation is

$$x_{n+1} = x_n + \Delta t(f(\mathbf{x}_n, t_n))$$

and reference to Fig. 60 indicates that the error ϵ_{n+1}, which results from assuming a constant slope $\dot{x}_n$ for the function over the computation interval, is proportional to the length Δt of this interval. In other words the error can be controlled by making Δt appropriately small.

Once x_{n+1} is approximated

$$x_{n+1} = x_n + \Delta t(\dot{x}_n), \tag{1a}$$

the new value is used to compute a derivative to serve as a slope over the next computation interval (t_{n+1}, t_{n+2})

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{1b}$$

A sequence of calculations beginning at any arbitrary time t_n would then be

$$\begin{aligned} \dot{x}_n &= f(\mathbf{x}_n, t_n) \\ x_{n+1} &= x_n + \Delta t(\dot{x}_n) \\ \dot{x}_{n+1} &= f(\mathbf{x}_{n+1}, t_{n+1}) \\ x_{n+2} &= x_{n+1} + \Delta t(\dot{x}_{n+1}) \\ &\vdots \end{aligned}$$

The errors ϵ at each calculation accumulate, limiting the period of time over which a response can be calculated with usable accuracy.

This method was implemented in Examples 10, 12, 13, and program SILVER SPRINGS in the following way, as illustrated by the SILVER SPRINGS linear model herbivore compartment (Table IV):

Procedure	*Example*
$\dot{x}_n = f(\mathbf{x}_n, t_n)$	Herbivore equation: $\dot{x}_2 = F_{02}(t) + \tau_{12}x_1 - x_2(\rho_{20} + \mu_{25} + \tau_{23})$
$\Delta x_n = \Delta t(\dot{x}_n)$	DX2 = DT * (F02 + TAU12 * X1 − X2 * (RHO20 + MU25 + TAU23))
$x_{n+1} = x_n + \Delta x_n$	X2 = X2 + DX2
$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1})$	
⋮	

2. *Adams–Bashforth (Predictor) Methods*

In the Euler method inaccuracy results from assuming a constant slope in each solution interval. The problem then is to estimate how the slope of the solution equation actually changes in each interval Δt. The general approach of "predictor" methods is to use past values of x and $\dot{x}$ to estimate an average slope over the next computation interval by fitting a polynomial to the past and present values. The one-step method uses one past value.

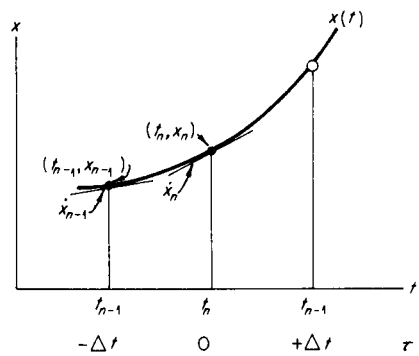


FIG. 61

Referring to Fig. 61, and letting τ be a relative time variable with origin at t_n (i.e., $\tau = 0$ when $t = t_n$), the approach is to define a polynomial (quadratic) with slope $\dot{x}_{n-1}$ at t_{n-1}, and which passes through the

point (t_n, x_n) with slope $\dot{x}_n$. The polynomial is then to be extended to t_{n+1} to approximate x_{n+1}.

(1) Define a quadratic: $x = a + b\tau + c\tau^2$.

(2) The slope at any point is: $\dot{x} = b + 2c\tau$.

(3) The coefficients a, b, and c must satisfy the following conditions:

(a) At $t = t_n$, $\tau = 0$ and from the quadratic equation

$$a = x_n .$$

(b) Similarly, at $t = t_n$ the second equation gives

$$b = \dot{x}_n .$$

(c) At $t = t_{n-1}$, $\tau = -\Delta t$, and substituting into the second equation

$$b - 2c(\Delta t) = \dot{x}_{n-1} \qquad \text{and} \qquad c = \frac{\dot{x}_n - \dot{x}_{n-1}}{2\Delta t} .$$

(d) At $t = t_{n+1}$, $\tau = \Delta t$; substituting the above-derived values of a, b, and c into the quadratic equation

$$\begin{aligned} x_{n+1} &= x_n + (\dot{x}_n)\tau + \left(\frac{\dot{x}_n - \dot{x}_{n-1}}{2\Delta t}\right)\tau^2 \\ &= x_n + \tau\left(\frac{3}{2}\dot{x}_n - \frac{1}{2}\dot{x}_{n-1}\right) \\ x_{n+1} &= x_n + \frac{\Delta t}{2}(3\dot{x}_n - \dot{x}_{n-1}). \end{aligned} \tag{2a}$$

This is the same basic form as in the Euler method, but $(\dot{x}_n)$ in the latter is now replaced by a weighted mean of the current and past slopes, $(\frac{3}{2}\dot{x}_n - \frac{1}{2}\dot{x}_{n-1})$. Using the new value x_{n+1}, the derivative is updated as before for use in the next calculation

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{2b}$$

In this "second-order" version of the Adams–Bashforth predictor approach, errors are proportional to $(\Delta t)^2$ instead of Δt, a reduction since $0 < \Delta t < 1$ always in applications. The fourth-order method based on the use of three past slopes and a fourth-degree polynomial is

$$x_{n+1} = x_n + \frac{\Delta t}{24}(55\dot{x}_n - 59\dot{x}_{n-1} + 37\dot{x}_{n-2} - 9\dot{x}_{n-3}) \tag{3a}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{3b}$$

The error in this method is even further reduced to being proportional to $(\Delta t)^4$.

3. *Predictor–Corrector Methods*

a. *Constant Step-Size (Adams–Moulton).* In predictor–corrector methods, x_{n+1} and $\dot{x}_{n+1}$ are calculated by a predictor method, but these are then regarded only as preliminary estimates, $\hat{x}_{n+1}$ and $\hat{\dot{x}}_{n+1}$. The estimate of the next slope is then included in the fitted polynomial and, for example, the fourth-order equations become

$$x_{n+1} = x_n + \frac{\Delta t}{24}(9\hat{\dot{x}}_{n+1} + 19\dot{x}_n - 5\dot{x}_{n-1} + \dot{x}_{n-2}) \tag{4a}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}), \tag{4b}$$

where $\hat{\dot{x}}_{n+1}$ is as yielded by Eq. (3b).

In iterated variants of the predictor–corrector rationale, the last-computed slope in Eq. (4b) is still regarded as an estimate $\hat{\hat{\dot{x}}}_{n+1}$—a very refined estimate—to be cycled back through Eq. (4a) in an iterative loop

$$x_{n+1} = x_n + \frac{\Delta t}{24}(9\hat{\hat{\dot{x}}}_{n+1} + 19\dot{x}_n - 5\dot{x}_{n-1} + \dot{x}_{n-2}) \tag{5a}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{5b}$$

b. *Variable Step-Size (Milne).* Methods which vary the length of the integration interval Δt do so in response to an estimate of the error at each step of the calculation. If estimated error exceeds a specified bound, Δt is reduced until the error remains in bounds. The Milne fifth-order predictor–corrector method is

$$\hat{x}_{n+1} = x_{n-1} + \frac{\Delta t}{3}(8\dot{x}_n - 5\dot{x}_{n-1} + 4\dot{x}_{n-2} - \dot{x}_{n-3}) \tag{6a}$$

$$\hat{\dot{x}}_{n+1} = f(\hat{\mathbf{x}}_{n+1}, t_{n+1}) \tag{6b}$$

$$\hat{\hat{\dot{x}}}_{n+1} = \frac{1}{8}(x_n + 7x_{n-1}) + \frac{\Delta t}{192}(65\hat{\dot{x}}_{n+1} + 243\dot{x}_n + 51\dot{x}_{n-1} + \dot{x}_{n-2}) \tag{6c}$$

$$x_{n+1} = 0.96116\hat{x}_{n+1} + 0.03884\hat{\hat{\dot{x}}}_{n+1} \tag{6d}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{6e}$$

Note how this method, unlike preceding ones, makes use of information about the past *state* x_{n-1} of the system.

4. *Simpson's Rule Method*

With methods that look at the past history (states and/or derivatives) of a system's behavior, the first few points must be computed by some other means (e.g., Euler method) since there is no history to look back to. Simpson's rule and Runge–Kutta methods (below) search forward. With $t_{n+1/2}$ signifying $\Delta t/2$, and $x_{n+1/2}$ the state a half-step forward, the Simpson's rule method can be summarized as

$$x_{n+1/2} = x_n + \frac{\Delta t}{2}(\dot{x}_n) \tag{7a}$$

$$\dot{x}_{n+1/2} = f(\mathbf{x}_{n+1/2}, t_{n+1/2}) \tag{7b}$$

$$\hat{x}_{n+1} = x_{n+1/2} + \frac{\Delta t}{2}(\dot{x}_{n+1/2}) \tag{7c}$$

$$\hat{\dot{x}}_{n+1} = f(\hat{\mathbf{x}}_{n+1}, t_{n+1}) \tag{7d}$$

$$x_{n+1} = x_n + \frac{\Delta t}{6}(\dot{x}_n + 4\dot{x}_{n+1/2} + \hat{\dot{x}}_{n+1}) \tag{7e}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{7f}$$

The procedure of this method, which is basically a predictor–corrector method, will become clear in the discussion of Runge–Kutta methods below.

5. *Runge–Kutta Methods*

Following is a description of the fourth-order Runge–Kutta method. Referring to Fig. 62:

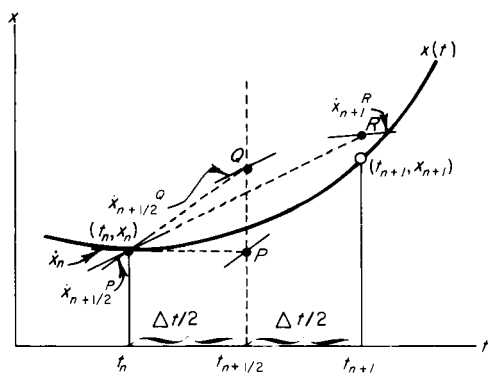


FIG. 62

(1) Go halfway ($\Delta t/2$) through the step to point P using $\dot{x}_n$

$$x^P_{n+1/2} = x_n + \frac{\Delta t}{2}(\dot{x}_n) \tag{8a}$$

$$\dot{x}^P_{n+1/2} = f(\mathbf{x}^P_{n+1/2}, t_{n+1/2}). \tag{8b}$$

(2) Repeat the same half-step through the interval $(t_n, t_{n+1/2})$, this time using the slope just computed

$$x^Q_{n+1/2} = x_n + \frac{\Delta t}{2}(\dot{x}^P_{n+1/2}) \tag{8c}$$

$$\dot{x}^Q_{n+1/2} = f(\mathbf{x}^Q_{n+1/2}, t_{n+1/2}). \tag{8d}$$

(3) Take a whole step Δt with this new slope to reach the point x^R_{n+1}

$$x^R_{n+1} = x_n + \Delta t(\dot{x}^Q_{n+1/2}) \tag{8e}$$

$$\dot{x}^R_{n+1} = f(\mathbf{x}^R_{n+1}, t_{n+1}). \tag{8f}$$

(4) The field forward has now been well explored, and a weighted mean of the various slopes is used to carry out the final, accurate step forward

$$x_{n+1} = x_n + \frac{\Delta t}{6}(\dot{x}_n + 2\dot{x}^P_{n+1/2} + 2\dot{x}^Q_{n+1/2} + \dot{x}^R_{n+1}) \tag{8g}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{8h}$$

A one-parameter family of second-order Runge–Kutta methods in which the step-length forward is arbitrary ($0 < \alpha \leqslant 1$) is

$$x_{n+\alpha} = x_n + \alpha\,\Delta t(\dot{x}_n) \tag{9a}$$

$$\dot{x}_{n+\alpha} = f(\mathbf{x}_{n+\alpha}, t_{n+\alpha}) \tag{9b}$$

$$x_{n+1} = x_n + \Delta t\left(\left(1 - \frac{1}{2\alpha}\right)\dot{x}_n + \frac{1}{2\alpha}\dot{x}_{n+\alpha}\right) \tag{9c}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{9d}$$

6. *Trapezoidal Method*

When $\alpha = 1$, the second-order Runge–Kutta method collapses to the trapezoidal or improved Euler method

$$\hat{x}_{n+1} = x_n + \Delta t(\dot{x}_n) \tag{10a}$$

$$\hat{\dot{x}}_{n+1} = f(\hat{\mathbf{x}}_{n+1}, t_{n+1}) \tag{10b}$$

$$x_{n+1} = x_n + \frac{\Delta t}{2}(\dot{x}_n + \hat{\dot{x}}_{n+1}) \tag{10c}$$

$$\dot{x}_{n+1} = f(\mathbf{x}_{n+1}, t_{n+1}). \tag{10d}$$

7. *Matrix Exponential (Paynter's) Method*

Consider an unforced (homogeneous) system of linear differential equations written, as in Example 12, in vector–matrix notation

$$\dot{\mathbf{x}} = A\mathbf{x},$$

where $\mathbf{x}$ is the solution vector and A the coefficient matrix. Just as in Example 4 where the solution of $\dot{N} = rN$ was shown to be $N(t) = N(0)e^{rt}$, so the matrix equation above has the solution

$$\mathbf{x}(t) = e^{At}\mathbf{x}(0).$$

Over a computational time interval (t_n, t_{n+1}) this solution can be expressed as

$$\mathbf{x}_{n+1} = e^{A\Delta t}\mathbf{x}_n$$

or, letting τ be a variable representing step-length,

$$\mathbf{x}(t_n + \tau) = e^{A\tau}\mathbf{x}(t_n).$$

The *matrix exponential* $e^{A\tau}$ is defined operationally by a truncated Taylor series

$$e^{A\tau} \doteq I + A\tau + \frac{(A\tau)^2}{2!} + \frac{(A\tau)^3}{3!} + \cdots + \frac{(A\tau)^k}{k!},$$

where I is the identity matrix (diagonal elements = 1, off-diagonal elements = 0) with the same number of rows and columns as A.

For forced systems the corresponding differential equations are

$$\dot{\mathbf{x}} = A\mathbf{x} + \mathbf{z},$$

where $\mathbf{z}$ is the forcing vector as in Example 12. The general incremental solution is

$$\mathbf{x}(t_n + \tau) = e^{A\tau}\mathbf{x}(t_n) + e^{A(t_n+\tau)} \int_{t_n}^{t_n+\tau} e^{-A\tau}\mathbf{z}(\tau)\, d\tau$$

whose exact solution in the case where $\mathbf{z}$ is constant over the step-length is

$$\mathbf{x}(t_n + \tau) = e^{A\tau}\mathbf{x}(t_n) + (e^{A\tau} - I)\, A^{-1}\mathbf{z}(t_n). \tag{11}$$

This is the basic equation of the method. The symbol A^{-1} is the inverse of matrix A (i.e., $A^{-1}A = AA^{-1} = I$), but it does not have to be calculated since it can be shown that

$$(e^{A\tau} - I)\, A^{-1} \doteq \tau \left(I + \frac{A\tau}{2!} + \frac{(A\tau)^2}{3!} + \cdots + \frac{(A\tau)^{k-1}}{k!}\right).$$

Because this series is so similar to that which represents $e^{A\tau}$, it becomes very economical to compute both matrices (i.e., $e^{A\tau}$ and $(e^{A\tau} - I)A^{-1}$) in a single computer program, and to use these to solve the system by applying Eq. (11). Such a program is described below.

D. A General-Purpose Program: MATEXP

MATEXP (Ball and Adams, 1967) is a general purpose Fortran IV program for solving large systems of differential equations by the matrix exponential method. The program is highly efficient, and is said to yield virtually exact solutions. It is available for both nonlinear and linear equations, with constant or time-varying coefficients and forcings. Discussion here will be restricted to linear constant-coefficient systems, with the Silver Springs linear model (Section III.H) taken as an illustrative example.

In the program the $e^{A\tau}$ matrix is termed the "C" matrix and the $(e^{A\tau} - I)A^{-1}$ matrix is called the "HP" matrix. These matrices are computed to nearly any desired accuracy (specified in the data input). Solution proceeds in the following manner

$$\mathbf{x}(t_n + \tau) = \text{C}\,\mathbf{x}(t_n) + \text{HP}\,\mathbf{z}(t_n).$$

Just one time increment $\tau = \Delta t$ is required, and therefore the C and HP matrices need to be evaluated only once.

The basic parts of the MATEXP program are the main program MATEXP, a utility subprogram OUTPUT called as a subroutine for outputting, and DISTRB, a subroutine for calculating nonconstant forcing functions and also coefficient sensitivities $\partial\mathbf{x}/\partial a_{ij}$. *Sensitivity analysis* is an important subject in systems analysis, and the MATEXP program permits ready implementation of the sensitivity concept (see Volume II, Chapters 1 and 2). There are many options available within the context of the basic program, e.g., time-varying coefficients, nonlinear differential equations, arbitrary function generation (comparable to the VDFG capabilities of analog computers), variable transport lags, etc. In general, it is a good program to have in one's library for implementing dynamic models of ecological systems. Following is a brief description of the basic information required to use it.

The data to be read in include the initial $\mathbf{x}$ vector, the coefficient matrix A, and the constant forcing vector $\mathbf{z}$. Additional information required for each run includes the number of equations, initial time, computation time interval, final time, and printing interval—much as for program SILVER SPRINGS. Since many elements of the coefficient matrix often are zero, only nonzero elements need to be read in. This

makes it necessary to enter also the row and column index numbers of the corresponding coefficients. Similarly, only nonzero initial conditions and forcings are read in with their row numbers. Since successive cases in a run may require only one or a few changes, options are available so that only altered data need to be entered.

For each case in a MATEXP run, four types of data input cards are necessary as shown in the Type 1–4 tabulations below.

TYPE 1

MATEXP Control Card[a]

Column:	1–2	3–5	6–7	8–10	11–20	21–30	31–40	41–50	51–60	61–62
Format:	I2		I2		F10.0	F10.0	F10.0	F10.0	F10.0	I2
Input:	NE	③	LL	③	P	TZERO	T	TMAX	PLTINC	MATYES

Type 1 (cont.)

Column:	63–64	65–66	67–69	70	71–72	73–74	75–80
Format:	I2	I2	I3	I1	I2	I2	F6.0
Input:	ICSS	JFLAG	ITMAX	LASTCC	I1Z	ICONTR	VAR

[a] Key to control card variables: NE is number of equations; LL is coefficient matrix tag number; P is precision of C and HP (recommend 10^{-6} or less); TZERO is zero time; T is computation time interval; TMAX is maximum time; PLTINC is printing time interval; MATYES is coefficient matrix (A) control flag: 1 is use previous A and T, 2 is read new coefficients to alter A, 3 is read entire new A (nonzero values), 4 is DISTRB to calculate entire new A, 5 is read some, DISTRB to calculate others, 6 is DISTRB to alter some A elements. ICSS is initial condition vector (XIC) flag: 1 is read in all new nonzero values, 2 is read new values to alter previous vector, 3 is use previous vector, 4 is vector = 0, 5 is use last value of X vector from previous run. JFLAG is forcing function (Z) flag: 1–4 is same as for ICSS for constant Z, 5 is call DISTRB at each time step for variable Z. ITMAX is maximum number of terms in series approximation of exp(AT). LASTCC is nonzero for last case (blank otherwise); I1Z is row of Z if only one nonzero, otherwise = 0; ICONTR for internal control options: 0 is read new control card for next case, 1 is go to 212 call DISTRB for new A or T, −1 is go to 215 call DISTRB for new initial conditions. VAR is maximum allowable value of largest coefficient matrix element times T (Recommend VAR = 1.0).

TYPE 2

Coefficient Matrix A[a,b]

Column:	1–3	4–6	7–18	
Format:	I3	I3	E12.3	Repeat, 4 per card
Input:	Row No.	Column No.	Coefficient	

[a] Include if MATYES = 2, 3, or 5.

[b] *Notes:* (1) All row and column number entries on a card must be nonzero. (2) Insert blank card after last A-matrix card. (3) Format option: data can be entered in F format.

TYPE 3

Initial Conditions Vector XIC[a,b]

Column:	1–2	3–5	6–17	Repeat columns 3–17,
Format:	I2	I3	E12.3	5 per card
Input:	MM[c]	Row No.	I.C. value	

[a] Include if ICSS = 1 or 2.

[b] *Notes:* (1) All row number entries on a card must be nonzero. (2) Insert blank card after last XIC card. (3) Format option: data can be entered in F format.

[c] MM is initial state vector tag number.

TYPE 4

Forcing Vector Z[a,b]

Column:	1–2	3–5	6–17	Repeat columns 3–17,
Format:	I2	I3	E12.3	5 per card
Input:	KK[c]	Row No.	Z Value	

[a] Include if JFLAG = 1 or 2.

[b] *Notes:* same as for Type 3 cards.

[c] KK is forcing vector tag number.

For further details on the use of DISTRB and other subprograms, Ball and Adams' report should be consulted directly. A listing of the MATEXP main program, and the two subroutines DISTRB and a version of OUTPUT appears in Appendix A. Table VI is a sample of output for the linear Silver Springs model: its free response which can be compared to that computed by the Euler method in Table V. The MATEXP output is the more accurate.

E. Digital Simulation Languages: S/360 CSMP

1. *Introduction*

Simulation languages essentially attempt to provide access to digital computers for purposes of studying time-behavior of dynamic systems without programming in a complex general purpose language such as Fortran. They are special purpose languages based on the common features of all simulation problems, and as such they are relatively simple and easy to use. The latest entries into the field, one of which is described below, incorporate virtually every feature of analog computers—except instantaneous turnaround. There is little question that simulation langu-

ages, because of their great power, versatility, and simplicity, will become of leading significance to ecological modeling in the years ahead.

Some of these languages, without translating their acronyms or discussing their characteristics or interrelationships, are: GPSS, DYNAMO, MIDAS, PACTOLUS, MIMIC, DSL/90, CSSL, 1130 CSMP, and S/360 CSMP. The last one, IBM's System/360 Continuous System Modeling Program, is introduced below. Benyon (1968, Table 4) summarizes the numerical integration methods used with most of these languages.

TABLE VI

FREE RESPONSE OF SILVER SPRINGS LINEAR SYSTEM BY PROGRAM MATEXP[a]

```
MATEXP CASE  1
NO. OF EQUATIONS  5
SPECIFIED PRECISION  0.00000010
TIME INTERVAL        0.01000000
PLOT INCREMENT       0.09999996

CONTROL FLAGS -
     MATYPE   3
     ICSS     1
     JFLAG    4
     ICONTR   0

MAX. TERMS IN EXPONENTIAL APPROX.    30
SINGLE Z ROW   0
MAX. ALLOWABLE A*DT    1.000
MAX. ALLOWABLE OPT ELEMENT      10.000

MAX.COEFF. MATRIX ELEMENT = A( 5, 5) =     -0.1986E 03
MAX. A*DT =   0.94299936  WITH DELTA T =      0.00500000

MINIMUM NON-ZERO ELEMENT = A( 4,  3) =      0.3390E 00
RATIO AMAX/AMIN =      0.5563E 03

NO. OF TERMS IN SERIES APPROX. OF MATEXP = 11

TOTAL NO. OF T HALVINGS =  1

A 1
 -6.080E 00  0.0         0.0         0.0         0.0
  8.400E-01 -1.578E 01   0.0         0.0         0.0
  0.0         1.790E 00 -6.179E 00   0.0         0.0
  0.0         0.0         3.390E-01 -2.142E 00   0.0
  1.010E 00   5.130E 00   7.410E-01   6.760E-01 -1.886E 02

C
  9.410E-01   0.0         0.0         0.0         0.0
  7.533E-03   8.540E-01   0.0         0.0         0.0
  6.849E-05   1.604E-02   9.401E-01   0.0         0.0
  7.880E-08   2.801E-05   3.252E-03   9.788E-01   0.0
  4.484E-03   2.088E-02   3.209E-03   2.999E-03   1.517E-01

HP
  1.994E-79 -7.721E 40   2.013E 55   6.644E 12 -1.013E-39
  1.994E-79   8.431E-01   3.141E-61   9.336E-46 -5.173E-60
  0.0        -4.175E 27   1.106E 01  -2.911E-78   6.350E-02
  0.0        -1.253E 27   3.841E 03  -2.670E-20   1.088E-78
  0.0         7.569E-01   1.153E 19   1.085E 09   5.947E-78
T = 0.0       X =
      3.42125977E 03 2.13439987E 02 6.20599976E 01 9.75999928E 00 2.43999939E 01
T = 1.000E-01 X =
      1.86246382E 03 1.44206619E 02 5.70476379E 01 9.71701050E 00 1.45943232E 01
T = 2.000E-01 X =
      1.01410449E 03 9.42907257E 01 4.53344269E 01 9.40783405E 00 8.18982601E 00
T = 3.000E-01 X =
      5.521164556E 02 4.70937708E 01 3.27357788E 01 8.775158888E 00 4.54010868E 00
T = 4.000E-01 X =
      3.005925298E 02 2.588031018E 01 2.223820538E 01 7.909334188E 00 2.50835991E 00
T = 5.000E-01 X =
```

[a] MATEXP = matrix exponential method.

Table continued

TABLE VI (*continued*)

```
      1.63653824E 02 1.41409941E 01 1.45029402E 01 6.93385029E 00 1.38639069E 00
T = 6.00OE-01 X =
      8.99993347E 01 7.70938587E 00 9.19054031E 00 5.95010567E 00 7.68251181E-01
T = 7.000E-01 X =
      4.85090637E 01 4.19944572E 00 5.70220461E 00 5.02429581E 00 4.27632749E-01
T = 8.000E-01 X =
      2.64101410E 01 2.28678036E 00 3.48118591E 00 4.19183540E 00 2.39640176E-01
T = 9.00CE-01 X =
      1.43786440E 01 1.24509811E 00 2.09837723E 00 3.46627331E 00 1.35587990E-01
T = 1.000E 00 X =
      7.82828140E 00 6.77898109E-01 1.25191784E 00 2.84751225E 00 7.77454972E-02
T = 1.100E 00 X =
      4.26201249E 00 3.69077623E-01 7.40613163E-01 2.32792950E 00 4.53864075E-02
T = 1.200E 00 X =
      2.32039928E 00 2.00940430E-01 4.35035765E-01 1.89643478E 00 2.71196254E-02
T = 1.300E 00 X =
      1.26331043E 00 1.09399498E-01 2.54001915E-01 1.54094315E 00 1.66778713E-02
T = 1.400E 00 X =
      6.87794030E-01 5.95611185E-02 1.47534251E-01 1.24974346E 00 1.06068850E-02
T = 1.500E 00 X =
      3.74461234E-01 3.24274153E-02 8.53073597E-02 1.01220035E 00 6.99791312E-03
T = 1.600E 00 X =
      2.03870933E-01 1.76547170E-02 4.91313823E-02 8.19015920E-01 4.79221717E-03
T = 1.700E 00 X =
      1.10994875E-01 9.61187854E-03 2.81974711E-02 6.62237644E-01 3.39925452E-03
T = 1.800E 00 X =
      6.04296289E-02 5.23305312E-03 1.61326006E-02 5.35201907E-01 2.48705433E-03
T = 1.900E 00 X =
      3.29001918E-02 2.84907361E-03 9.20410082E-03 4.32380438E-01 1.86693249E-03
T = 2.000E 00 X =
      1.79121122E-02 1.55114522E-03 5.23794815E-03 3.49233733E-01 1.42999878E-03
T = 2.100E 00 X =
      9.75203142E-03 8.44501657E-04 2.97404919E-03 2.82008946E-01 1.11214397E-03
T = 2.200E 00 X =
      5.30936196E-03 4.59778123E-04 1.68512575E-03 2.27701843E-01 8.74645775E-04
T = 2.300E 00 X =
      2.89061549E-03 2.50319717E-04 9.52992123E-04 1.83836281E-01 6.93380134E-04
T = 2.400E 00 X =
      1.57376099E-03 1.36283837E-04 5.38005959E-04 1.48411512E-01 5.52778132E-04
T = 2.500E 00 X =
      8.56814906E-04 7.41981203E-05 3.03239562E-04 1.19807541E-01 4.42413148E-04
```

2. s/360 CSMP

This simulation language is described by Brennan and Silberberg (1968), and in IBM Application Program Manuals H20-0240-1 and H20-0367-3, the last being a user's manual with full details.

a. *Elements of the Language.* *Numeric constants* are either integer or real, and represented essentially as in Fortran. *Symbolic names* of one to six alphameric (alphabetic A through Z, numeric 0 through 9) characters are used to represent real variables. Certain words reserved by the language are exluded as symbolic names. Integer variables are specified with a FIXED translation control statement (one of the kinds of control statements used to specify operations associated with translation, execution, and output segments of a program). Symbolic names can be subscripted according to the normal rules of Fortran. *Operators* [+, −, *, /, **, =, ( )] are as in Fortran, including the order in which they are performed.

Functions are operators which perform complex mathematical or other simulation-relevant operations. The basic s/360 CSMP library includes all the standard functions found in analog computers, plus a number of special purpose functions often encountered in simulation problems. Additional functions can also be supplied by the user. Examples from the standard library include those listed in Table VII.

TABLE VII

Name of function	General form	Operation
Integrator	Y = INTGRL(IC, X) where: IC = Y(0)	$Y = \text{IC} + \int_0^t X\,dt$
Derivative	Y = DERIV(IC, X) where: IC = X(0)	$Y = dX/dt$
Time delay	Y = DELAY(N, P, X) where: N = number of points in interval P; P = delay time	$Y(t) = X(t-P)$ when $t \geqslant P$ $Y(t) = 0$ when $t < P$
Function switch	Y = FCNSW(X_1, X_2, X_3, X_4)	$Y = X_2$ when $X_1 < 0$ $Y = X_3$ when $X_1 = 0$ $Y = X_4$ when $X_1 > 0$
Comparator	Y = COMPAR(X_1, X_2)	$Y = 0$ when $X_1 < X_2$ $Y = 1$ when $X_1 \geqslant X_2$
Arbitrary function generator (linear interpolation)	Y = AFGEN(FUNCT, X)	$Y = \text{FUNCT}(X)$
Arbitrary function generator (quadratic interpolation)	Y = NLFGEN(FUNCT, X)	$Y = \text{FUNCT}(X)$
Step function	Y = STEP(P)	$Y = 0$ when $t < P$ $Y = 1$ when $t \geqslant P$
Ramp function	Y = RAMP(P)	$Y = 0$ when $t < P$ $Y = t - P$ when $t \geqslant P$
Sine wave with delay, frequency, and phase parameters	Y = SINE(P_1, P_2, P_3) where: P_1 = delay, P_2 = radian frequency, P_3 = phase shift	$Y = 0$ when $t < P_1$ $Y = \text{SIN}(P_2(t-P_1)+P_3)$ when $t \geqslant P_1$
Largest value (real)	Y = AMAX1(X_1, X_2,..., X_n)	$Y = \text{MAX}(X_1, X_2, \ldots, X_n)$

The first word of s/360 CSMP data and control statements is a *label.* It identifies the statement as of a particular type. Examples include TITLE, INITIAL, INCON, CONSTANT, DYNAMIC, FIXED, MACRO, PARAMETER, PRINT, PRTPLOT, LABEL, TERMINAL, TIMER, END, STOP, ENDJOB. Some of these labels will be explained in an example later.

b. *Program Structure.* The S/360 CSMP formulation of a model consists of three *program segments*, identified by statements containing the labels INITIAL, DYNAMIC, and TERMINAL. Computations preliminary to solving the system differential equations are performed in the INITIAL segment, and subsequent ones in the TERMINAL segment. The equations are solved numerically in the DYNAMIC segment. The INITIAL and TERMINAL segments are optional in a program, but the DYNAMIC segment is mandatory. An END statement is used to complete specification of the model's structure.

Structure statements define the model to be simulated. They have the general form $Y = f(X_1, X_2, ..., P_1, P_2, ...)$, where X's are inputs, P's parameters, and Y the output from the "device" (e.g., a *function*) represented by the structure statement. Examples of structure statements include

```
NDOT  = R * N
FIJ   = PHIIJ * XI * XJ
X2DOT = F02 + TAU12 * X1 - X2 * (RHO20 + MU25 + TAU23)
X2    = INTGRL (IC2, X2DOT)
```

In general, rules for structure statements follow those for Fortran statements. Some particular points are: (1) If an INTGRL function is included in an expression, it must be the rightmost part of the expression (e.g., Z = INTGRL (IC, X) + Y is incorrect, but Z = Y + INTGRL (IC, X) is correct). (2) *Continuation cards* are identified by "···" as the last entry on cards which precede them. There may be up to nine cards in a statement. Cards should not be continued in the middle of variable names or constants. (3) *Comment cards* are denoted by an asterisk in column 1. (4) As in Fortran, columns 73–80 are not processed by the compiler.

c. *Data Statements.* *Data statements* are used to assign numerical values to constants, parameters, initial conditions, and variables with fixed values during a run. Referring to data for the Silver Springs linear model (Section III.H and IV.C), some sample data statements are

```
PARAMETER  A11 = -6.08, A22 = -15.78, A33 = -6.179,...
           A44 = -2.142, A55 = -188.6
CONSTANT   F01 = 20810., TAU12 = .84, MU15 = 1.01,...
           RHO10 = 3.5, LAMD10 = .73,...
           F02 = 486., TAU23 = 1.79, MU25 = 5.13, RHO20 = 8.86,...
           TAU34 = .339, MU35 = .74, RHO30 = 5.1, MU45 = .676,...
           RHO40 = 1.466, RHO50 = 188.6
INCON      IC1 = 3421.26, IC2 = 213.44, IC3 = 62.06,...
           IC4 = 8.87, IC5 = 24.38
```

Some rules for data statements include: (1) Each data type is identified by an appropriate label, such as PARAMETER, CONSTANT, and INCON, among others. The label does not have to start in column 1, but it must be followed by at least one blank before data is entered. (2) Data statements may be continued on an indefinite number of cards. (3) Data may appear anywhere on a card following the card label. (4) Unlike Fortran, data-card columns 73–80 are not processed by S/360 CSMP.

d. *Control Statements.* Certain operations related to translation, execution, and output segments of a program are specified by *control statements.*

TRANSLATION CONTROL STATEMENTS

EXAMPLE LABELS	PURPOSE
FIXED	Converts real variables to integer variables.
MACRO ⋮ ENDMAC	These labels identify a group of statements defining a "MACRO," a large functional block constructed by the user.
INITIAL DYNAMIC TERMINAL	These three labels identify the major segments of the program.
END	This statement marks completion of the model's structural description.
CONTINUE	Replaces the END card when a run is to continue from some arbitrary point where a preceding run terminates. Neither time nor IC's are initialized. This statement allows a control statement to be changed during a simulation.
SORT NOSORT	These cards determine whether a sequence of cards is to be machine-sorted into correct order or not.
STOP	This card follows the last END statement in the program.
ENDJOB	This card denotes the end of a job and must follow the STOP card (or otherwise any Fortran subroutine used). The label ENDJOB must be punched in columns 1–6.

EXECUTION CONTROL STATEMENTS

TIMER This label is used (e.g., TIMER FINTIM = 10., DELT = .001) with the following CSMP-specified variables:

- PRDEL Output print increment
- OUTDEL Print–plot output print increment
- FINTIM Maximum time for simulation
- DELT Integration step-size, Δt. If DELT is not specified, it is automatically set equal to the smaller of PRDEL and OUTDEL. If neither of these is specified, DELT is adjusted to be a submultiple of FINTIM/100
- DELMIN Minimum allowable integration interval for variable-step integration methods.

FINISH Used to specify run-terminating conditions other than FINTIM.

RELERR Used to specify relative error when variable-step integration methods are used.

ABSERR Controls absolute error when the Runge–Kutta variable-step method is used.

METHOD Used (e.g., METHOD MILNE) to specify the integration routine used. If none specified, the RKS method is used. Integration-method labels are:

- ADAMS Eqs. (2)
- CENTRL A dummy routine to be replaced by a user-supplied method
- MILNE Eqs. (6), variable-step
- RECT Eqs. (1)
- RKS Eqs. (8), variable-step, Simpson's Rule to estimate error
- RKSFX Eqs. (8), fixed integration interval
- SIMP Eqs. (7)
- TRAPZ Eqs. (10).

OUTPUT CONTROL STATEMENTS

PRINT	Specifies variables whose values are to be printed at each PRDEL interval.
TITLE	For naming the program, etc.
PRTPLOT	Specifies variables whose values are to be print-plotted (e.g., Table VIII) at each OUTDEL interval.
LABEL	Used to specify headings for each page of print–plot output. Up to 10 per run permitted.
RANGE	Used to obtain maximum and minimum values of specified variables (done automatically for PRTPLOT variables).

Example 14

A S/360 CSMP program to obtain the free response of the Silver Springs linear model (Sections III.H and IV.C) by the Milne method is as follows:

```
TITLE SILVER SPRINGS LINEAR SYSTEM

* INITIAL PROGRAM SEGMENT.
INITIAL

* ENTER DATA.
INCON IC1 = 3421.26, IC2 = 213.44, IC3 = 62.06, IC4 = 8.87, IC5 = 24.38
CONSTANT F01 = 0., F02 = 0., TAU12 = .84, TAU23 = 1.79, TAU34 = .339,...
    MU15 = 1.01, MU25 = 5.13, MU35 = .74, MU45 = .676,...
    LAMD10 = .73, RHO10 = 3.5, RHO20 = 8.86, RHO30 = 5.1,...
    RHO40 = 1.466, RHO50 = 188.6

* COMPUTE MINUS TURNOVER RATES (A-MATRIX ELEMENTS).
    A11 = -(TAU12 + MU15 + LAMD10 + RHO10)
    A22 = -(TAU23 + MU25 + RHO20)
    A33 = -(TAU34 + MU35 + RHO30)
    A44 = -(MU45 + RHO40)
    A55 = -RHO50

* DYNAMIC PROGRAM SEGMENT.
DYNAMIC
    X1 = INTGRL (IC1, F01 + A11 * X1)
```

```
      X2 = INTGRL (IC2, F02 + TAU12 * X1 + A22 * X2)
      X3 = INTGRL (IC3, TAU23 * X2 + A33 * X3)
      X4 = INTGRL (IC4, TAU34 * X3 + A44 * X4)
      X5 = INTGRL (IC5, MU15 * X1 + MU25 * X2...
           + MU35 * X3 + MU45 * X4 + A55 * X5)
      SUMX = X1 + X2 + X3 + X4 + X5

* NO TERMINAL PROGRAM SEGMENT REQUIRED.

* SPECIFY INTEGRATION METHOD.
METHOD MILNE

* SPECIFY OUTPUT (PRINT-PLOT EACH X AND PRINT SUMX ALONGSIDE).
      PRTPLOT X1 (SUMX)
      LABEL X1
      PRTPLOT X2 (SUMX)
      LABEL X2
      PRTPLOT X3 (SUMX)
      LABEL X3
      PRTPLOT X4 (SUMX)
      LABEL X4
      PRTPLOT X5 (SUMX)
      LABEL X5

* SPECIFY RUN TIME AND PRINT-PLOT INCREMENT (DELT ADJUSTS
* AUTOMATICALLY).

TIMER FINTIM = 2.5, OUTDEL = 0.1
END
STOP
ENDJOB
```

The free response of the Silver Springs system, as computed by this program, is print-plotted in Table VIII, along with a printed output of SUMX. These results should be compared with behavior computed by the Euler method (Table V) and by the matrix exponential method (Table VI).

Exercise 13

(1) Write a S/360 CSMP program to solve the Silver Springs nonlinear system (Sections III.H and IV.C) by the fourth-order Runge–Kutta fixed step-length routine. Generate system behavior for 10yr, and print the results out at intervals of 0.2 yr.

TABLE VIII

FREE RESPONSE OF SILVER SPRINGS LINEAR SYSTEM BY S/360 CSMP[a]

X1

TIME	X1	MINIMUM 8.5676E-04 X1 VERSUS TIME MAXIMUM 3.4213E 03	SUMX
0.0	3.4213E 03	----------+	3.7300E 03
1.0000E-01	1.8627E 03	----------+	2.0875E 03
2.0000E-01	1.0141E 03	----------+	1.1608E 03
3.0000E-01	5.5211E 02	--------+	6.4478E 02
4.0000E-01	3.0059E 02	----+	3.5875E 02
5.0000E-01	1.6365E 02	--+	2.0031E 02
6.0000E-01	8.9098E 01	-+	1.1247E 02
7.0000E-01	4.8508E 01	+	6.3663E 01
8.0000E-01	2.6410E 01	+	3.6448E 01
9.0000E-01	1.4378E 01	+	2.1193E 01
1.0000E 00	7.8281E 00	+	1.2578E 01
1.1000E 00	4.2619E 00	+	7.6603E 00
1.2000E 00	2.3203E 00	+	4.8115E 00
1.3000E 00	1.2633E 00	+	3.1290E 00
1.4000E 00	6.8777E-01	+	2.1106E 00
1.5000E 00	3.7445E-01	+	1.4755E 00
1.6000E 00	2.0386E-01	+	1.0652E 00
1.7000E 00	1.1099E-01	+	7.9110E-01
1.8000E 00	6.0427E-02	+	6.0071E-01
1.9000E 00	3.2898E-02	+	4.6389E-01
2.0000E 00	1.7911E-02	+	3.6293E-01
2.1000E 00	9.7515E-03	+	2.8675E-01
2.2000E 00	5.3090E-03	+	2.2806E-01
2.3000E 00	2.8904E-03	+	1.8195E-01
2.4000E 00	1.5737E-03	+	1.4605E-01
2.5000E 00	8.5676E-04	+	1.1736E-01

X2

TIME	X2	MINIMUM 7.4193E-05 X2 VERSUS TIME MAXIMUM 2.1344E 02	SUMX
0.0	2.1344E 02	----------+	3.7300E 03
1.0000E-01	1.4421E 02	----------+	2.0875E 03
2.0000E-01	8.4291E 01	----------+	1.1608E 03
3.0000E-01	4.7084E 01	----------+	6.4478E 02
4.0000E-01	2.5880E 01	------+	3.5875E 02
5.0000E-01	1.4141E 01	---+	2.0031E 02
6.0000E-01	7.7093E 00	-+	1.1247E 02
7.0000E-01	4.1994E 00	+	6.3663E 01
8.0000E-01	2.2868E 00	+	3.6448E 01
9.0000E-01	1.2451E 00	+	2.1193E 01
1.0000E 00	6.7788E-01	+	1.2578E 01
1.1000E 00	3.6907E-01	+	7.6603E 00
1.2000E 00	2.0094E-01	+	4.8115E 00
1.3000E 00	1.0940E-01	+	3.1290E 00
1.4000E 00	5.9559E-02	+	2.1106E 00
1.5000E 00	3.2426E-02	+	1.4755E 00
1.6000E 00	1.7654E-02	+	1.0652E 00
1.7000E 00	9.6115E-03	+	7.9110E-01
1.8000E 00	5.2328E-03	+	6.0071E-01
1.9000E 00	2.8489E-03	+	4.6389E-01
2.0000E 00	1.5511E-03	+	3.6293E-01
2.1000E 00	8.4446E-04	+	2.8675E-01
2.2000E 00	4.5975E-04	+	2.2806E-01
2.3000E 00	2.5030E-04	+	1.8195E-01
2.4000E 00	1.3628E-04	+	1.4605E-01
2.5000E 00	7.4193E-05	+	1.1736E-01

[a] Results obtained by the Milne method.

TABLE VIII (*continued*)

X3

MINIMUM X3 VERSUS TIME MAXIMUM
3.0323E-04 6.2060E 01

TIME	X3	I	SUMX
0.0	6.2060E 01	----------+	3.7300E 03
1.0000E-01	5.7048E 01	----------+	2.0875E 03
2.0000E-01	4.5335E 01	---------+	1.1608E 03
3.0000E-01	3.2736E 01	--------+	6.4478E 02
4.0000E-01	2.2238E 01	-------+	3.5875E 02
5.0000E-01	1.4503E 01	------+	2.0031E 02
6.0000E-01	9.1905E 00	-----+	1.1247E 02
7.0000E-01	5.7022E 00	----+	6.3663E 01
8.0000E-01	3.4812E 00	---+	3.6448E 01
9.0000E-01	2.0984E 00	--+	2.1193E 01
1.0000E 00	1.2519E 00	--+	1.2578E 01
1.1000E 00	7.4060E-01	-+	7.6603E 00
1.2000E 00	4.3503E-01	-+	4.8115E 00
1.3000E 00	2.5400E-01	+	3.1290E 00
1.4000E 00	1.4753E-01	+	2.1106E 00
1.5000E 00	8.5306E-02	+	1.4755E 00
1.6000E 00	4.9130E-02	+	1.0652E 00
1.7000E 00	2.8197E-02	+	7.9110E-01
1.8000E 00	1.6132E-02	+	6.0071E-01
1.9000E 00	9.2039E-03	+	4.6389E-01
2.0000E 00	5.2378E-03	+	3.6293E-01
2.1000E 00	2.9740E-03	+	2.8675E-01
2.2000E 00	1.6851E-03	+	2.2806E-01
2.3000E 00	9.5297E-04	+	1.8195E-01
2.4000E 00	5.3799E-04	+	1.4605E-01
2.5000E 00	3.0323E-04	+	1.1736E-01

X4

MINIMUM X4 VERSUS TIME MAXIMUM
1.1560E-01 8.9986E 00

TIME	X4	I	SUMX
0.0	8.8700E 00	----------+	3.7300E 03
1.0000E-01	8.9986E 00	----------+	2.0875E 03
2.0000E-01	8.8279E 00	----------+	1.1608E 03
3.0000E-01	8.3071E 00	---------+	6.4478E 02
4.0000E-01	7.5315E 00	--------+	3.5875E 02
5.0000E-01	6.6288E 00	-------+	2.0031E 02
6.0000E-01	5.7039E 00	------+	1.1247E 02
7.0000E-01	4.8256E 00	-----+	6.3663E 01
8.0000E-01	4.0314E 00	----+	3.6448E 01
9.0000E-01	3.3368E 00	---+	2.1193E 01
1.0000E 00	2.7430E 00	--+	1.2578E 01
1.1000E 00	2.2435E 00	--+	7.6603E 00
1.2000E 00	1.8283E 00	-+	4.8115E 00
1.3000E 00	1.4859E 00	-+	3.1290E 00
1.4000E 00	1.2053E 00	+	2.1106E 00
1.5000E 00	9.7636E-01	+	1.4755E 00
1.6000E 00	7.9008E-01	+	1.0652E 00
1.7000E 00	6.3888E-01	+	7.9110E-01
1.8000E 00	5.1635E-01	+	6.0071E-01
1.9000E 00	4.1716E-01	+	4.6389E-01
2.0000E 00	3.3694E-01	+	3.6293E-01
2.1000E 00	2.7209E-01	+	2.8675E-01
2.2000E 00	2.1970E-01	+	2.2806E-01
2.3000E 00	1.7738E-01	+	1.8195E-01
2.4000E 00	1.4320E-01	+	1.4605E-01
2.5000E 00	1.1560E-01	+	1.1736E-01

TABLE VIII (*continued*)

```
X5                                                              PAGE    1

                    MINIMUM              X5     VERSUS TIME          MAXIMUM
                  3.4473E-04                                     2.4380E 01
TIME          X5          I                                          I        SUMX
0.0           2.4380E 01  ----------------------------------------------+    3.7300E 03
1.0000E-01    1.4591E 01  ------------------------------+               +    2.0875E 03
2.0000E-01    8.1962E 00  ----------------+                             +    1.1608E 03
3.0000E-01    4.5382E 00  ----------+                                   +    6.4478E 02
4.0000E-01    2.5079E 00  -----+                                        +    3.5875E 02
5.0000E-01    1.3848E 00  --+                                           +    2.0031E 02
6.0000E-01    7.6716E-01  -+                                            +    1.1247E 02
7.0000E-01    4.2707E-01  +                                             +    6.3663E 01
8.0000E-01    2.3916E-01  +                                             +    3.6448E 01
9.0000E-01    1.3493E-01  +                                             +    2.1193E 01
1.0000E 00    7.7437E-02  +                                             +    1.2578E 01
1.1000E 00    4.5241E-02  +                                             +    7.6603E 00
1.2000E 00    2.6856E-02  +                                             +    4.8115E 00
1.3000E 00    1.6374E-02  +                                             +    3.1290E 00
1.4000E 00    1.0434E-02  +                                             +    2.1106E 00
1.5000E 00    6.9276E-03  +                                             +    1.4755E 00
1.6000E 00    4.4339E-03  +                                             +    1.0652E 00
1.7000E 00    3.4230E-03  +                                             +    7.9110E-01
1.8000E 00    2.5670E-03  +                                             +    6.0071E-01
1.9000E 00    1.7733E-03  +                                             +    4.6389E-01
2.0000E 00    1.2887E-03  +                                             +    3.6293E-01
2.1000E 00    1.0816E-03  +                                             +    2.8675E-01
2.2000E 00    9.0511E-04  +                                             +    2.2806E-01
2.3000E 00    4.8343E-04  +                                             +    1.8195E-01
2.4000E 00    6.0300E-04  +                                             +    1.4605E-01
2.5000E 00    5.2700E-04  +                                             +    1.1736E-01
```

VIII. Answers to Exercises

Exercise 1

(1) (a) See Fig. 63 (b) $E_0 = -(E_1 + 0.1E_2)$

(2) (a) See Figs. 64–66

(b) (i) $E_0 = -E_1$ (iii) $E_0 = -(10x + 0.1y + z)$

(ii) $E_0 = -10E_1$

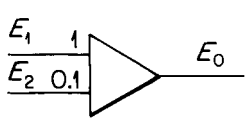


FIG. 63

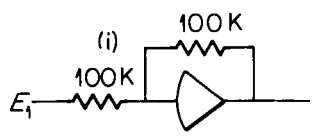


FIG. 64

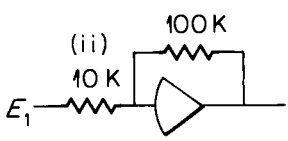


FIG. 65

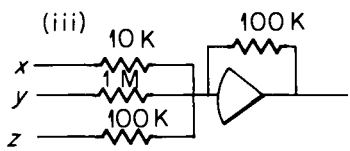


FIG. 66

Exercise 2

(1) (a) $1/(10^6 \cdot 10^{-5}) = 1/10$ (c) $1/(10^3 \cdot 10^{-6}) = 1000$
(b) $1/(10^4 \cdot 10^{-6}) = 100$ (d) $1/(10^5 \cdot 10^{-5}) = 1$

(2) See Fig. 67

(3) (a) See Fig. 68 (c) See Fig. 70
(b) See Fig. 69 (d) See Fig. 71

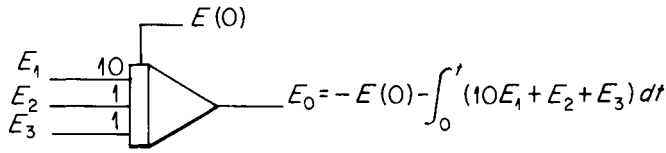


FIG. 67

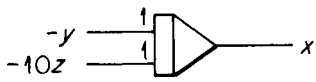


FIG. 68

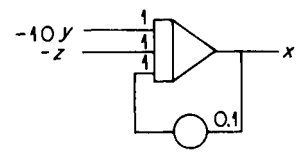


FIG. 69

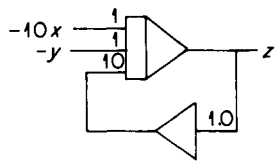


FIG. 70

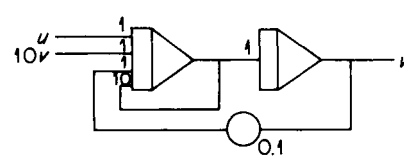


FIG. 71

Exercise 3

(1) (a) $E_0 = -0.43x$
(b) $E_0 = -(ax + 2by)$
(c) $E_0 = -(-50ax + 300y)$
(d) $E_0 = -(-50x - 50by - 10a)$
(e) $E_0 = -(10x + 0.1y + 10z)$
(f) $E_0 = -(10x + 10y)/a$
(g) $E_0 = -(10bx + y)/10b$
(h) $E_0 = 10a(x - y)$
(i) $E_0 = 10a(x - y)$
(j) $E_0 = 10bx - (b^2/a)y$
(k) $E_0 = -\int_0^t (8x - 5y + aE_0)\, dt$
(l) $E_0 = (E_0 - 10ax)/b$

(2) (a) See Fig. 72 (d) See Fig. 75
(b) See Fig. 73 (e) See Fig. 76
(c) See Fig. 74 (f) See Fig. 77

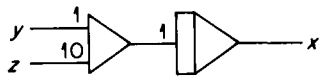


FIG. 72

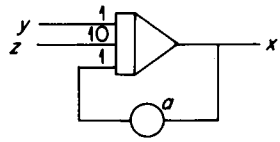


FIG. 73

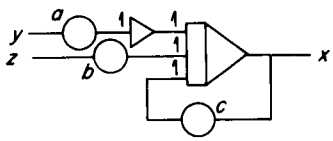


FIG. 74

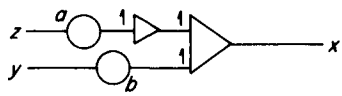


FIG. 75

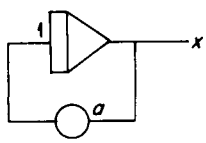


FIG. 76

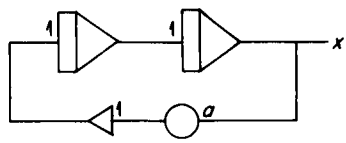


FIG. 77

Exercise 4

(1) See Fig. 78
(2) See Fig. 79
(3) See Fig. 80
(4) See Fig. 81

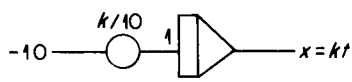


FIG. 78

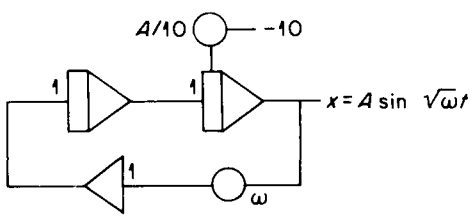


FIG. 79

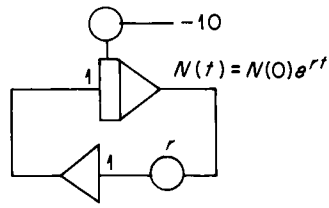


FIG. 80

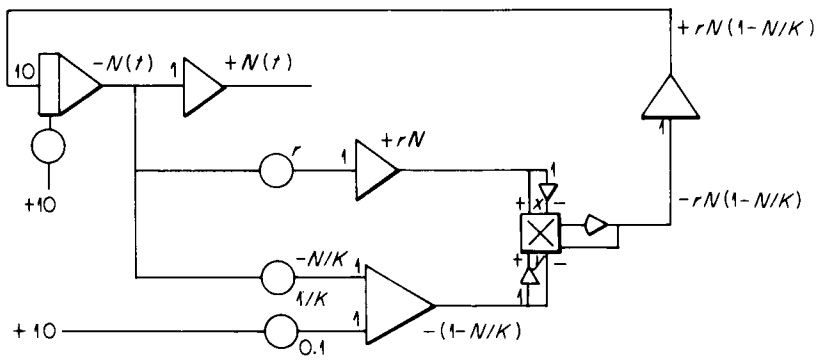


FIG. 81

Exercise 5

(1) Model II: Fig. 82; Model III: Fig. 83

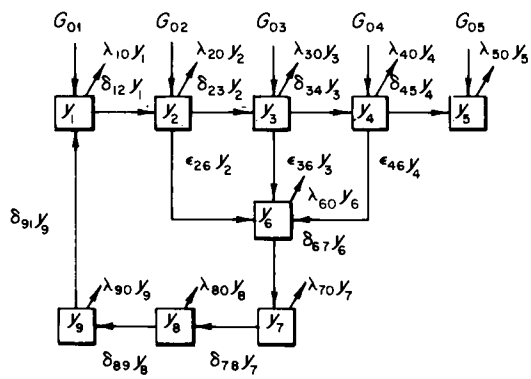


FIG. 82

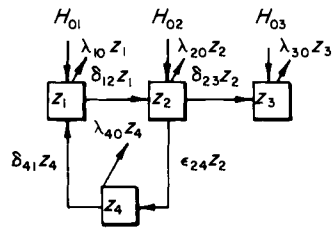


FIG. 83

(2) Model II:

$$\dot{y}_1 = G_{01}(t) + \delta_{91}y_9 - (\delta_{12} + \lambda_{10})\,y_1$$
$$\dot{y}_2 = G_{02}(t) + \delta_{12}y_1 - (\delta_{23} + \epsilon_{26} + \lambda_{20})\,y_2$$
$$\dot{y}_3 = G_{03}(t) + \delta_{23}y_2 - (\delta_{34} + \epsilon_{36} + \lambda_{30})\,y_3$$
$$\dot{y}_4 = G_{04}(t) + \delta_{34}y_3 - (\delta_{45} + \epsilon_{46} + \lambda_{40})\,y_4$$
$$\dot{y}_5 = G_{05}(t) + \delta_{45}y_4 - \lambda_{50}y_5$$
$$\dot{y}_6 = \epsilon_{26}y_2 + \epsilon_{36}y_3 + \epsilon_{46}y_4 - (\delta_{67} + \lambda_{60})\,y_6$$
$$\dot{y}_7 = \delta_{67}y_6 - (\delta_{78} + \lambda_{70})\,y_7$$
$$\dot{y}_8 = \delta_{78}y_7 - (\delta_{89} + \lambda_{80})\,y_8$$
$$\dot{y}_9 = \delta_{89}y_8 - (\delta_{91} + \lambda_{90})\,y_9$$

Model III:

$$\dot{z}_1 = H_{01}(t) + \delta_{41}z_4 - (\delta_{12} + \lambda_{10})\,z_1$$
$$\dot{z}_2 = H_{02}(t) + \delta_{12}z_1 - (\delta_{23} + \epsilon_{24} + \lambda_{20})\,z_2$$
$$\dot{z}_3 = H_{03}(t) + \delta_{23}z_2 - \lambda_{30}z_3$$
$$\dot{z}_4 = \epsilon_{24}z_2 - (\delta_{41} + \lambda_{40})\,z_4$$

(3) Model II (initial conditions omitted): Fig. 84

Model III (initial conditions omitted): Fig. 85

Exercise 6

(1) The original program (Section IV.D) has more than one rate constant lumped on a potentiometer in many cases, e.g., $a_{11} = -(\tau_{12} + \mu_{15} + \lambda_{10} + \rho_{10})$, $a_{22} = -(\tau_{23} + \mu_{25} + \rho_{20})$, etc. To represent these individually by separate potentiometers in effect removes constraints on the potentiometers. For example, in the program of Section IV.D the potentiometer labeled ".608" represents $-(0.1a_{11})$, where $a_{11} = -(\tau_{12} + \mu_{15} + \lambda_{10} + \rho_{10})$. The coefficient τ_{12} also is represented

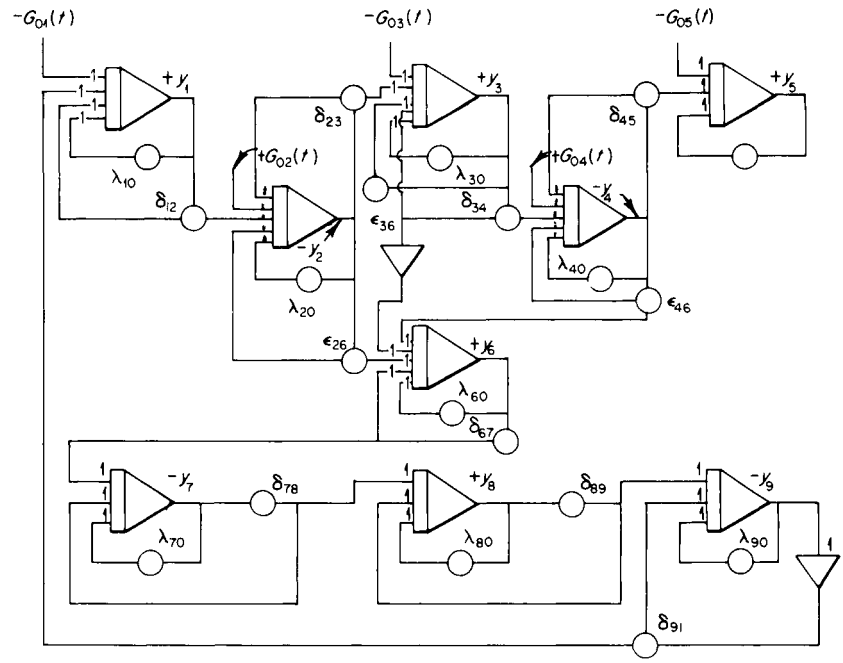


FIG. 84

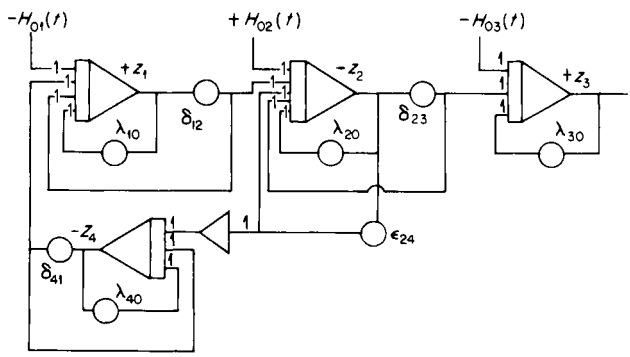


FIG. 85

by the potentiometer labeled ".84." In simulation, any change in value of the ".608" pot may or may not imply a change in τ_{12}. If it does, then the ".84" pot must be altered accordingly. If τ_{12} is ever changed for a simulation run, then the a_{11} pot must always be adjusted. Mutual dependency of potentiometers in a program creates operational problems,

and consequently is to be discouraged. In this example, only ρ_{10} and λ_{10} can be lumped onto one potentiometer without impairing operational convenience. The disadvantage of not lumping parameters is, of course, that more potentiometers are required in a program, which may cause computer capacity to be exceeded.

The scaled equations for Section IV.A can be rewritten as follows.

$$
\begin{aligned}
[\alpha_1\dot{x}_1] &= 5[\sigma_1 F_{01}] - (\tau_{12})[\alpha_1 x_1] - (\mu_{15})[\alpha_1 x_1] - (\lambda_{10} + \rho_{10})[\alpha_1 x_1] \\
&= 10(.5)[\sigma_1 F_{01}] - (.84)[\alpha_1 x_1] - 10(.101)[\alpha_1 x_1] - 10(.423)[\alpha_1 x_1] \\
&= 10(.5)[\sigma_1 F_{01}] - (\tau_{12})[\alpha_1 x_1] - 10(\mu_{15}/10)[\alpha_1 x_1] \\
&\quad - 10((\lambda_{10} + \rho_{10})/10)[\alpha_1 x_1]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_2\dot{x}_2] &= [\sigma_2 F_{02}] + 10(\tau_{12})[\alpha_1 x_1] - (\tau_{23})[\alpha_2 x_2] - (\mu_{25})[\alpha_2 x_2] - (\rho_{20})[\alpha_2 x_2] \\
&= [\sigma_2 F_{02}] + 10(.84)[\alpha_1 x_1] - 10(.179)[\alpha_2 x_2] \\
&\quad -10(.513)[\alpha_2 x_2] - 10(.886)[\alpha_2 x_2] \\
&= [\sigma_2 F_{02}] + 10(\tau_{12})[\alpha_1 x_1] - 10(\tau_{23}/10)[\alpha_2 x_2] \\
&\quad - 10(\mu_{25}/10)[\alpha_2 x_2] - 10(\rho_{20}/10)[\alpha_2 x_2]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_3\dot{x}_3] &= 2.5(\tau_{23})[\alpha_2 x_2] - (\tau_{34})[\alpha_3 x_3] - (\mu_{35})[\alpha_3 x_3] - (\rho_{30})[\alpha_3 x_3] \\
&= 25(.179)[\alpha_2 x_2] - (.339)[\alpha_3 x_3] - (.74)[\alpha_3 x_3] - 10(.51)[\alpha_3 x_3] \\
&= 25(\tau_{23}/10)[\alpha_2 x_2] - (\tau_{34})[\alpha_3 x_3] - (\mu_{35})[\alpha_3 x_3] - 10(\rho_{30}/10)[\alpha_3 x_3]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_4\dot{x}_4] &= 10(\tau_{34})[\alpha_3 x_3] - (\mu_{45})[\alpha_4 x_4] - (\rho_{40})[\alpha_4 x_4] \\
&= 10(.339)[\alpha_3 x_3] - (.676)[\alpha_4 x_4] - 10(.1466)[\alpha_4 x_4] \\
&= 10(\tau_{34})[\alpha_3 x_3] - (\mu_{45})[\alpha_4 x_4] - 10(\rho_{40}/10)[\alpha_4 x_4]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_5\dot{x}_5] &= 100(\mu_{15})[\alpha_1 x_1] + 10(\mu_{25})[\alpha_2 x_2] + 4(\mu_{35})[\alpha_3 x_3] \\
&\quad + 0.4(\mu_{45})[\alpha_4 x_4] - (\rho_{50})[\alpha_5 x_5] \\
&= 1000(.101)[\alpha_1 x_1] + 100(.513)[\alpha_2 x_2] + 4(.74)[\alpha_3 x_3] \\
&\quad + 0.4(.676)[\alpha_4 x_4] - 1000(.1886)[\alpha_5 x_5] \\
&= 1000(\mu_{15}/10)[\alpha_1 x_1] + 100(\mu_{25}/10)[\alpha_2 x_2] + 4(\mu_{35})[\alpha_3 x_3] \\
&\quad + 0.4(\mu_{45})[\alpha_4 x_4] - 1000(\rho_{50}/1000)[\alpha_5 x_5].
\end{aligned}
$$

The corresponding program (initial conditions omitted) is shown in Fig. 86. This diagram does not show how unusual gains (0.4, 4, 25, 100, 1000) can be obtained. The program has to be modified (e.g., as in Section IV.D) to achieve this.

(2) Scaled equations from the nonlinear system equations (Section III.H) are as follows.

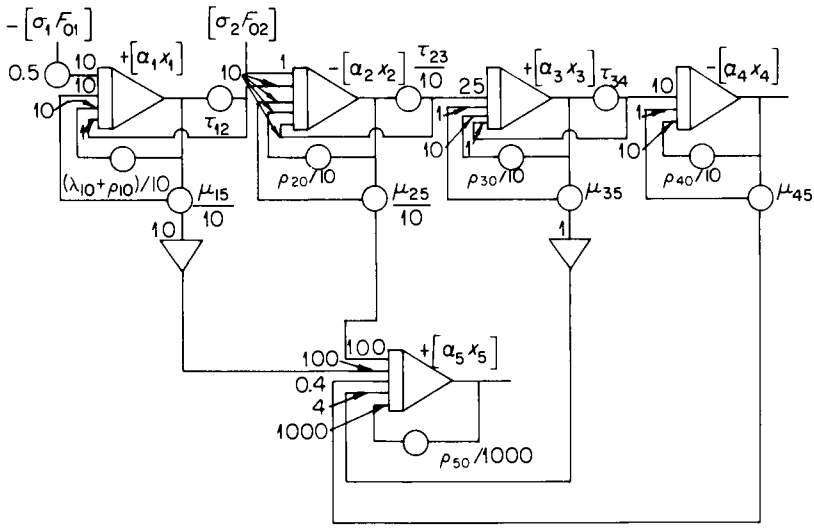


FIG. 86

$$[\alpha_1\dot{x}_1] = (\alpha_1/\sigma_1)[\sigma_1 F_{01}] - (\tau'_{12}/\alpha_2)[\alpha_2 x_2][\alpha_1 x_1] - (\mu_{15})[\alpha_1 x_1] - (\lambda_{10} + \rho_{10})[\alpha_1 x_1]$$

$$= 5[\sigma_1 F_{01}] - 50(\tau'_{12})[\alpha_2 x_2][\alpha_1 x_1] - (\mu_{15})[\alpha_1 x_1] - (\lambda_{10} + \rho_{10})[\alpha_1 x_1]$$

$$= 5[\sigma_1 F_{01}] - 50(.0039)[\alpha_2 x_2][\alpha_1 x_1] - 10(\mu_{15}/10)[\alpha_1 x_1]$$
$$- 10((\lambda_{10} + \rho_{10})/10)[\alpha_1 x_1]$$

$$= 5[\sigma_1 F_{01}] - 10(5\tau'_{12})[\alpha_2 x_2][\alpha_1 x_1] - 10(\mu_{15}/10)[\alpha_1 x_1]$$
$$-10((\lambda_{10} + \rho_{10})/10)[\alpha_1 x_1]$$

$$[\alpha_2\dot{x}_2] = (\alpha_2/\sigma_2)[\sigma_2 F_{02}] + (\tau'_{12}/\alpha_1)[\alpha_2 x_2][\alpha_1 x_1] - (\tau'_{23}/\alpha_3)[\alpha_3 x_3][\alpha_2 x_2]$$
$$- (\mu_{25})[\alpha_2 x_2] - (\rho_{20})[\alpha_2 x_2]$$

$$= 1[\sigma_2 F_{02}] + 500(\tau'_{12})[\alpha_2 x_2][\alpha_1 x_1] - 20(\tau'_{23})[\alpha_3 x_3][\alpha_2 x_2]$$
$$- (\mu_{25})[\alpha_2 x_2] - (\rho_{20})[\alpha_2 x_2]$$

$$= [\sigma_2 F_{02}] + 500(.0039)[\alpha_2 x_2][\alpha_1 x_1] - 20(.0288)[\alpha_3 x_3][\alpha_2 x_2]$$
$$- 10(\mu_{25}/10)[\alpha_2 x_2] - 10(\rho_{20}/10)[\alpha_2 x_2]$$

$$= [\sigma_2 F_{02}] + 100(5\tau'_{12})[\alpha_2 x_2][\alpha_1 x_1] - 10(2\tau'_{23})[\alpha_3 x_3][\alpha_2 x_2]$$
$$- 10(\mu_{25}/10)[\alpha_2 x_2] - 10(\rho_{20}/10)[\alpha_2 x_2]$$

$$
\begin{aligned}
[\alpha_3\dot{x}_3] &= (\tau'_{23}/\alpha_2)[\alpha_3x_3][\alpha_2x_2] - (\tau'_{34}/\alpha_4)[\alpha_4x_4][\alpha_3x_3] - (\mu_{35})[\alpha_3x_3] - (\rho_{30})[\alpha_3x_3] \\
&= 50(\tau'_{23})[\alpha_3x_3][\alpha_2x_2] - 2(\tau'_{34})[\alpha_4x_4][\alpha_3x_3] - (\mu_{35})[\alpha_3x_3] - (\rho_{30})[\alpha_3x_3] \\
&= 50(.0288)[\alpha_3x_3][\alpha_2x_2] - 2(.0382)[\alpha_4x_4][\alpha_3x_3] \\
&\quad - (\mu_{35})[\alpha_3x_3] - 10(\rho_{30}/10)[\alpha_3x_3] \\
&= 25(2\tau'_{23})[\alpha_3x_3][\alpha_2x_2] - (2\tau'_{34})[\alpha_4x_4][\alpha_3x_3] \\
&\quad - (\mu_{35})[\alpha_3x_3] - 10(\rho_{30}/10)[\alpha_3x_3]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_4\dot{x}_4] &= (\tau'_{34}/\alpha_3)[\alpha_4x_4][\alpha_3x_3] - (\mu_{45})[\alpha_4x_4] - (\rho_{40})[\alpha_4x_4] \\
&= 20(\tau'_{34})[\alpha_4x_4][\alpha_3x_3] - (\mu_{45})[\alpha_4x_4] - (\rho_{40})[\alpha_4x_4] \\
&= 20(.0382)[\alpha_4x_4][\alpha_3x_3] - (\mu_{45})[\alpha_4x_4] - 10(\rho_{40}/10)[\alpha_4x_4] \\
&= 10(2\tau'_{34})[\alpha_4x_4][\alpha_3x_3] - (\mu_{45})[\alpha_4x_4] - 10(\rho_{40}/10)[\alpha_4x_4]
\end{aligned}
$$

$$
\begin{aligned}
[\alpha_5\dot{x}_5] &= 1000(\mu_{15}/10)[\alpha_1x_1] + 100(\mu_{25}/10)[\alpha_2x_2] + 4(\mu_{35})[\alpha_3x_3] \\
&\quad + 0.4(\mu_{45})[\alpha_4x_4] - 1000(\rho_{50}/1000)[\alpha_5x_5]
\end{aligned}
$$

The program (without initial conditions) corresponding to these equations is shown in Fig. 87.

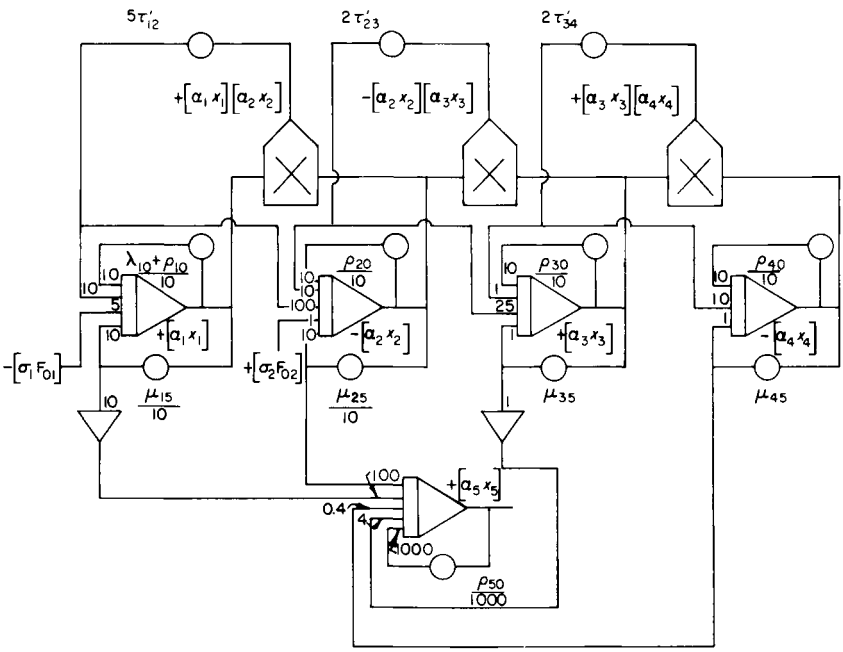


FIG. 87

Exercise 7

(1) (a) 7.84 (c) 7.84E − 03 (e) 1.E + 09
(b) 7.84 (d) −7.84E − 05 (f) −7.84E + 09

(2) Unacceptable: (b) period (d) commas
(c) comma (e) period

(3) Columnwise: *i*, *r*, *r*, *u* (too many characters); *r*, *r*, *i*, *r*; *r*, *u* (special characters), *r*, *i*

(4) (a) X + Y ** 2
(b) (X + Y) ** 2
(c) X + Y/Z
(d) (X + Y)/Z
(e) 1.+X+X ** 2/2.+X ** 3/3.
(f) ((A+B)/(C−3.))*(3.* C+2.)
(g) B = N
A/(B−1.)*(4. * B ** 2+1.)
(h) (1./A ** 2)*(R/10.) * A
(i) A+X * (B+X * (C+D * X))
(j) SIN(X/2.)/COS(X/2.)
(k) 1. − EXP(−A * T)
(l) 1. + SIN(THETA) * COS(2. * PHI) ** 2

(5) (a) A = 3.1416 * R ** 2
(b) C = K
Y = −C * SIN(OMEGA * T)
(c) J = (Q * P)/T; $j = (5 \cdot 20)/3 = 100/3 = 33.333\ldots = 33$
(d) X = −B + SQRT(B ** 2 − 4. * A * C)
(e) ENDOT = R * EN
(f) C = K
ENDOT = R * EN * ((C − EN)/C)
(g) F(I, J) = PHI(I, J) * X(I) * X(J) (see Subscripted Variables, Section VI.I)
(h) X2DOT = F02 + TAU12 * X1 − TAU23 * X2
− AMU25 * X2 − RHO20 * X2
(i) Y = .5 * LOG((1. + SIN(X))/(1.−SIN(X)))

Exercise 8

```
C       MAKE THE VARIABLES N, NDOT, AND MU REAL.
        REAL N, NDOT, MU
        READ (5, 100) BETA, MU, C, N
  100   FORMAT (4F10.0)
C       COMPUTE GROWTH RATE CONSTANT.
        R = BETA − MU
```

```
C       COMPUTE POPULATION RATE OF CHANGE.
        NDOT = (R - C * N) * N
C       CARRYING CAPACITY K IS MAX N, DENOTED WHEN FIRST AND
C       SECOND DERIVATIVES VANISH: K = R/(2 * C).
C       COMPUTE K AS AN INTEGER VARIABLE.
        K = R/(2. * C) + .5
        WRITE (6,101) NDOT, K
  101   FORMAT (1H1, F10.4, I10)
        STOP
        END
```

Exercise 9

```
C       MAKE THE VARIABLES N1, N2, K1, K2, NIC1, NIC2 REAL (NIC1 AND
C       NIC2 ARE THE INITIAL POPULATION SIZES).
        REAL N1, N2, K1, K2, NIC1, NIC2
        READ (5,20) R1, R2, K1, K2, ALPHA, BETA, NIC1, NIC2, DT, TMAX
   20   FORMAT (10F8.0)
C       INITIALIZE TIME (T) AND POPULATION SIZES.
        T = 0.
        N1 = NIC1
        N2 = NIC2
C       PRINT INITIAL POPULATION SIZES.
        WRITE (6, 21) T, N1, N2
   21   FORMAT (1H1, 3F12.4)
C       COMPUTE POPULATION DIFFERENTIALS.
  100   DN1 = DT * (R1 * N1 * (1. - N1/K1 - (ALPHA * N2)/K1))
        DN2 = DT * (R2 * N2 * (1. - N2/K2 - (BETA * N1)/K2))
C       INCREMENT POPULATION SIZES.
        N1 = N1 + DN1
        N2 = N2 + DN2
C       INCREMENT TIME.
        T = T + DT
C       PRINT NEW POPULATION SIZES.
        WRITE (6, 21) T, N1, N2
C       REPEAT COMPUTATION FOR NEXT TIME INTERVAL.
        IF (T.LT.TMAX) GO TO 100
        STOP
        END
```

Exercise 10

(1) See Fig. 88.

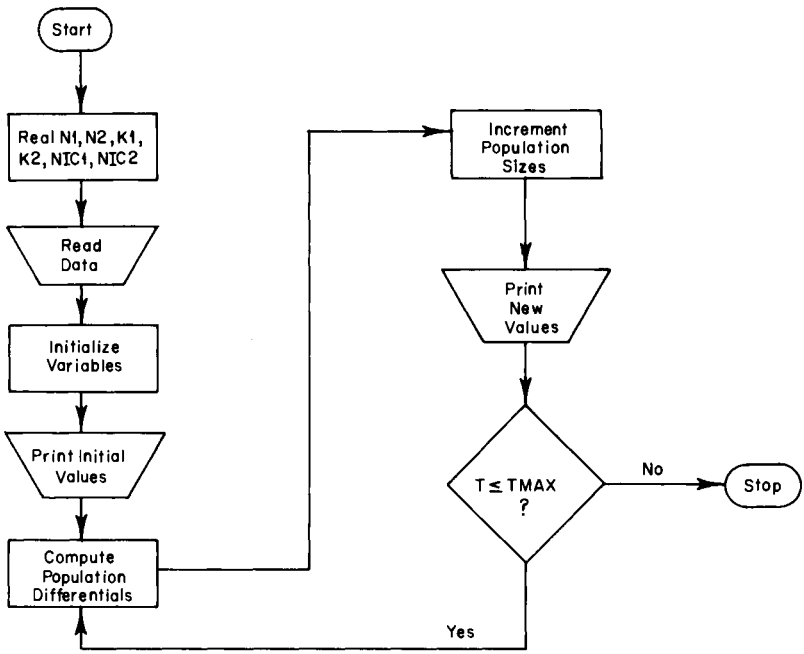


FIG. 88

Exercise 11

(1) The model III rotifer system differential equations are given in the answers to Exercise 5 above. The equivalent system in matrix notation is

$$\dot{\mathbf{z}} = \mathbf{h} + A\mathbf{z},$$

where

$$\dot{\mathbf{z}} = \begin{bmatrix} \dot{z}_1 \\ \dot{z}_2 \\ \dot{z}_3 \\ \dot{z}_4 \end{bmatrix}, \qquad \mathbf{h} = \begin{bmatrix} H_{01} \\ H_{02} \\ H_{03} \\ 0 \end{bmatrix}, \qquad \mathbf{z} = \begin{bmatrix} z_1 \\ z_2 \\ z_3 \\ z_4 \end{bmatrix},$$

and

$$A = \begin{bmatrix} -(\delta_{12} + \lambda_{10}) & 0 & 0 & \delta_{41} \\ \delta_{12} & -(\delta_{23} + \epsilon_{24} + \lambda_{20}) & 0 & 0 \\ 0 & \delta_{23} & -\lambda_{30} & 0 \\ 0 & \epsilon_{24} & 0 & -(\delta_{41} + \lambda_{40}) \end{bmatrix}.$$

A program to solve this system, using subscripted variables, is as follows.

```
C       DIMENSION THE VARIABLES.
        DIMENSION Z(4), H(4), A(4, 4), DZ(4)

C       READ H, A AND INITIAL Z, ALSO TMAX AND DT.
        READ (5, 50) Z, H, A, TMAX, DT
   50 FORMAT (8F10.0/ 8F10.0/ 8F10.0/ 2F10.0)

C       IN STATEMENT 50, SLASHES INDICATE NEW DATA CARDS. THE FIRST

C       CARD CONTAINS THE Z AND H VECTORS; THE SECOND AND THIRD

C       CARDS CONTAIN THE A MATRIX (ELEMENTS MUST BE READ IN

C       COLUMNWISE, A11, A21, A31, A41, A12, ETC., TO BE SUBSCRIPTED

C       CORRECTLY); AND THE FOURTH CARD CONTAINS TMAX AND DT.

C       COMPUTE SOLUTIONS OF SYSTEM EQUATIONS.
        T = 0.
        WRITE (6,51) T, Z
   60 I = 1
   61 SUM = 0.
        J = 1
   62 SUM = A(I, J) * Z(J) + SUM
        J = J + 1
        IF (J.LE.4) GO TO 62
        DZ(I) = DT * (H(I) + SUM)
        Z(I) = Z(I) + DZ(I)
        I = I + 1
        IF (I.LE.4) GO TO 61

C       INCREMENT TIME.
        T = T + DT

C       PRINT SOLUTIONS.
        WRITE (6,51) T, Z
   51 FORMAT (1H(1), F5.3, 4F10.4)

        IF (T.LT.TMAX) GO TO 60
        STOP
        END
```

A flowchart is shown in Fig. 89.

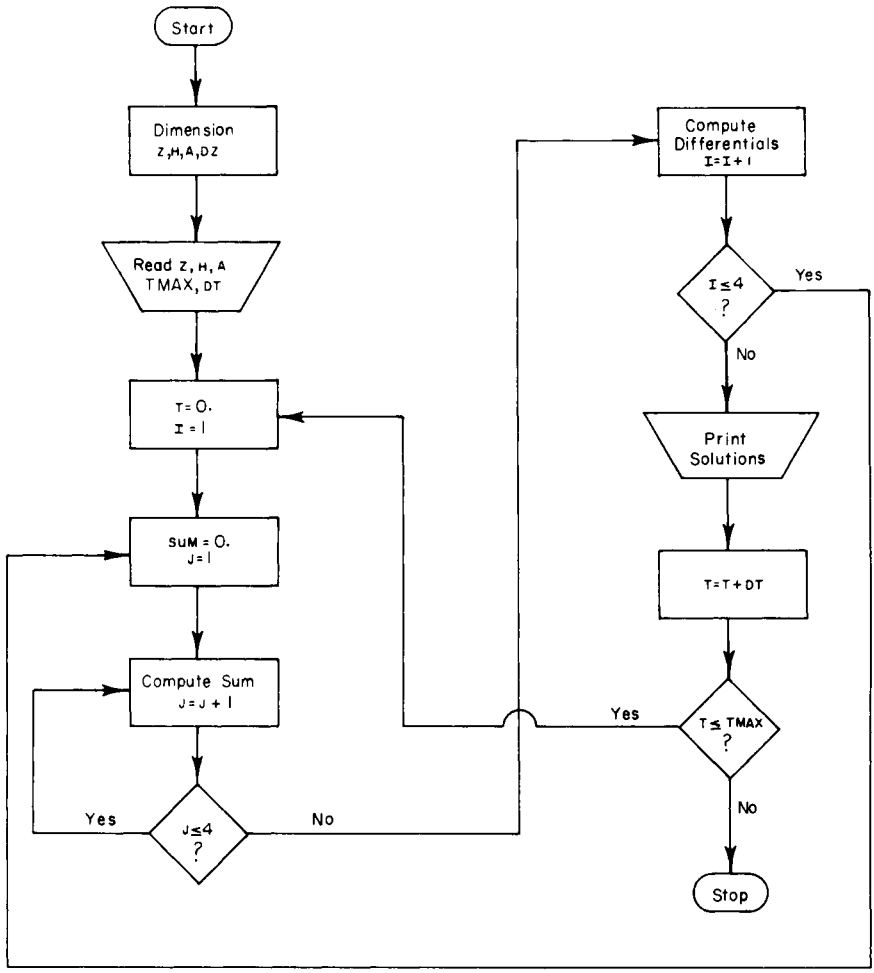


FIG. 89

Exercise 12

(1) (a) Program for the Lotka–Volterra system.

```
C       IN THIS PROBLEM IT IS NOT EFFICIENT TO DIMENSION THE
C       STATE VARIABLES. HOWEVER, TIME ITERATIONS CAN BE
C       ACHIEVED BY A DO LOOP.
        REAL N1, N2, K1, K2, NIC1, NIC2
        READ (5,100) R1, R2, K1, K2, ALPHA, BETA, NIC1, NIC2, DT, TMAX
  100 FORMAT (10F8.0)
```

```
C       INITIALIZE TIME (T) AND POPULATION SIZES.
        T = 0.
        N1 = NIC1
        N2 = NIC2
C       PRINT INITIAL CONDITIONS.
        WRITE (6, 101) T, N1, N2
  101   FORMAT (1H①, 3F12.4)
C       CALCULATE NUMBER OF COMPUTATIONS.
        NCOMP = TMAX/DT + .5
        DO 20 J = 1, NCOMP
C       REAL THE DO LOOP INDEX.
        RJ = J
        T = DT * RJ
C       POPULATION DIFFERENTIALS.
        DN1 = DT * (R1 * N1 * (1. - N1/K1 - (ALPHA * N2)/K1))
        DN2 = DT * (R2 * N2 * (1. - N2/K2 - (BETA * N1)/K2))
C       INCREMENT.
        N1 = N1 + DN1
        N2 = N2 + DN2
C       PRINT RESULTS.
        WRITE (6, 101) T, N1, N2
   20   CONTINUE
        STOP
        END
```

(b) Program for the model III rotifer system.

```
        DIMENSION Z(4), H(4), A(4, 4), DZ(4)
        READ (5, 40) Z, H, A, TMAX, DT
   40   FORMAT (8F10.0/ 8F10.0/ 8F10.0/ 2F10.0)
        T = 0.
C       PRINT INITIAL CONDITIONS.
        WRITE (6, 41) T, Z
   41   FORMAT (1H①, F10.4, 4F12.4)
C       OUTER DO LOOP TO INCREMENT TIME.
        NCOMP = TMAX/DT + .5
        DO 50 K = 1, NCOMP
        RK = K
        T = DT * RK
```

```
C       NESTED DO WITH INDEX I (NUMBER OF EQUATIONS).
        DO 51 I = 1,4
        SUM = 0.
C       NESTED DO WITH INDEX J (NUMBER OF TERMS IN EACH EQUATION).
        DO 52 J = 1, 4
   52   SUM = A(I, J) * Z(J) + SUM
        DZ(I) = DT * (H(I) + SUM)
   51   Z(I) = Z(I) + DZ(I)
C       PRINT RESULTS.
        WRITE (6, 41) T, Z
   50   CONTINUE
        STOP
        END
```

Exercise 13

(1) s/360 CSMP program for Silver Springs nonlinear model.

```
TITLE SILVER SPRINGS NONLINEAR SYSTEM
INCON IC1 = 3421.26, IC2 = 213.44, IC3 = 62.06, IC4 = 8.87, IC5 = 24.38
CONSTANT  F01 = 20810., F02 = 486., TAU12 = .84, TAU23 = 1.79,...
          TAU34 = .339, MU15 = 1.01, MU25 = 5.13, MU35 = .74,...
          MU45 = .676, LAMD10 = .73, RHO10 = 3.5, RHO20 = 8.86,...
          RHO30 = 5.1, RHO40 = 1.466, RHO50 = 188.6
* COMPUTE NONLINEAR RATE CONSTANTS
          TTAU12 = TAU12/X2
          TTAU23 = TAU23/X3
          TTAU34 = TAU34/X4
DYNAMIC
          X1 = INTGRL (IC1, F01 - X1 * (TTAU12 * X2 + MU15...
               + LAMD10 + RHO10))
          X2 = INTGRL (IC2, F02 + TTAU12 * X2 * X1...
               - X2 * (TTAU23 * X3 + MU25 + RHO20))
          X3 = INTGRL (IC3, TTAU23 * X3 * X2...
               - X3 * (TTAU34 * X4 + MU35 + RHO30))
          X4 = INTGRL (IC4, TTAU34 * X4 * X3 - X4 * (MU45 + RHO40))
          X5 = INTGRL (IC5, MU15 * X1 + MU25 * X2 + MU35 * X3...
               + MU45 * X4 - RHO50 * X5))
METHOD    RKSFX
PRINT     X1, X2, X3, X4, X5
```

```
LABEL     x1, x2, x3, x4, x5
TIMER     FINTIM = 10., OUTDEL = 0.2
*         NOTE: PRDEL WILL AUTOMATICALLY EQUAL OUTDEL.
END
STOP
ENDJOB
```

Appendix A. MATEXP Program Listing

MAIN

```
C     PROGRAM MATEXP FOR TIME RESPONSE OF LINEAR SYSTEMS
C
C     THIS PROGRAM CALCULATES THE SOLUTION OF A MATRIX OF FIRST
C     ORDER, SIMULTANEOUS DIFFERENTIAL EQUATIONS W/ CONSTANT COEFFICIENTS
C     OF THE FORM DX/DT = AX + Z.
C
C     THE METHOD IS PAYNTER-S MATRIX EXPONENTIAL METHOD
C
C     THE SOLUTION IS GIVEN FOR INCREMENTS OF THE INDEPENDENT
C     VARIABLE (T) FROM TZERO THROUGH TMAX
C
C     COMPUTES MATRICES C = EXP(A*T) AND
C                        HP = (C-I)*A INVERSE
C     SOLUTION X(N*T) = C*X((N-1)*T)+HP*Z((N-1)*T)
C     SERIES CALCULATION OF C AND HP MONITORED TO
C          ASSURE SPECIFIED SIGNIFICANCE.
C     IF T IS REDUCED FOR C AND HP CALCS.,
C     ORIGINAL ARGUMENTS ARE RESTORED BY-
C          C(2*T)=C(T)*C(T)
C          HP(2*T)=HP(T)+C(T)*HP(T)
C
C     OUTPUT FROM THE PROGRAM IS PRINTED AT INTERVALS PLTINC.
C     THE PROGRAM USES SUBROUTINES DISTRB AND OUTPUT
C
C     INPUT FOR THE PROGRAM CONSISTS OF
C          ONE CONTROL CARD
C          THE COEFFICIENT MATRIX A (UP TO 60 X 60)
C          THE INITIAL CONDITION VECTOR X
C          A FIXED DISTURBANCE VECTOR Z
C
C     A VARYING Z CAN BE GENERATED BY DISTRB
C     VARIABLE COEFFICIENT EQUATIONS MAY BE SOLVED BY APPROPRIATE
C     FUDGING OF THE DISTURBANCE FUNCTION SUBROUTINE.
C
C     CONTROL CARD INPUT INFORMATION
C          NE=NO. OF EQUATIONS (I2)
C          LL=COEFF. MATRIX TAG NO.  (I2)
C          P=PRECISION OF C AND HP (F10.0) -  RECOMMEND 1.0E-6 OR LESS
C          TZERO=ZERO TIME  (F10.0)
C          T=COMPUTATION TIME INTERVAL (F10.0)
C          TMAX=MAXIMUM TIME  (F10.0)
C          PLTINC=PRINTING TIME INTERVAL (F10.0)
C          MATYES=COEFF. MATRIX (A) CONTROL FLAG (I2)
C            1=USE PREVIOUS A AND T
C            2=READ NEW COEFF.S TO ALTER A
C            3=READ ENTIRE NEW A  (NON-ZERO VALUES)
C            4=DISTRB TO CALC. ENTIRE NEW A
C            5=READ SOME, DISTRB TO CALC. OTHERS
C            6=DISTRB TO ALTER SOME A ELEMENTS
C          ICSS=INITIAL CONDITION VECTOR (XIC) FLAG (I2)
C            1=READ IN ALL NEW NON-ZERO VALUES
C            2=READ NEW VALUES TO ALTER PREVIOUS VECTOR
C            3=USE PREVIOUS VECTOR
C            4=VECTOR=0
C            5=USE LAST VALUE OF X VECTOR FROM PREVIOUS RUN
C          JFLAG=FORCING FUNCTION (Z) FLAG (I2)
C            1 THRU 4=SAME AS FOR ICSS FOR CONSTANT Z
C            5=CALL DISTRB AT EACH TIME STEP FOR VARIABLE Z
C     ITMAX = MAX. NO. OF TERMS IN SERIES APPROX.
C          OF EXP(AT).  (I3)
C     LASTCC = NON-ZERO FOR LAST CASE (I1)
C     IIZ = ROW NO. OF Z IF ONLY ONE NON-ZERO,
C          OTHERWISE =0     (I2)
C     ICONTR - FOR INTERNAL CONTROL OPTIONS   (I2)
C          0=READ NEW CONTROL CARD FOR NEXT CASE
C          1=GO TO 212 CALL DISTRB FOR NEW A OR T
C         -1=GO TO 215 CALL DISTRB FOR NEW I.C.-S
```

```
C      VAR = MAX. ALLOWABLE VALUE OF LARGEST COEFF. MATRIX ELEMENT * T
C      (RECOMMEND VAR=1.0)    (F6.0)
C
       DIMENSION A(60,60),C(60,60),HP(60,60),QPT(60,60),
      1X(60),Y(60),Z(60),XIC(60),TQP(60),ANORM(60),PX(60)
C
      COMMON C,HP,A,QPT,X,Z,Y,ITMAX,KK,LL,MM,
      1JJFLAG,XIC,NI,TIME,TMAX,TZERO,NE,TQP,T,
      2I1Z,ICONTR,PLTINC,MATYES,ICSS,JFLAG,PLT,NFLAG,ANORM
C
C      K=CASE NUMBER
C      NI=0 ON 1-ST PASS.  SET TO 1 ON 1-ST CALL OF OUTPUT.
       K=1
       NI=0
C
    1  READ (5,100)            NE,LL,P,TZERO,T,TMAX,PLTINC,MATYES,ICSS,
      1JFLAG,ITMAX,LASTCC,I1Z,ICONTR,VAR
  100 FORMAT(2(I2,3X),5F10.0,3I2,I3,I1,2I2,F6.0)
C
C      COEFFICIENT MATRIX INPUT
       GO TO (3,99,2,2,2,3),MATYES
C
    2  DO 90 I=1,NE
       DO 90 J=1,NE
   90  A(I,J)=0.0
       IF(MATYES-4)99,3,99
   99  DO 91 I=1,1379
C      MATRIX ELEMENTS  5(ROW, COLUMN, VALUE)
C      ALL I AND J ENTRIES ON CARD MUST BE NON-ZERO.
C      A BLANK CARD IS REQUIRED AFTER ALL ELEMENTS ARE READ IN.
       READ (5,101)            I1,J1,D1,I2,J2,D2,I3,J3,D3,I4,J4,D4
  101  FORMAT (4(2I3,E12.3))
C
       IF(I1)3,3,92
   92  A(I1,J1)=D1
       A(I2,J2)=D2
       A(I3,J3)=D3
   91  A(I4,J4)=D4
C
C      INITIAL CONDITION VECTOR XIC INPUT
    3  GO TO(4,120,6,5,6),ICSS
C
    4  DO 93 I=1,NE
   93  XIC(I)=0.0
  120  DO 94 I=1,15
C      ALL ROW (I) ENTRIES MUST BE NON-ZERO
C      A BLANK CARD IS REQUIRED AFTER ALL ELEMENTS ARE READ IN.
       READ(5,95)              MM,I11,D11,I12,D12,I13,D13,I14,D14,I15,D15
   95  FORMAT(I2,5(I3,E12.3))
       IF (I11)6,6,96
   96  XIC(I11)=D11
       XIC(I12)=D12
       XIC(I13)=D13
       XIC(I14)=D14
   94  XIC(I15)=D15
C
    5  MM=0
       DO 7 I=1,NE
    7  XIC(I)=0.0
    6  IF(ICSS-5)81,214,81
   81  DO 82 I=1,NE
   82  X(I)=XIC(I)
  214  IF(MATYES-3)213,213,212
  212  CALL DISTRB
  213  JJFLAG=0
C      QPTMP = MAX. PERMISSIBLE ELEMENT OF QPT FOR  8 DECIMAL COMPUTER
C      MATRIX CALC. LOSES SIGNIFICANCE IF LARGEST
C        ELEMENT IN SERIES APPROX. MATRIX QPT IS
C        GREATER THAN P*1.0E8
```

```
      QPTMP=P*1.0E8
C
      WRITE(6,211) LL,NE,P,T,
     1PLTINC,MATYES,ICSS,JFLAG,ICONTR,ITMAX,I17,VAR,QPTMP
C
  2110FORMAT(12HOMATEXP CASE,I3/17H NO. OF EQUATIONS,
     113/20H SPECIFIED PRECISION,E12.8/6H TIME ,
     28HINTERVAL,E18.8/15H PLOT INCREMENT,E17.8//
     316H CONTROL FLAGS -/1H ,5X,6HMATYES,I4/1H ,
     45X,4HICSS,I6/1H ,5X,5HJFLAG,I5/1H ,5X,6HICONTR,I4/
     534HOMAX. TERMS IN EXPONENTIAL APPROX.,I5/
     613H SINGLE Z ROW,I4/20H MAX. ALLOWABLE A*DT,E9.3/
     727H MAX. ALLOWABLE QPT ELEMENT,E11.3)
C
      PLTINC=PLTINC*0.9999
C
      JFK=0
      IF(MATYES-1)20,20,806
C     SCAN MATRIX FOR MAX. AND MIN. NON-ZERO ELEMENTS.
 806  IMAX=1
      JMAX=1
      AMAX=ABS (A(1,1))
      DO 401 I=1,NE
      DO 401 J=1,NE
      IF(AMAX-ABS (A(I,J)))402,401,401
 402  AMAX=ABS (A(I,J))
      IMAX=I
      JMAX=J
 401  CONTINUE
      IMIN=IMAX
      JMIN=JMAX
      AMIN=AMAX
      DO 409 I=1,NE
      DO 409 J=1,NE
      IF(A(I,J)) 407,409,407
 407  IF(ABS (A(I,J))-AMIN) 408,409,409
 408  AMIN=ABS (A(I,J))
      IMIN=I
      JMIN=J
 409  CONTINUE
      RATIO=AMAX/AMIN
C     AMIN = MINIMUM NON-ZERO ELEMENT
      ISTOR=0
      ADT=AMAX*T
      DO 403 I=1,11
      IF(VAR-ADT) 413,404,404
 413  ISTOR=ISTOR+1
 403  ADT=ADT*0.5
 404  T=ADT/AMAX
C     COMPUTATION INTERVAL T IS HALVED ISTOR
C       TIMES (10=MAX.) SO MAX. ELEMENT IN A*T
C       IS LESS THAN VAR.
      WRITE (6,405)              IMAX,JMAX,A(IMAX,JMAX),ADT,T,
     1 IMIN,JMIN,A(IMIN,JMIN),RATIO
 405  FORMAT (31HOMAX.COEFF. MATRIX ELEMENT = A(,I2,1H,,I2,3H) =,
     1 E15.4/13H MAX. A*DT = ,F12.8,2X,14HWITH DELTA T =,F15.8/
     230HOMINIMUM NON-ZERO ELEMENT = A(,I2,1H,,I2,3H) =,E15.4/
     318H RATIO AMAX/AMIN =,E15.4)
C
      IF(ISTOR-10)8,410,410
 410  WRITE (6,411)
 4110FORMAT(34HOA*DT STILL GREATER THAN ALLOWABLE,
     119H AFTER 10 HALVINGS.)
      GO TO 37
C     CALCULATION OF MATRIX EXPONENTIALS C AND HP
   8  DO 9 I=1,NE
      DO 9 J=1,NE
   9  C(I,J)=0.
```

```
C
      DO 10 I=1,NE
   10 C(I,I)=1.
C
C     SKIP HP CALCS. FOR HOMOGENEOUS EQUATIONS
      IF (JFLAG-4)48,51,48
   48 DO 49 I=1,NE
      DO 49 J=1,NE
   49 HP(I,J)=0.
C
      DO 50 I=1,NE
   50 HP(I,I)=T
C
   51 PE=0.0
C
      DO 11 I=1,NE
      DO 11 J=1,NE
  11  QPT(I,J)=C(I,J)
C
C NOW FORM THE MATRIX EXPONENTIALS C=EXP(A*T) AND HP=((C-I)*A INVERSE)
C
      AL=1.0
C
   12 DO 16 KL=1,ITMAX
C
      KLM=KL
      ALL=T/AL
      AL=AL+1.0
      TALLL=T/AL
C
      DO 18 I=1,NE
C
C
      DO 13 J=1,NE
      TQP(J)=0.0
      DO 13 KX=1,NE
  13  TQP(J)=TQP(J)+QPT(I,KX)*A(KX,J)
C
      DO 18 J=1,NE
  18  QPT(I,J)=TQP(J)*ALL
C
C     QPT=MATRIX TERM IN SERIES APPROX. =((A*T)**K)/K FACTORIAL
C
      DO 44 I=1,NE
      DO 44 J=1,NE
   44 C(I,J)=C(I,J)+QPT(I,J)
C
      IF (JFLAG-4)45,47,45
C
  45  IF(ITMAX-KL)47,47,145
  145 DO 46 I=1,NE
      DO 46 J=1,NE
   46 HP(I,J)=HP(I,J)+QPT(I,J)*TALLL
C
C
C FIND MAX ABS ELEMENT IN QPT AND CALL IT PMK
C
C     LARGEST QPT ELEMENT USUALLY IN ROW IMAX, COLUMN JMAX
  47  PMK=ABS (QPT(IMAX,JMAX))
      IF(QPTMP-PMK) 83,83,502
 502  IF(PMK-P) 406,406,16
C     SCAN OTHER QPT ELEMENTS ONLY WHEN QPT(IMAX, JMAX) IS LESS THAN P
 406  DO 14 I=1,NE
      DO 14 J=1,NE
  14  PMK=AMAX1(PMK,ABS (QPT(I,J)))
      IF(PMK-P)17,17,16
C
C     PRESENT MAX. QPT ELEMENT SHOULD BE LESS THAN
C       HALF PREVIOUS MAX. TO INSURE CONVERGENCE
   17 IF(PE-2.*PMK)16,21,21
```

```
   16 PE=PMK
C
   21  WRITE (6,200)            KLM
C
  200 FORMAT(44HONO. OF TERMS IN SERIES APPROX. OF MATEXP = ,I2)
C
      IF(ITMAX-1)20,20,538
  538 IF(KLM-ITMAX) 414,83,83
C
   83  T=T*0.5
      JFK=JFK+1
      IF(JFK-7)303,304,304
  304  WRITE (6,305)            PMK
  305 0FORMAT(32H07 TRIES AT HALVING T N.G., PMK=,F12.6)
C     ALL ROW (I) ENTRIES MUST BE NON-ZERO
C     A BLANK CARD IS REQUIRED AFTER ALL ELEMENTS ARE READ IN.
      READ (5,95)          KK,I21,D21,I22,D22,I23,D23,I24,D24,I25,D25
      IF(I21)27,27,78
   78 Z(I21)=D21
      Z(I22)=D22
      Z(I23)=D23
      Z(I24)=D24
   98  Z(I25)=D25
C
   25 KK=0
      DO 28 I=1,NE
   28 Z(I)=0.
C
C     ON 1-ST CALL OF OUTPUT NI SET TO 1
   27 CALL OUTPUT
C
C NOW COMES THE EQUATION SOLUTION BASED ON
C     X(NT)=M*X(NT-1)+((M-I)A INV.)*Z(NT-1)
C
   24 IF (JJFLAG-4)29,54,56
   54 DO 53 I=1,NE
      Y(I)=C(I,1)*X(1)
      DO 53 J=2,NE
   53 Y(I)=Y(I)+C(I,J)*X(J)
      IF(I1Z)52,52,702
   56 IF(JJFLAG)30,29,30
   30 CALL DISTRB
   29 IF(I1Z)700,700,54
C     ONLY ONE Z-TERM CALC. IF I1Z IS GREATER THAN ZERO
  702 DO 703 I=1,NE
  703 Y(I)=Y(I)+HP(I,I1Z)*Z(I1Z)
      GO TO 52
  700 DO 32 I=1,NE
      Y(I)=C(I,1)*X(1)+HP(I,1)*Z(1)
      DO 32 J=2,NE
   32 Y(I)=Y(I)+C(I,J)*X(J)+HP(I,J)*Z(J)
   52 DO 31 I=1,NE
   31 X(I)=Y(I)
C
C ONE TIME INCREMENT OF THE SOLUTION HAS JUST BEEN FOUND
C
C NOW PLOT AND PRINT IF PLTINC INTERVAL HAS ELAPSED
C
      JJFLAG=1
      TIME=TIME+T
      PLT=PLT+T
      IF(PLT-PLTINC)35,33,33
      GO TO 37
  303  WRITE (6,210)            KLM,PMK,T
  210  FORMAT(21HOMAX. ELEMENT IN TERM,I3,9HOF OPT =,E11.3/
     1 35H TRY HALVED TIME INTERVAL DELTA T =,F15.8)
      GO TO 8
  414 ISTOR=ISTOR+JFK
C     ORIGINAL ARGUMENTS OF C AND HP MATRICES RESTORED IF ISTOR GREATER THAN 0
```

```
      IF(ISTOR) 20,20,416
  416 WRITE (6,415)            ISTOR
  415 FORMAT(26HOTOTAL NO. OF T HALVINGS =,I3)
      DO 417 KR=1,ISTOR
      IF(JFLAG-4) 419,418,419
C     SKIP HP CALCS. FOR HOMOGENEOUS EQUATIONS
  419 DO 420 I=1,NE
      DO 421 J=1,NE
      TQP(J)=0.0
      DO 421 KX=1,NE
  421 TQP(J)=TQP(J)+HP(I,KX)*C(KX,J)
      DO 420 J=1,NE
  420 HP(I,J)=TQP(J)+HP(I,J)
C
  418 DO 430 I=1,NE
      DO 430 J=1,NE
  430 QPT(I,J)=0.0
      DO 431 I=1,NE
      DO 431 J=1,NE
      DO 431 KX=1,NE
  431 QPT(I,J)=QPT(I,J)+C(I,KX)*C(KX,J)
      DO 432 I=1,NE
      DO 432 J=1,NE
  432 C(I,J)=QPT(I,J)
  417 T=2.0*T
C
C     C(I,J) IS THE MATRIX EXPONENTIAL C=EXP(A*T)
C     AND HP(I,J) IS THE ((C-I)*A INVERSE) MATRIX
C NOW WE READ (OR CALL SUBROUTINE FOR) DISTURBANCE VECTOR
C
   20 TIME=TZERO
      PLT=0.
      GO TO (26,121,27,25,55),JFLAG
   55 IF(MATYES-3)215,215,27
  215 CALL DISTRB
      I1Z=I17
      GO TO 27
C
   26 DO 97 I=1,NE
   97 Z(I)=0.0
  121 DO 98 I=1,15
   31 I1Z=IS(IST)
C     COL. I1Z OF HP MATRIX MULT. BY Z
      WRITE(6,101)            IS(IST),JS(IST)
  101 FORMAT(18HOSENSITIVITY TO A(,I3,1H,,I3,1H))
      TIME=TZERO
      NDT=1
      DO 41 I=1,NE
      X(I)=0.0
   41 Z(I)=0.0
      JJFLAG=0
C     DURING EACH SENSITIVITY RUN -
    7 Z(I17)=XT(IST,NDT)
      NDT=NDT+1
   30 RETURN
      END
```

DISTRB

```
      SUBROUTINE DISTRB
C     DISTRB FOR TIME RESPONSE SENSITIVITIES OF LINEAR SYSTEMS
      DIMENSION A(60,60),C(60,60),HP(60,60),QPT(60,60),
     1X(60),Y(60),Z(60),XIC(60),TQP(60)
     0COMMON C,HP,A,QPT,X,Z,Y,ITMAX,KK,LL,MM,
     1JJFLAG,XIC,NI,TIME,TMAX,TZERO,NE,TQP,T,
     2IIZ,ICONTR,PLTINC,MATYES,ICSS,JFLAG,PLT
     0DIMENSION IR(5),IS(15),JS(15),IQ(30),XT(5,1000),
     1XSEN(15,30),XPSI(30)
      IF(NI)1,1,2
    1 IF(ICONTR+2)5,4,3
    2 IF(ICONTR+2)7,6,6
C     INITIAL INPUTS AND CALCS.
    3 READ(5,100)(IS(I),JS(I),I=1,5),NTI,NSENS
  100 FORMAT(6(2I3,4X))
      NDT=1
      ICONTR=-2
      NTIMO=NTI-1
      DO 8 I=1,NE
    8 Z(I)=0.0
      READ(5,103)(Z(I),I=1,NE)
  103 FORMAT(8E10.0)
C     DURING SOLUTION OF SYSTEM EQUATIONS
    6 DO 20 I=1,NSENS
      ICO=JS(I)
   20 XT(I,NDT)=X(ICO)
      NDT=NDT+1
      GO TO 30
C
C     JUST AFTER SYSTEM SOLUTION IS COMPLETED
    4 IST=0
      ICONTR=-3
      DO 21 I=1,NSENS
      DO 21 J=1,NTIMO
   21 XT(I,J)=0.5*(XT(I,J)+XT(I,J+1))
C     XT = AVG VALUES OF SENSITIVITY EQN INPUTS
      WRITE(6,102)              ((XT(I,J),J=1,NTI),I=1,NSENS)
  102 FORMAT(3H0XT/(1H ,10E11.3))
C
C     AFTER COMPLETING EACH SENSITIVITY RUN -
    5 IST=IST+1
      IF(IST-NSENS)31,31,32
C     GO TO NEXT CASE
   32 ICONTR=0
      PLTINC=TMAX
      TMAX=0.0
      NI=1
      GO TO 30
   33 CALL OUTPUT
      PLT=0.
   35 IF(TIME-TMAX)24,37,37
   37 IF(LASTCC)40,34,40
   34 K=K+1
      NI=0
      PLT=0.0
      IF(ICONTR)215,1,212
   40 STOP
      END
```

OUTPUT

```
      SUBROUTINE OUTPUT
C
      DIMENSION A(60,60),C(60,60),HP(60,60),QPT(60,60),
     1X(60),Y(60),Z(60),XIC(60),TOP(60),ANORM(60),PX(60)
C
     COMMON C,HP,A,QPT,X,Z,Y,ITMAX,KK,LL,MM,
     1JJFLAG,XIC,NI,TIME,TMAX,TZERO,NE,TOP,T,
     2IIZ,ICONTR,PLTINC,MATYES,ICSS,JFLAG,PLT,NFLAG,ANORM
C
      IF(NI)2,1,2
    1 NI=1
      NC=10
      DO 11 NCM=1,51,10
      WRITE(6,200) LL,((A(I,J),J=NCM,NC),I=1,NE)
  200 FORMAT (2H0A,I2/(1H ,1P10E11.3))
      IF(NE-NC) 10,10,11
   11 NC=NC+10
C
   10 NC=10
      DO 21 NCM=1,51,10
      WRITE(6,201) ((C(I,J),J=NCM,NC),I=1,NE)
  201 FORMAT (2H0C/(1H ,1P10E11.3))
      IF(NE-NC) 20,20,21
   21 NC=NC+10
C
   20 NC=10
      DO 31 NCM=1,51,10
      WRITE(6,202) ((HP(I,J),J=NCM,NC),I=1,NE)
  202 FORMAT (3H0HP/(1H ,1P10E11.3))
      IF(NE-NC) 2,2,31
   31 NC=NC+10
C
    2 WRITE(6,203)TIME,(X(I),I=1,NE)
  203 FORMAT(4H T =,1PE10.3,4H X =,       /(1H ,5X,10E15.8))
      IF(JFLAG.NE.5) GO TO 30
C
      WRITE(6,204) (Z(I),I=1,NE)
  204 FORMAT(6H0Z =  ,1P10E11.3/(1H ,5X,10E11.3))
   30 RETURN
      END
```

Appendix B. Selected Bibliography

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2

A Rationale for Modeling Dynamic Ecological Systems

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I. Mathematical Models

A. Introduction

Scientific hypotheses and theories never deal directly with the real world, only with arbitrary variables and other concepts, such as statements of relationships among variables. There may be many levels of concepts, all somehow connected to the real world through the operations of measurements.

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An excellent example of relationships among different levels of concepts, and between concepts and the real world comes from the field of thermodynamics. Dixon and Emery (1965) view all concepts of "operational thermodynamics" as being defined in terms of seven directly measured variables: pressure, volume, mass, time, length, force, and temperature. All concepts in successive levels of abstraction are defined in terms of these variables, from concentration and velocity to Gibbs free energy and chemical potentials. This is the basic structure of theory throughout empirical science.

These concepts and the expressed relationships among them are the models. I am dealing here with mathematical models, but in certain situations one might use physical models as well, e.g., graphs, springs, rubber balls, and miniature replicas.

Although the intelligent use of models requires explicit connection of measurements with concepts, ecologists in the past have been prone to remain satisfied with one or the other alone. Thus plant ecologists have accumulated measurements, yielding endless statistics and descriptions, with few connections to concepts. On the other hand, some ecologists have constructed elaborate models, never satisfactorily connecting them to the real world, e.g., some models of ecological succession or of the niche concept.

Ideally the scientist should work both ends simultaneously—the man who formulates the model should also make the measurements. I do not think that this is an unreasonable suggestion. The current problems ecology is called upon to solve demand it, and the current mathematical training received by young ecologists facilitates it.

B. Nature of Mathematical Models

In order to understand the nature of mathematical models one must understand the nature of mathematical theory, i.e., a body of knowledge constructed by the axiomatic method.

> One begins with certain undefined concepts. One then makes certain statements about the properties possessed by, and the relations between, these concepts. These statements are called the axioms of the theory. Then, by means of logical deduction, without any appeal to experience, various propositions (called *theorems*) are obtained from the axioms. Although the propositions do not refer directly to the real world, but are merely logical consequences of the axioms, they do represent conclusions about real phenomena, namely those real phenomena one is willing to assume possess the properties postulated in the axioms.

The theory is used as the mathematical model. Continuing:

> We are thus led to the notion of a *mathematical model of a real phenomenon.* A mathematical theory constructed by the axiomatic method is said to be a *model* of

> a real phenomenon, if one gives a rule for translating propositions of the mathematical theory into propositions about the real phenomenon. This definition is vague, for it does not state the character of the rules of translation one must employ. . . . Generally speaking, to use a mathematical theory as a model for a real phenomenon, one needs only to give a rule for identifying the abstract objects about which the axioms of the mathematical theory speak with aspects of the real phenomenon. It is then expected that the theorems of the theory will depict the phenomenon to the same extent that the axioms do, for the theorems are merely logical consequences of the axioms (quoted with permission from Parzen, 1960).

The abstract objects of the mathematical theory are variables of the mathematical model; the axioms are statements of relationships among the variables. Henceforth the "mathematical theory" used as a mathematical model will be called the "mathematical structure," since the former term is usually used in a more restricted sense.

The mathematical models then lead to "new" conclusions, i.e., ideas and predictions. But the conclusions to which this technique leads assert nothing that is *theoretically new* in the sense of not being implicit in the mathematical model. But they may well be *psychologically new;* in fact, they usually are (Hempel, 1945). An apparent requirement for this method to work is that the real world operates with the same logic that human beings think in. The fact that mathematical arguments do lead to practical results suggests that this may be true, but, of course, man will never know.

In the acts of identifying variables of the mathematical model with aspects of the real world lie many of the problems in formulating mathematical models. These acts of identification must be operational definitions (Bridgman, 1927) of the variables, i.e., specific instructions on how to make measurements which evaluate the variables. If the variables are not operationally defined, predictions generated by the model do not correspond to any real-world measurements, and thus the model cannot be tested. Such a model may be intellectually stimulating, but is not useful in applications to the real world.

Each variable used in the model is an abstract concept, connected to the real world directly or indirectly through specific physical measurements (Fig. 1). Thus the same real-world phenomenon might underly (in a metaphysical sense) many different variables, e.g., NaCl concentration and osmotic pressure. Moreover, the way a variable is defined is often determined by convenience, e.g., availability of certain kinds of data, instruments, or talent, and different definitions lead to different variables (Bridgman, 1927), e.g., the various concepts of productivity.

If a model is to be tested by comparing its predictions with data from the real world, the model then becomes a hypothesis, although often a

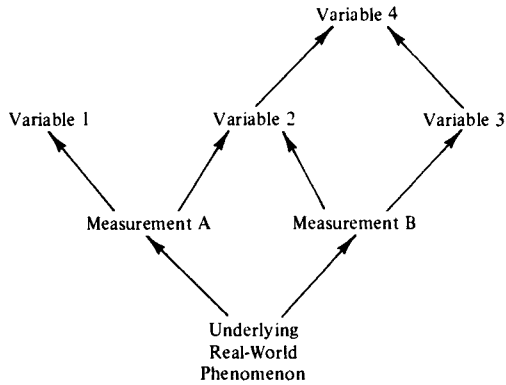

FIG. 1. Relationships between different variables and same real-world phenomenon.

very complex one, consisting of numerous "subhypotheses." Since the predictions and real-world data must usually be compared statistically (chi-square, *t*-test, etc.) using an arbitrary confidence level, it is often the case that several different models may be accepted as "explaining" the same set of real-world data. There is no philosophical conflict here, since a model is an abstract concept arbitrarily identified with the real world.

The predictions themselves are often regarded as the hypotheses, rather than the model which generated them. Since the predictions are necessary consequences of the model, one can view the model as including the predictions (Hempel, 1945), and thus it seems more reasonable to consider the model as the hypothesis. Moreover, in hypothesis-testing one does not accept or reject predictions; one compares predictions of a model with real-world observations, and then accepts or rejects (usually later to modify) the model.

The formulation of mathematical models of complex real-world phenomena thus requires one to (1) operationally define the important real-world variables, and (2) precisely state the hypothetical relationships among these variables. The model then represents a complex hypothesis which can generate predictions about the real world. The predictions can then be tested against real-world measurements, and the model then either accepted as it is or modified in some way. If the model is modified, the cycle must be repeated until predictions agree with measurements at some satisfactory level of statistical significance. In engineering terms, the whole process is called "system identification"; in more general terms, this is nothing more than the traditional method of empirical science.

C. Types of Mathematical Models

1. *Introduction*

Since such a large number of different types of mathematical structures exists for use as mathematical models, one should have some set of guidelines in making a choice. Probably as good a set as any is the following: (1) Naturalness with which the mathematical theory represents the real-world phenomenon, e.g., continuous versus discrete functions, one versus several variables, (2) ability to generate predictions, (3) comprehensiveness and esthetics, (4) tractability of mathematics, and (5) consistency with other existing models.

At this point it is advantageous to comment on the word "system." Mathematically, a "system" is a mapping (Sell, 1967). We shall, in this chapter, concern ourselves only with the special type of system defined by the first-order ordinary differential equation

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, t), \tag{1}$$

where the vector-valued function $\mathbf{f}$ maps the real 1-space (whose elements are time t) and the real n-space (vector space) (whose elements are the vectors $\mathbf{x}$) into the same real n-space. In other words, our system will be defined by a set of coupled first-order ordinary differential equations, one for each of the "state variables" x_i (to be defined later).

Notice that the definition of a system refers to concepts—coupled equations in this case—and not directly to the real world. This indicates that the identification of and the limits on a system are arbitrary; they are a matter of definition. Of course, one always tries to identify the idea of a system with some set of real-world phenomena (the "real-world system") in such a way that is psychologically satisfying, but arguments about what is or is not a system in the real world, or what the limits "really" are on a particular system, are largely futile. It should be obvious that, mathematically, the system is the mathematical model; in this paper the word will usually be used in its real-world intuitive sense.

At this point it is also advantageous to comment on vector and matrix notation. Boldface symbols like $\mathbf{x}$ will be used to represent vectors (usually column vectors). Capital letters like A will represent matrices. Thus, $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, t)$ is shorthand for

$$\begin{aligned}
\dot{x}_1 &= f_1(x_1, x_2, \ldots, x_n, t), \\
\dot{x}_2 &= f_2(x_1, x_2, \ldots, x_n, t), \\
&\vdots \\
\dot{x}_n &= f_n(x_1, x_2, \ldots, x_n, t),
\end{aligned}$$

and $\dot{\mathbf{x}} = A\mathbf{x}$ is shorthand for

$$\begin{aligned}
\dot{x}_1 &= a_{11}x_1 + a_{12}x_2 + \cdots + a_{1n}x_n , \\
\dot{x}_2 &= a_{21}x_1 + a_{22}x_2 + \cdots + a_{2n}x_n , \\
&\vdots \\
\dot{x}_n &= a_{n1}x_1 + a_{n2}x_2 + \cdots + a_{nn}x_n .
\end{aligned}$$

The question often arises whether one should use deterministic or probabilistic models. The question really involves two problems—one philosophical, one practical.

The philosophical problem is nicely put to rest by the following quotation:

> The controversy of determinism and causality versus randomness and probability has been the topic of extensive discussions. In our opinion, the difference lies not in the nature of this or that phenomenon, but in the quantities in which the observer is interested. If he is interested in the outcome of *one* experiment, then his statement is deterministic; if he is interested in certain averages of a large number n of experiments, then his statement is probabilistic. In either case no categorical assertion is possible. In the first case, the uncertainty of his conclusions takes the form *within certain errors and in certain ranges of the relevant parameters*; in the second case, *with a high degree of certainty if n is large enough.*

But, it is often objected, the universe *really* is deterministic, and

> ··· The phenomenon is thus inherently deterministic, and probabilistic considerations are necessary only because of our ignorance. Our answer is that the physicist is not concerned with what *is* true, but only with what he can measure. Such explanations are therefore outside the sphere of his scientific interests (Papoulis, 1965). (From "Probability, Random Variables, and Stochastic Processes," pp. 15–16, by A. Papoulis. Copyright © 1965, McGraw-Hill. Used with permission of McGraw-Hill Book Company.)

The practical problem is that the theory of probability has, up to now, produced only rather simple models limited to one or only a few variables changing in time. If one wishes to formulate probabilistic models of complex phenomena, it is probably best to use an essentially deterministic model, and introduce randomness into this model in some fashion; then multiple digital computer solutions are obtained (Monte Carlo techniques). The randomness can be introduced either in the input or somewhere in the system itself, depending on the nature of the physical problem.

In the three brief sections which follow are indicated those mathematical structures which, in my opinion, are the most useful as models of ecological phenomena. Ecological phenomena are grouped into three categories: changes in time, changes in space or in space and time, and classification.

2. *Changes in Time*

This category includes those phenomena in which the values of dependent variables change with the passage of time, but not in space. Thus it includes only those phenomena which may be considered to be spatially homogeneous (in engineering: "lumped"), i.e., without space effects. Although for some purposes such a restriction may be too unrealistic, the gain in tractability of the mathematical model is usually great. Ecological examples are: energy and material flow in food webs, ecological succession within small areas (so that spatial variation is not relevant), and population changes.

There is but one independent variable, time, and the state of the system at any point in time is affected by the state of the system at a previous point in time, i.e., the system has a finite memory, or is state-determined. Thus the system is dynamic, and may be represented by the methods of classical physics. Probably the most useful mathematical structures to use as the models of such systems are ordinary differential equations. Where the variables are measured, or have meaning, only at regular discrete points in time, the corresponding ordinary difference equations can be used. Integral equations might be used as an alternative to the differential equations, but their theory has not been well developed (Hart, 1967).

For probabilistic models with only one dependent variable, one can use Markov chains, birth-and-death processes, and queueing.

3. *Changes in Space, or in Space and Time*

This category includes those phenomena in which values of dependent variables change in physical space (surface or volume), and, perhaps, time as well. Thus it includes those phenomena which are considered to be spatially heterogeneous (in engineering: "distributed"). Ecological examples are: (1) time not an independent variable: distribution of organisms, ecological gradients, niches, and distribution of genotypes, (2) time an independent variable: energy and material flow in food webs in spatially heterogeneous systems, and ecological succession over broad areas.

Since there is more than one independent variable (two or three for space, and, perhaps, one for time), the required mathematical theory becomes very complex and difficult to work with analytically. The most useful mathematical structures to use as models of such systems are partial differential equations, or the corresponding partial difference equations. Since analytical solutions (predictions) to systems of partial differential equations are very difficult to find, these models will probably

always be solved by numerical approximation on digital computers. Probability density functions may also be used.

4. *Classification*

Schemes of classification differ from other models in that they are not testable, and thus are not hypotheses. Ecological examples are: classification of vegetation types, of communities, and of species (taxonomy). Useful mathematical structures are: sets (Rosen, 1967), mappings (Rashevsky, 1959), and information (Hairston *et al.*, 1968).

II. Formulation of Models of Dynamic Ecological Systems

A. Formulation as Sets of Algebraic and Ordinary Differential Equations

1. *Formulation*

a. *Introduction.* Through the remainder of this chapter, it is assumed that one is interested in making a mathematical model of a continuous, dynamic system (using the term, "system," loosely) which is spatially homogeneous, or in which space effects are negligible, i.e., a lumped system. The mathematical disadvantages of trying to account for the space effects, i.e., dealing with a distributed system, are tremendous (Schwarz and Friedland, 1965).

The objective of this section is to suggest a procedure for formulating a model as a set of coupled first-order ordinary differential equations. This is best done in two steps, first by formulating the model with both algebraic and differential equations, and second by eliminating the algebraic equations. A simple procedure for numerical approximation of solutions is also given.

The formulation of a mathematical model as a set of coupled algebraic and ordinary differential equations is divided into five steps:

(1) specification of variables of interest,

(2) construction of control diagram,

(3) classification of variables, operational definition of variables, and specification of variable units,

(4) specification of forms of equations,

(5) evaluation of constants.

Each of these steps will be considered in turn, together with an example from the pine–mor food web.

b. *Specification of Variables of Interest.* A mathematical model may be constructed for a number of reasons, such as for the experience, for pleasure, or for a publication, but usually the objective will be the solution of some specific problem. The problem will usually be the causal explanation of the values or changes in the values of some particular variables as functions of other particular variables. The values must be in either numerical or logical, e.g., true–false or present–absent, terms. In ecology, the variables of interest will often be biomasses (total or of some component), fluxes, rates, or characteristics of the physical environment.

As one formulates the model, new variables will probably need to be recognized and defined, and old ones omitted. In any case the choice of variables must be explicitly stated. Which particular variables are chosen depends upon the nature of the problem, knowledge and personal interests of the researcher, and ability to measure the variables.

In the case of the pine–mor food web, I am interested in explaining the changes in time of biomass of the major components of pine mor (the forest floor of a pine forest). These components consist of decomposing plant material (with contained fungi and bacteria, since not operationally separable) of several types, frass, materials from throughfall, numerous animal taxa, feces (with contained fungi and bacteria), and exuviae (with contained fungi and bacteria). These biomasses are considered to be controlled by each other, several litterfall types and other inputs, air temperature, and precipitation.

In order to keep the model relatively simple, I have chosen as the variables of the model only what I consider to be the most important of all the possibilities.

A fairly complete list of decomposing plant material types would include: Pine—leaves, branches, bark, cones and seeds, bud scales, male strobili, and pollen; Understory species—leaves, etc.; Groundcover species—leaves, etc. Of these, only pine litter, taken as a whole, is chosen as a variable.

Frass, materials from throughfall, feces, and exuviae are ignored in the present model, partly because of the difficulty of measuring them.

A fairly complete list of the animal taxa in pine mor would be quite extensive. Of these, nine arthropod taxa are chosen as variables: Lithobiomorpha (Chilopoda), Symphypleona (Collembola), Entomobryomorpha (Collembola), Poduromorpha (Collembola), Formicidae (Hymenoptera), Araneae, Mesostigmata (Acarina), Trombidiformes (Acarina), and Oribatei (Acarina).

The litterfall types (the input fluxes), of course, are the same as the decomposing plant material types, and thus only pine litterfall is chosen

as a variable. The characteristics of the physical environment, air temperature and precipitation, are also chosen as variables.

c. *Construction of Control Diagram.* Once the variables of interest have been chosen, it is then necessary to indicate paths in which immediate cause-and-effect relationships ("controls," "signals," "communications," "flows of information," etc.) operate among the variables. To do this it is almost always necessary to add new variables, gradually building up a "control diagram," until all "first causes" are variables outside the system of interest (Fig. 2). These latter variables have causes not expressed in the mathematical model, and may be regarded as inputs to the system. The extent of the diagram, i.e., the number of variables to be used and how far back one should go for first causes, depends upon objectives of the model, availability of information, degree of accuracy required, etc.

The number of variables used between first causes and the other variables of interest depends upon the level at which one wishes to explain the variables' behavior. For example, suppose one wishes to explain variations in a mouse population as a function of weather variations. One could attempt an explanation on a coarse level by introducing no new variables, and set up an equation expressing mouse population directly as a function of weather variables. One could attempt an explanation on a finer level by introducing food supply, natality, and mortality as new variables. Or one could go still further by adding plant photosynthesis and respiration, ingestion, mouse respiration, and various mouse behavior variables. The process could be continued almost indefinitely, each time attempting an explanation on a finer level, or "higher magnification." Each shift to a finer level might be regarded as substituting an "explanation" for a "description" (Bradley, 1968), but, of course, all explanations are descriptions.

The procedure of starting with variables which have no or few effects on the other variables (i.e., are at the bottom of the effects chain), and working backwards to immediate causes is to be strongly recommended. This procedure helps to overcome preconceived notions of what affects what. Where a variable, e.g., biomass, changes due to a rate, e.g., respiration, making that rate into a separate variable will greatly simplify formulation of the mathematical model.

Each arrow on the control diagram indicates only that a cause-and-effect relationship *exists* from one variable to the other; the exact nature of the relationship will be stated later in the formulation. The diagram represents an outline of a complex hypothesis concerning the time behavior of the variables of interest.

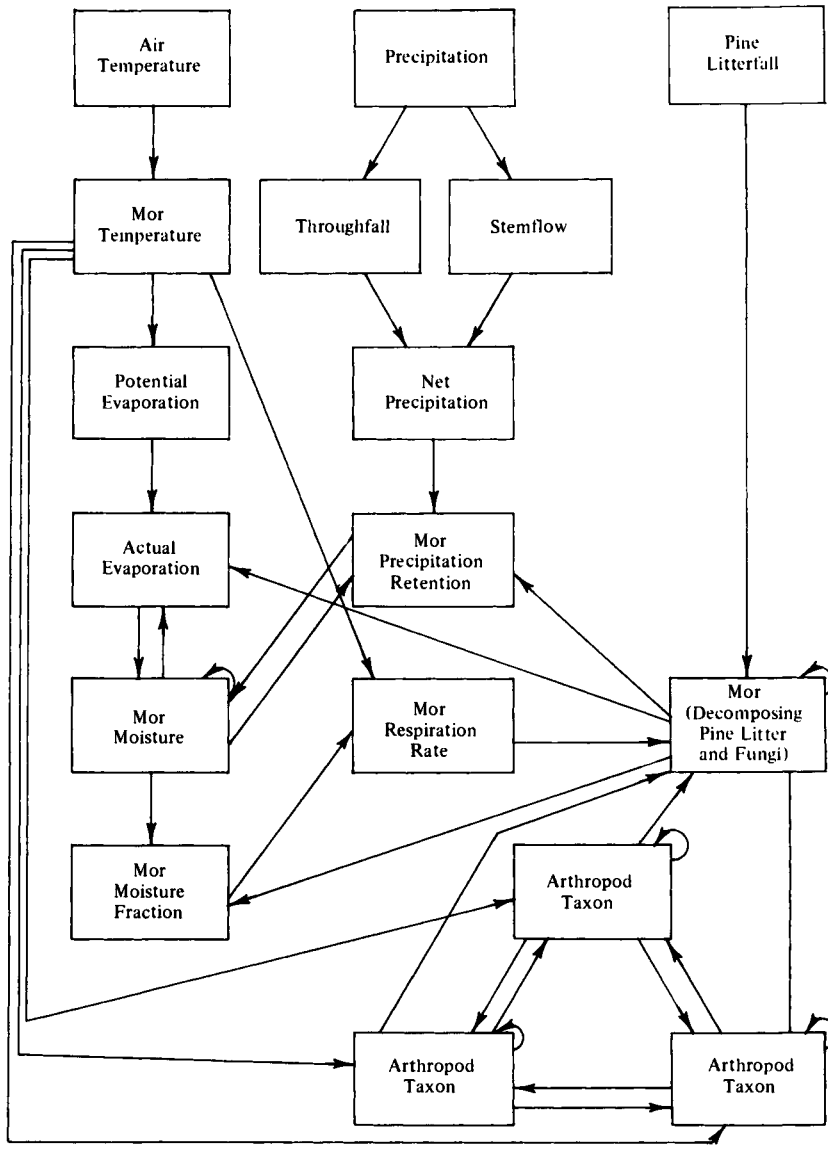

FIG. 2. Control diagram for pine-mor model.

(The control diagram is obviously a type of block diagram, but it must be kept in mind that the blocks are variables, rather than operators. The latter is the most comman usage in engineering literature. The

arrows signify mappings or functions. Thus the control diagram is similar to "signal-flow graphs" in engineering literature, with the important distinction that the units of the "signals" impinging on a variable are nonuniform.)

The control diagram for the pine–mor food web model is presented in Fig. 2. Where an effect is indicated from a variable back to itself, this means that at any point in time the value of that variable depends upon its previous value. This would be true of any variable representing mass or stored energy, changing in time. (Only three of the nine arthropod taxa have been included, to avoid confusion.)

d. *Classification of Variables, Operational Definitions of Variables, and Specification of Variable Units.* Once the control diagram is completed, the variables can be classified into three types: "input variables" (v_i), "nondynamic state variables" (n_j), and "dynamic state variables"(x_k). (This formulation is leading up to the analysis of dynamic ecological systems using the "state variable approach" of differential equations theory (DeRusso *et al.* 1965). This approach utilizes only the input variables and the dynamic state variables. The nondynamic state variables are used here to simplify formulation of the mathematical model; they will later be eliminated.)

The input variables are the "first causes" of the control diagram, and lie outside of the system being represented by the mathematical model. In ecological systems they will usually represent input fluxes (e.g., litterfall, immigration, fallout, and input current) or environmental controls (e.g., temperature and humidity).

The state variables represent the system, i.e., at any point in time the set of values of the state variables is the state of the system. The nondynamic state variables are those considered to be zero-memory, instantaneous, or, in the language of the engineer, non-energy-storing, e.g., rates. Thus, at any point in time the value of a nondynamic state variable does not depend upon its previous value, and the variable may be defined by an algebraic equation. The dynamic state variables are those considered to be finite-memory or energy-storing, e.g., biomass. Thus, at any point in time the value of a dynamic state variable depends upon its previous value, and the variable must be defined by a differential equation. The existence of dynamic state variables in a system results in the system itself being state-determined.

Since the model must later be tested by comparing measured values of state variables with predicted values of state variables (as functions of themselves and measured values of input variables), operational definitions must be given for each input variable and state variable. These

definitions are often implicit, since many ecological measuring techniques are standardized, but it is better to make definitions explicit, since different definitions yield different variables. For example, the term, "plankton biomass," has been used as a label for several essentially different variables, including in their operational definitions different net meshes or filter grades, different drying temperatures, etc.; certainly these variables are based upon the same real-world phenomenon, but they cannot be used interchangeably in a mathematical model. In many cases it will be necessary for the researcher to compromise his ideal operational definition of a variable because of the availability of data based on other definitions. In some cases it may be necessary to omit certain variables entirely, because of the difficulty or expense of measuring them.

One particular problem, which has led to a great deal of confusion in ecological modeling, is the use of trophic levels, saprophage levels, biophage levels, etc. as variables. It is practically impossible to measure, thus to operationally define, such functional groups of organisms in a psychologically satisfying manner. Thus it is better to use easily recognizable taxonomic groups as the variables of the model, and, perhaps, later construct a new model by partitioning the taxonomic variables among the functional variables. In this way an indefinite number of new models may be constructed, using different definitions of the functional variables.

Since the statements of relationships among model variables are mathematical equations, the units of each variable must be explicitly stated. As with the operational definitions, the best units to be used depend upon the objective of the model and availability of data. Where relevant, most variable dimensions will contain three types of units: (1) a measure of amount, e.g., weight, length, or number of individuals; (2) a measure of distribution in space, e.g., inverse area or inverse volume; and (3) a measure of distribution in time, i.e., inverse time. Where possible, identical units should be used to simplify computation, e.g., all weights in grams.

Input, nondynamic state variables, and dynamic state variables used in the pine–mor model, together with their units, are listed in Table I. The system is defined as a pure pine forest with no undergrowth.

Mean air temperature (v_1) and precipitation (v_2) are defined in the same way as does the US Weather Bureau, in order to utilize Weather Bureau records. Pine litterfall (v_3) is defined as ash-free, oven-dry (105 C) weight of litter collected in litter baskets at two-week intervals.

Mor (x_2) is defined as ash-free, oven-dry (105 C) weight of the total forest floor. The arthropod taxa (x_3–x_{11}) are defined as total oven-dry

TABLE I

PINE–MOR MODEL VARIABLES

Symbol	Description	Units[a]
Input variables (v_i)		
v_1	Mean air temperature	C
v_2	Precipitation	g water m^{-2} day^{-1}
v_3	Pine litterfall	g PL m^{-2} day^{-1}
Nondynamic state variables (n_j)		
n_1	Mor temperature	C
n_2	Throughfall	g water m^{-2} day^{-1}
n_3	Stemflow	g water m^{-2} day^{-1}
n_4	Net precipitation	g water m^{-2} day^{-1}
n_5	Potential evaporation from mor	g water m^{-2} day^{-1}
n_6	Actual evaporation from mor	g water m^{-2} day^{-1}
n_7	Precipitation retention	g water m^{-2} day^{-1}
n_8	Mor moisture fraction	(pure number)
n_9	Mor respiration rate	g M respired g M^{-1} day^{-1}
Dynamic state variables (x_k)		
x_1	Mor moisture	g water m^{-2}
x_2	Mor (decomposing pine litter and fungi)	g M m^{-2}
x_3	Araneae	g A m^{-2}
x_4	Mesostigmata (Acarina)	g Me m^{-2}
x_5	Trombidiformes (Acarina)	g T m^{-2}
x_6	Oribatei (Acarina)	g O m^{-2}
x_7	Symphypleona (Collembola)	g S m^{-2}
x_8	Poduromorpha (Collembola: Arthropleona)	g P m^{-2}
x_9	Entomobryomorpha (Collembola: Arthropleona)	g E m^{-2}
x_{10}	Formicidae (Hymenoptera)	g F m^{-2}
x_{11}	Lithobiomorpha (Chilopoda)	g L m^{-2}

[a] PL = pine litterfall, M = mor, A = Araneae, Me = Mesostigmata, T = Trombidiformes, O = Oribatei, S = Symphypleona, P = Poduromorpha, E = Entomobryomorpha, F = Formicidae, and L = Lithobiomorpha.

(65 C) weights of the respective taxa, extracted in a micro-Tullgren funnel (Auerbach and Crossley, 1960).

The unit of time used for all rates and fluxes in the model is the (inverse) day; the unit of area, the (inverse) square meter. There are several possible choices for the unit representing biomass, e.g., grams oven-dry weight, number of individuals, joules, grams carbon, grams calcium, grams nitrogen, and grams of other elements. The choice among these possible units is very important since this is the unit with which most of the model will operate. All data used in calculation of equation constants will have to be in this unit; all predictions from the model will

be in this unit, and must be compared with similar data from other sources.

I have chosen grams of oven-dry weight (square meters per day) as the unit since this is most easily, most accurately, and most often measured. In most experimental work this is the unit actually measured, and then used to calculate one or more other units by means of a conversion factor. If predictions in some other unit are desired, it is easy to convert from grams of oven-dry weight, using conversion factors which are empirically determined. These factors would vary among variables and, perhaps, with time, e.g., joules per gram varies among arthropod taxa and among life stages within any given taxon.

e. *Specification of Forms of Equations.* Specifying the equation forms represents the filling in of details of the control diagram. Each equation expresses a state variable as a function of both input and other state variables which have effects on the variable. The arguments of each function are the causes or controls of variable behavior, or the sources of signals, communication, or information flowing to the variable; the reader may choose the most satisfying phrase. The equations are the axioms of the mathematical structure which is the model.

The set of equations is a complex hypothesis, in which each equation can be regarded as an independent subhypothesis, subject to being independently tested and modified. The terms of each equation, and even the constants, may be so regarded. Thus, the forms of the equations should be based upon mathematical, physical, chemical, and biological principles, as well as the literature, personal knowledge, and intelligent guesses.

The equation forms should not be purely empirical, and probably cannot be, since an empirical equation is really a hypothesis that the future behavior of a variable will be the same as a sample of its past behavior was. Some empirical equations might be resorted to in order to calculate variable behavior necessary for the model to operate, but in whose genesis one is not particularly interested, e.g., the temperature of a biological system. The forms of such equations will often be statistical regressions or power series.

Each nondynamic state variable is expressed as a function of other variables by an algebraic equation; each dynamic state variable, by a first-order ordinary differential equation. The differential equations are of the form

$$\dot{x}_k = \text{gain fluxes} - \text{loss fluxes}, \tag{2}$$

where $\dot{x}_k = dx_k/dt$. The algebraic equations could be condensed into the differential equations, and the nondynamic state variables eliminated,

but they are best retained for the present to ease formulation of the model and the digital computer program. They will later be eliminated to put the model into a form amenable to analysis.

Each equation will contain a number of constants k_1 . (These are often called "parameters," a word which leads to confusion because it is sometimes used, although not here, for the independent variables.) They will remain in an unevaluated form until the equations are fully specified. While I prefer to use a single letter, such as "k," to denote the constants, one might choose to use several letters (as in Chapter 1) so as to clearly identify several classes of constants, e.g., temperatures, ingestion rates, and respiration rates. The advantage of the single-letter approach is that the variables and the constants are immediately distinguishable by the reader, and the equation forms made obvious.

Since both sides of each equation must have the same units, the constants will often have unusual ones, e.g., inverse degrees Celsius. In the case of the differential equations, all of the right-hand terms must be fluxes, often rate times mass (or density).

Each term on the right-hand side of each equation (of course, some equations might have but one term) is a function of one or several variables. These arguments of the function are the sources of control. The question arises whether time should be considered as a possible argument. The question is an important one, since when one is dealing with a linear differential equation the inclusion of time as an argument produces an equation with variable coefficients (leading to "time-varying," "variable," or "nonstationary" systems), while the exclusion of time as an argument produces an equation with constant coefficients (leading to "time-invariant," "fixed," or "stationary" systems). While the solution of the latter is routine, the solution of the former usually cannot be obtained in exact literal form (Coddington, 1961).

Since in this type of mathematical model time is the only independent variable, all dependent variables (input and state) are functions of time. The state variables (the only variables for which equations are written), however, are only indirectly functions of time, so that time does not appear as an argument, and the system described by the model is time-invariant. Where time is included explicitly as an argument of a variable, one is just describing the behavior of that variable in time without attempting to hypothesize the cause of that behavior. Such a variable would lie outside the system. This is the case with the input variables, which are just described as functions of time, and are sometimes merely constants ("constant forcing function"). Thus, in my opinion, all models of dynamic ecological systems should be so formulated as to be time-invariant, except for the existence of input variables, which are defined

as functions of time. Such models might be considered to be "explanatory" or "cause-and-effect" models.

As an example of the two different approaches described above—time-invariant versus time-varying models—consider the pine–mor system which is affected by temperature, precipitation, and litterfall. The ecologist would consider all three of these to be input variables, with the resulting model being nonlinear, but time-invariant. In this case the concept of an "unforced system" would not be meaningful. On the other hand, the engineer or physicist would probably consider litterfall to be the only input variable, with the resulting model being, perhaps, linear, but time-varying (the variable coefficients would include the effects of temperature and precipitation as functions of time). In this case the concept of an "unforced system" would be meaningful.

In ecological models, many dynamic state variables will often be biomasses (or biomass densities) of some taxon of organisms. Terms on the right-hand sides of the differential equations for these variables represent fluxes. (These fluxes are identical to the flows between compartments of "compartment models," special cases of general dynamic models discussed here.) The question arises of what variables, besides physical environmental controls, are the sources of control for each flux, i.e., whether the source taxon (or other foodstuff) or the receiver taxon or both exert control. (Other taxa might be hypothesized as exerting control, e.g., through competition, to further complicate the question.)

Where the flux represents a physiological process, such as respiration or excretion, the assumption of total control by the source taxon is probably reasonable. The answer is more difficult when the flux represents a flow of food from the source to the receiver.

It is sometimes assumed that feeding fluxes are completely controlled by the food source compartment. The biological interpretation of this assumption is that feeders are controlled by competition for a limited food supply or, perhaps, niches; the biomass of feeder has no effect on the amount eaten. A more realistic assumption would be that each feeding flux is controlled by both the source and the receiver. Thus, the more feeder present the more there is eaten, as well as the more food the more there is eaten. A biological interpretation of this assumption is that food supply and feeders mutually control each other.

One might choose the "Hairston–Smith–Slobodkin" alternative (Hairston *et al.*, 1960) for the sources of control of feeding fluxes. In this case feeding fluxes from plants (or detritus) to herbivores (or saprovores) would be controlled solely by the receivers; feeding fluxes from herbivores (or saprovores) to predators would be controlled by

both sources and receivers. The biological interpretation of this assumption is that competition for a limited food supply does not control herbivores; herbivores are controlled by predators, and predators are controlled by competition for supply of herbivores. Increased herbivores decrease the amount of plant material, but the amount of plant material has no effect on the feeding flux to herbivores. This last consequence seems somewhat unrealistic, unless there are unlimited supplies of plant material, or the model is only used when the plant material supply is high, i.e., for a certain range of conditions.

In the case of the predator–prey feeding flux, it is common to assume that flux is expressed by a function of the form: constant times prey density times predator density. This is the Lotka–Volterra assumption that the rate of interaction of two species is directly proportional to the product of their populations—the mass action law of chemistry and physics. Watt (1962) has criticized this assumption (or hypothesis), but very rarely is enough information available to justify a better one.

The above example is one of the simplest types of nonlinear functions (see Chapter 1 for a hierarchy), and serves to bring up the extremely important question of whether one should use linear or nonlinear functions in the equations. Certainly almost all real-world relationships are more accurately represented by nonlinear mathematical models than linear ones (I hestitate to say "are nonlinear"), but there is a great advantage in using linear models since most of the techniques developed by engineers and mathematicians for the analysis of dynamic systems are based upon linear mathematical models (DeRusso *et al.*, 1965, Schwarz and Friedland, 1965). The disadvantage of a linear formulation is that it is usually a cruder approximation than the nonlinear, and, moreover, is usually valid for only a limited range of the model variables, including time.

If it is felt necessary to use a nonlinear model, the analysis must usually be done by (1) the time-consuming process of digital (or analog) computer simulation (numerical approximation), or (2) linearizing the model about an equilibrium state and then using conventional linear techniques. The latter method is valid only for small deviations (or "perturbations") from equilibrium (Schwarz and Friedland, 1965).

Time lags are sometimes thought desirable in ecological models. For a spatially homogeneous continuous dynamic system, time lags should not be necessary in the model equations. If they appear to be necessary, this is an indication that the state of the system has not been properly defined; in particular, more state variables are probably needed. This makes sense—a dynamic system is a state-determined system. Thus, the state of the system at any given instant of time is a function of the state of the

system and the inputs at the immediately previous instant of time. Any effect from a distant time must act through the immediately previous instant of time. For example, growth of an animal may be considered to be a function of food intake at some previous time, since an obvious time lag exists. But if one increases the reality of the model by adding new state variables such as gut content and stored food, the necessity of time lags largely disappears. However, in some complex models, e.g., population models, it might not be feasible to redefine state in this way (Wangersky and Cunningham, 1957). If time lags are deemed necessary, a good introduction to the literature on the resulting differential–difference equations and functional–differential equations may be found in the book by Hale and LaSalle (1967).

If the system is spatially heterogeneous, then pure time delays ("transport lags") may be necessary. This is the simplest space effect, and may often be used in formally spatially homogeneous models (Ball and Adams, 1967), and does not violate the system's property of being state-determined.

Tables II and III contain the forms of the equations used for the nondynamic state variables (algebraic equations) and the dynamic state variables (differential equations), respectively, of the pine–mor model.

The mean daily temperature within the mor (n_1) has been made equal to the mean daily air temperature (v_1). Some preliminary measurements in an Oak Ridge, Tennessee, shortleaf pine forest indicate this to be approximately true. In a future version of the model it might be wise to make mor temperature a function of a dynamic state variable, soil heat; in this way the temperature time lag could be accounted for.

Throughfall (n_2) and stemflow (n_3) have each been made equal to constant fractions of open-air precipitation (v_2), and net precipitation (n_4) equal to their sum. This is, in general, consistent with the assumptions of foresters (Helvey, 1967, Hoover, 1953). A nonlinear relationship would be more realistic because of the initial period of saturation of branches and leaves during a storm.

Potential evaporation from mor (n_5) is assumed to be a function solely of mor temperature (n_1). This is a tremendous oversimplification compared with other extant models, e.g., those of Thornthwaite, Penman, Budyko, and others, but is used here as a first approximation. The form of the potential evaporation curve (against temperature) is assumed to be the same as that of vapor pressure deficit (VPD) (millimeters of mercury, 0% relative humidity), which is assumed to be of the form: $\text{VPD} = ae^{bn_1}$. Values of $a = 4.58$ and $b = 0.065$ closely approximate the original VPD curve. ("b" is k_4 in the actual model equation.)

TABLE II

EQUATIONS FOR NONDYNAMIC STATE VARIABLES

$$n_1 = v_1$$

$$n_2 = k_1 v_2$$

$$n_3 = k_2 v_2$$

$$n_4 = n_2 + n_3$$

$$n_5 = k_3 e^{k_4 n_1}$$

$$n_6 = \frac{x_1 - k_6 x_2}{k_5 x_2 - k_6 x_2} n_5 = \frac{x_1/x_2 - k_6}{k_5 - k_6} n_5 = \frac{n_8 - k_6}{k_5 - k_6} n_5$$

$$n_7 = \frac{k_5 x_2 - x_1}{k_5 x_2 - k_6 x_2} n_4 = \frac{k_5 - x_1/x_2}{k_5 - k_6} n_4 = \frac{k_5 - n_8}{k_5 - k_6} n_4$$

$$n_8 = \frac{x_1}{x_2}$$

$$n_9 = k_8 \exp(k_7(n_1 - k_9)) \left(\frac{n_8 - k_6}{k_{10} - k_6}\right)$$

TABLE III

EQUATIONS FOR DYNAMIC STATE VARIABLES

$$\dot{x}_1 = n_7 - n_6$$

$$\begin{aligned}\dot{x}_2 = {} & v_3 - n_9 x_2 - k_{11} \exp(k_{12}(n_1 - k_{13})) x_6 - k_{14} \exp(k_{15}(n_1 - k_{16})) x_7 \\ & - k_{17} \exp(k_{18}(n_1 - k_{19})) x_8 - k_{20} \exp(k_{21}(n_1 - k_{22})) x_9 \\ & - k_{120} \exp(k_{147}(n_1 - k_{121})) x_{10}\end{aligned}$$

$$\begin{aligned}\dot{x}_3 = {} & k_{48} k_{50} \exp(k_{23}(n_1 - k_{49})) x_3 x_4 + k_{51} k_{53} \exp(k_{23}(n_1 - k_{52})) x_3 x_5 \\ & + k_{54} k_{56} \exp(k_{23}(n_1 - k_{55})) x_3 x_6 + k_{57} k_{59} \exp(k_{23}(n_1 - k_{58})) x_3 x_7 \\ & + k_{60} k_{62} \exp(k_{23}(n_1 - k_{61})) x_3 x_8 + k_{63} k_{65} \exp(k_{23}(n_1 - k_{64})) x_3 x_9 \\ & + k_{66} k_{68} \exp(k_{23}(n_1 - k_{67})) x_3 x_{10} + k_{69} k_{71} \exp(k_{23}(n_1 - k_{70})) x_3 x_{11} \\ & - k_{26} \exp(k_{23}(n_1 - k_{27})) x_3 - k_{72} \exp(k_{24}(n_1 - k_{73})) x_3 x_4 \\ & - k_{96} \exp(k_{25}(n_1 - k_{97})) x_3 x_5 - k_{123} \exp(k_{147}(n_1 - k_{124})) x_3 x_{10} \\ & - k_{148} \exp(k_{172}(n_1 - k_{149})) x_3 x_{11}\end{aligned}$$

$$\begin{aligned}\dot{x}_4 = {} & k_{72} k_{74} \exp(k_{24}(n_1 - k_{73})) x_4 x_3 + k_{75} k_{77} \exp(k_{24}(n_1 - k_{76})) x_4 x_5 \\ & + k_{78} k_{80} \exp(k_{24}(n_1 - k_{79})) x_4 x_6 + k_{81} k_{83} \exp(k_{24}(n_1 - k_{82})) x_4 x_7 \\ & + k_{84} k_{86} \exp(k_{24}(n_1 - k_{85})) x_4 x_8 + k_{87} k_{89} \exp(k_{24}(n_1 - k_{88})) x_4 x_9 \\ & + k_{90} k_{92} \exp(k_{24}(n_1 - k_{91})) x_4 x_{10} + k_{93} k_{95} \exp(k_{24}(n_1 - k_{94})) x_4 x_{11} \\ & - k_{28} \exp(k_{24}(n_1 - k_{29})) x_4 - k_{48} \exp(k_{23}(n_1 - k_{49})) x_4 x_3 \\ & - k_{99} \exp(k_{25}(n_1 - k_{100})) x_4 x_5 - k_{126} \exp(k_{147}(n_1 - k_{127})) x_4 x_{10} \\ & - k_{151} \exp(k_{172}(n_1 - k_{152})) x_4 x_{11}\end{aligned}$$

TABLE III *(continued)*

$$\dot{x}_5 = k_{96}k_{98}\exp(k_{25}(n_1 - k_{97}))\,x_5x_3 + k_{99}k_{101}\exp(k_{25}(n_1 - k_{100}))\,x_5x_4 + k_{102}k_{104}\exp(k_{25}(n_1 - k_{103}))\,x_5x_6 + k_{105}k_{107}\exp(k_{25}(n_1 - k_{106}))\,x_5x_7 + k_{108}k_{110}\exp(k_{25}(n_1 - k_{109}))\,x_5x_8 + k_{111}k_{113}\exp(k_{25}(n_1 - k_{112}))\,x_5x_9 + k_{114}k_{116}\exp(k_{25}(n_1 - k_{115}))\,x_5x_{10} + k_{117}k_{119}\exp(k_{25}(n_1 - k_{118}))\,x_5x_{11} - k_{30}\exp(k_{25}(n_1 - k_{31}))\,x_5 - k_{51}\exp(k_{23}(n_1 - k_{52}))\,x_5x_3 - k_{75}\exp(k_{24}(n_1 - k_{76}))\,x_5x_4 - k_{129}\exp(k_{147}(n_1 - k_{130}))\,x_5x_{10} - k_{154}\exp(k_{172}(n_1 - k_{155}))\,x_5x_{11}$$

$$\dot{x}_6 = k_{11}k_{44}\exp(k_{12}(n_1 - k_{13}))\,x_6 - k_{32}\exp(k_{12}(n_1 - k_{33}))\,x_6 - k_{54}\exp(k_{23}(n_1 - k_{55}))\,x_6x_3 - k_{78}\exp(k_{24}(n_1 - k_{79}))\,x_6x_4 - k_{102}\exp(k_{25}(n_1 - k_{103}))\,x_6x_5 - k_{132}\exp(k_{147}(n_1 - k_{133}))\,x_6x_{10} - k_{157}\exp(k_{172}(n_1 - k_{158}))\,x_6x_{11}$$

$$\dot{x}_7 = k_{14}k_{15}\exp(k_{15}(n_1 - k_{16}))\,x_7 - k_{34}\exp(k_{15}(n_1 - k_{35}))\,x_7 - k_{57}\exp(k_{23}(n_1 - k_{58}))\,x_7x_3 - k_{81}\exp(k_{24}(n_1 - k_{82}))\,x_7x_4 - k_{105}\exp(k_{25}(n_1 - k_{106}))\,x_7x_5 - k_{135}\exp(k_{147}(n_1 - k_{136}))\,x_7x_{10} - k_{160}\exp(k_{172}(n_1 - k_{161}))\,x_7x_{11}$$

$$\dot{x}_8 = k_{17}k_{46}\exp(k_{18}(n_1 - k_{19}))\,x_8 - k_{36}\exp(k_{18}(n_1 - k_{37}))\,x_8 - k_{60}\exp(k_{23}(n_1 - k_{61}))\,x_8x_3 - k_{84}\exp(k_{24}(n_1 - k_{85}))\,x_8x_4 - k_{108}\exp(k_{25}(n_1 - k_{109}))\,x_8x_5 - k_{138}\exp(k_{147}(n_1 - k_{139}))\,x_8x_{10} - k_{163}\exp(k_{172}(n_1 - k_{164}))\,x_8x_{11}$$

$$\dot{x}_9 = k_{20}k_{47}\exp(k_{21}(n_1 - k_{22}))\,x_9 - k_{38}\exp(k_{21}(n_1 - k_{39}))\,x_9 - k_{63}\exp(k_{23}(n_1 - k_{64}))\,x_9x_3 - k_{87}\exp(k_{24}(n_1 - k_{88}))\,x_9x_4 - k_{111}\exp(k_{25}(n_1 - k_{112}))\,x_9x_5 - k_{141}\exp(k_{147}(n_1 - k_{142}))\,x_9x_{10} - k_{166}\exp(k_{172}(n_1 - k_{167}))\,x_9x_{11}$$

$$\dot{x}_{10} = k_{120}k_{122}\exp(k_{147}(n_1 - k_{121}))\,x_{10} + k_{123}k_{125}\exp(k_{147}(n_1 - k_{124}))\,x_{10}x_3 + k_{126}k_{128}\exp(k_{147}(n_1 - k_{127}))\,x_{10}x_4 + k_{129}k_{131}\exp(k_{147}(n_1 - k_{130}))\,x_{10}x_5 + k_{132}k_{134}\exp(k_{147}(n_1 - k_{133}))\,x_{10}x_6 + k_{135}k_{137}\exp(k_{147}(n_1 - k_{136}))\,x_{10}x_7 + k_{138}k_{140}\exp(k_{147}(n_1 - k_{139}))\,x_{10}x_8 + k_{141}k_{143}\exp(k_{147}(n_1 - k_{142}))\,x_{10}x_9 + k_{144}k_{146}\exp(k_{147}(n_1 - k_{145}))\,x_{10}x_{11} - k_{40}\exp(k_{147}(n_1 - k_{41}))\,x_{10} - k_{66}\exp(k_{23}(n_1 - k_{67}))\,x_{10}x_3 - k_{90}\exp(k_{24}(n_1 - k_{91}))\,x_{10}x_4 - k_{114}\exp(k_{25}(n_1 - k_{115}))\,x_{10}x_5 - k_{169}\exp(k_{172}(n_1 - k_{170}))\,x_{10}x_{11}$$

$$\dot{x}_{11} = k_{148}k_{150}\exp(k_{172}(n_1 - k_{149}))\,x_{11}x_3 + k_{151}k_{153}\exp(k_{172}(n_1 - k_{152}))\,x_{11}x_4 + k_{154}k_{156}\exp(k_{172}(n_1 - k_{155}))\,x_{11}x_5 + k_{157}k_{159}\exp(k_{172}(n_1 - k_{158}))\,x_{11}x_6 + k_{160}k_{162}\exp(k_{172}(n_1 - k_{161}))\,x_{11}x_7 + k_{163}k_{165}\exp(k_{172}(n_1 - k_{164}))\,x_{11}x_8 + k_{166}k_{168}\exp(k_{172}(n_1 - k_{167}))\,x_{11}x_9 + k_{169}k_{171}\exp(k_{172}(n_1 - k_{170}))\,x_{11}x_{10} - k_{42}\exp(k_{172}(n_1 - k_{43}))\,x_{11} - k_{69}\exp(k_{23}(n_1 - k_{70}))\,x_{11}x_3 - k_{93}\exp(k_{24}(n_1 - k_{94}))\,x_{11}x_4 - k_{117}\exp(k_{25}(n_1 - k_{118}))\,x_{11}x_5 - k_{144}\exp(k_{147}(n_1 - k_{145}))\,x_{11}x_{10}$$

The ratio of actual evaporation (n_6) to potential evaporation (n_5) is assumed to be equal to the ratio of actual available moisture to maximum possible available moisture. The latter term is equal to maximum mor moisture content minus minimum mor moisture content. This assumption is commonly made in physical climatology (Sellers, 1965). That there is, indeed, a linear relationship between evaporation and available moisture is indicated by observed negative exponential drying curves of both pine and hardwood forest floors (Helvey, 1964, 1967).

Similarly, the ratio of precipitation retention (n_7) to net precipitation (n_4), i.e., the fraction of net precipitation retained by the forest floor (the rest becoming runoff or soil seepage) is assumed to be equal to the ratio of actual moisture deficit to maximum possible moisture deficit (which equals maximum possible available moisture). That there is a linear relationship between precipitation retention and moisture deficit is indicated by observed asymptotic moisture buildup curves of hardwood forest floors (Helvey, 1964).

The moisture fraction (n_8) is simply the ratio of mor moisture (x_1) to mor (x_2), and is included solely for convenience.

The mor respiration rate (n_9) is assumed to be a function of both mor temperature (n_1) and moisture fraction (n_8), when k_8 is the measured mor respiration rate, and k_9 and k_{10} are the temperature and moisture fraction, respectively, at which the measurement was made. Respiration is assumed to be an exponential function of temperature within the range of the model, allowing the use of a simple Q_{10} value with k_7, the temperature sensitivity of mor respiration, determined by the value of the Q_{10}, and "$n_1 - k_9$" is the difference in temperature of the mor from the original measurement. Data on the effect of moisture on the rate of mor respiration are very scarce. Those of Parkinson and Coups (1963) indicate that a linear relationship exists within the range they studied. A linear relationship is assumed here, although certainly a nonlinear one would be more realistic.

The assumption of a single respiration rate (or decomposition rate) for mor is a gross approximation, and a closer approximation could probably be obtained by using several respiration rates based on the mor components of sugars, hemicelluloses, cellulose, lignin, waxes, and phenols (Minderman, 1968). To do so would greatly complicate the model, since the dynamic state variable, "mor," would have to be broken down into at least six different dynamic state variables.

The dynamic state variable, mor moisture (x_1), is defined by a differential equation in which the change in mor moisture per unit time (a "flux") is made equal to the gain flux, precipitation retention (n_7), minus the loss flux, actual evaporation (n_6). Any transfer of moisture to

or from the mineral soil, not accounted for by the precipitation retention calculation, is ignored.

In the case of the mor (x_2), i.e., the decomposing pine litter with contained fungi, there is but one gain flux, pine litterfall (v_3), and several loss fluxes, respiration (n_9x_2), and ingestion by the arthropods, Oribatei (x_6), Symphyleona (x_7), Poduromorpha (x_8), Entomobryomorpha (x_9), and Formicidae (x_{10}).

Temperature is assumed to affect ingestion fluxes in the same fashion as it affects mor respiration rate, allowing, of course, each arthropod taxon to possess its own Q_{10} value, expressed as its temperature sensitivity. Moisture is assumed to have no effect on ingestion or respiration by arthropods; this is based on the observation (Kendrick and Burges, 1962) that the arthropods tend to concentrate in the rather uniformly moist F_2 layer. The insignificance of moisture is a questionable assumption, but sufficient information does not exist to make a different one.

Fluxes representing ingestion of mor by saprovore arthropods are assumed to be controlled solely by temperature and the saprovore biomass, the mor biomass (x_2) not having any effect. Predation fluxes, on the other hand, are assumed to be controlled by both prey and predator biomasses, as well as the temperature. Thus, I have adopted the "Hairston–Smith–Slobodkin" hypothesis.

The differential equation defining the biomass of an arthropod taxon, in order to be complete, would have to include as gain fluxes: the ingestion of each prey taxon (or plant material) and immigration; and as loss fluxes: egestion of each prey taxon (or plant material), excretion, respiration, production of exuviae, production of nonviable eggs, nonpredatory death, predatory death (including parts not ingested by the predator), and emigration. (This assumes that water intake contributes nothing to dry weight.) In this model ingestions minus egestions for each prey (or mor) are used as the gain fluxes, and respirations and predatory deaths for each predator are used as the loss fluxes.

The gain fluxes to each arthropod taxon (x_3–x_{11}) represent ingestion minus egestion, i.e., assimilation, of each food material, and thus are of the form: ingestion rate · assimilation fraction · temperature effect · feeding arthropod biomass · food arthropod biomass (for predators only). Assimilation fraction is assumed to be a constant. The predatory loss fluxes are similarly formulated, with ingestion rates based on the predator, and with the assimilation fraction absent since all ingested material is lost from the food compartment. (It should be noted that the predation ingestion rates do not have the usual units: grams of food ingested per grams feeder per day or, simply, inverse days, but,

grams of food ingested per grams feeder per grams food per day or, inverse grams food per day.)

f. *Evaluation of Constants.* The equations specified in the previous step contain a large number of unevaluated constants k_i. These constants must be evaluated if the mathematical model is to be tested and later (probably after modification) used for practical purposes. Of course, one might prefer to leave the constants in an unevaluated form, but I feel that this leads to rather empty models. Moreover, in nonlinear systems the qualitative behavior of the variables is often a function of the values of the constants.

In general, there are three possible sources of values for the constants. In some cases the value of one or more constants may be suggested as hypothesis, perhaps a major hypothesis of the model. More often, values will come from the literature, but one must be careful that equation forms and the operational definitions of variables associated with the constants are the same in both models (one's own and that in the literature). Since this requirement is seldom satisfied, values of constants obtained in this way should probably also be regarded as hypotheses. The last, perhaps ideal, source of constant values is, of course, actual measurement.

The actual measurement of constants, i.e., "parameter estimation," is where statistics makes its first major contribution to modeling. This is the area of least squares, regression, etc. In the case of fitting nonlinear curves (hypotheses) to sets of data, a very useful tool is the Taylor series gradient method developed by Marquardt (1963).

It is important to manage one's resources so that constants most influential in determining solution behavior are the constants most accurately measured. It is often possible to calculate their influences, i.e., the partial derivatives of solution behavior with respect to particular constants, in a sensitivity analysis (Tomović, 1963).

It is in the evaluation of model constants that mathematical modeling has great value in guiding activities of the researcher. The model indicates what kinds of measurements are important, and what kinds are not. It provides a definite goal for the researcher, leading him toward the most useful observations to be made in order to accomplish his objectives.

Table IV contains the evaluated constants of the pine–mor model. The sources of most of the values are indicated in the table. Ideally, all the constants should be measured in the same pine forest (the one on which the model is to be tested), since they are dependent upon local climate and topography, pine species, and species composition of arthropod taxa. Unfortunately, this has not been done.

Here k_3 is the scale factor for potential evaporation $n_5 = k_3 \exp(0.065 n_1)$. To calculate the value of k_3, I have used the data of Metz (1958). Metz measured a water loss from pine litter of 438 g m^{-2} day^{-1} immediately following rainstorms, during a period when the mean daily air temperature was 22.5 C. Using this data in the equation, and solving, $k_3 = 101.6$. Derivation of k_4 was explained in the previous section.

The standard mor respiration rate k_8 was calculated from a measurement (Kowal, 1969b) of *Pinus echinata* L-layer respiration rate (0.00275 day^{-1}) corrected for relative weights of layers and relative respiration rates of layers (Parkinson and Coups, 1963).

Predator ingestion "rates" were calculated from the assumptions that, at equilibrium, at 15 C all predator taxa ingest $\frac{1}{10}$ of their biomass per day, and ingestion of the various prey taxa is proportional to prey taxa biomass. The values used for equilibrium biomass come from some preliminary *P. echinata* mor data.

I recognize that many of the values used for constants are based upon crude data and unrealistic assumptions, but believe these to be the best available at the present time. Research is currently in progress to obtain better estimates of many of them, particularly the ingestion "rates."

2. *Digital Computer Programming (Numerical Approximation)*

Once the model has been formulated, it is necessary to obtain numerical solutions for use in system identification (testing of predictions and alteration of model) and, perhaps eventually, system analysis. this is most efficiently done (on the digital computer) by numerical approximation.

By a "numerical solution" is meant a set of numerical values of the state variables at one or more points in time, usually starting with the initial state. Exact (analytical, closed form) solutions might be feasible for some very simple models, but for most practical models an approximation will be necessary. If they are feasible, exact solutions, of course, should be used rather than approximations. Numerical solutions are calculated indirectly from the exact or approximate literal solution, or may be calculated directly by a computer algorithm (the digital computer program).

The model consists of a system of coupled algebraic and differential equations, and must be converted into a digital computer program. In formulating this program, algebraic equations pose no problems; they can be solved exactly. But, since the digital computer operates in discrete time steps, while differential equations are continuous, the differential equations must be approximated. This is most easily done by

TABLE IV

PINE–MOR MODEL CONSTANTS

Symbol	Physical description	Units	Value	Reference
k_1	Fraction of precipitation appearing as throughfall	(pure number)	0.80	Helvey (1967)
k_2	Fraction of precipitation appearing as stemflow	(pure number)	0.04	Helvey (1967)
k_3	Scale factor for potential evaporation	g H_2O m^{-2} day^{-1}	101.6	
k_4	Temperature sensitivity of potential evaporation	C^{-1}	0.065	
k_5	Maximum mor moisture fraction (max n_8)	(pure number)	2.30	Helvey (1967)
k_6	Minimum mor moisture fraction (min n_8)	(pure number)	0.40	Helvey (1967)
k_7	Temperature sensitivity of k_8	C^{-1}	0.069	$Q_{10} = 2$ (Drobník, 1962)
k_8	Standard mor respiration rate	g M g M^{-1} day^{-1}	0.00119	
k_9	Temperature at which k_8 determined	C	20	
k_{10}	Mor moisture fraction at which k_8 determined	(pure number)	1.00	
k_{11}	Standard Oribatei ingestion rate of mor	g M g O^{-1} day^{-1}	0.25	Kowal (1969a)
k_{12}	Temperature sensitivity of Oribatei	C^{-1}	0.139	Berthet (1967)
k_{13}	Temperature at which k_{11} determined	C	20	Kowal (1969a)
k_{14}	Standard Symphypleona ingestion rate of mor	g M g S^{-1} day^{-1}	0.14	Assumed same as Poduromorpha
k_{15}	Temperature sensitivity of Symphypleona	C^{-1}	0.139	Assumed same as Poduromorpha
k_{16}	Temperature at which k_{14} determined	C	15	Assumed same as Poduromorpha
k_{17}	Standard Poduromorpha ingestion rate of mor	g M g P^{-1} day^{-1}	0.14	Healey (1967)
k_{18}	Temperature sensitivity of Poduromorpha	C^{-1}	0.139	$Q_{10} = 4$ (Healey, 1967)
k_{19}	Temperature at which k_{17} determined	C	15	Healey (1967)
k_{20}	Standard Entomobryomorpha ingestion rate of mor	g M g E^{-1} day^{-1}	0.14	Assumed same as Poduromorpha
k_{21}	Temperature sensitivity of Entomobryomorpha	C^{-1}	0.139	Assumed same as Poduromorpha

Table continued

TABLE IV *(continued)*

Symbol	Physical description	Units	Value	Reference
k_{22}	Temperature at which k_{20} determined	C	15	Assumed same as Poduromorpha
k_{23}	Temperature sensitivity of Araneae	C^{-1}	0.139	Assumed same as Poduromorpha
k_{24}	Temperature sensitivity of Mesostigmata	C^{-1}	0.139	Assumed same as Poduromorpha
k_{25}	Temperature sensitivity of Trombidiformes	C^{-1}	0.139	Assumed same as Poduromorpha
k_{26}	Standard Araneae respiration rate	g A g A^{-1} day^{-1}	0.0047	MacFadyen (1963)
k_{27}	Temperature at which k_{26} determined	C	16	MacFadyen (1963)
k_{28}	Standard Mesostigmata respiration rate	g M g M^{-1} day^{-1}	0.0500	MacFadyen (1963)
k_{29}	Temperature at which k_{28} determined	C	16	MacFadyen (1963)
k_{30}	Standard Trombidiformes respiration rate	g T g T^{-1} day^{-1}	0.0500	Assumed same as Mesostigmata
k_{31}	Temperature at which k_{30} determined	C	16	Assumed same as Mesostigmata
k_{32}	Standard Oribatei respiration rate	g O g O^{-1} day^{-1}	0.00185	Berthet (1963)
k_{33}	Temperature at which k_{32} determined	C	16	Berthet (1963)
k_{34}	Standard Symphypleona respiration rate	g S g S^{-1} day^{-1}	0.0282	Assumed same as Poduromorpha
k_{35}	Temperature at which k_{34} determined	C	15	Assumed same as Poduromorpha
k_{36}	Standard Poduromorpha respiration rate	g P g P^{-1} day^{-1}	0.0282	Healey (1967)
k_{37}	Temperature at which k_{36} determined	C	15	Healey (1967)
k_{38}	Standard Entomobryomorpha respiration rate	g E g E^{-1} day^{-1}	0.0282	Assumed same as Poduromorpha
k_{39}	Temperature at which k_{38} determined	C	15	Assumed same as Poduromorpha
k_{40}	Standard Formicidae respiration rate	g F g F^{-1} day^{-1}	0.0500	Assumed same as Mesostigmata
k_{41}	Temperature at which k_{40} determined	C	16	Assumed same as Mesostigmata
k_{42}	Standard Lithobiomorpha respiration rate	g L g L^{-1} day^{-1}	0.0103	MacFadyen (1963)
k_{43}	Temperature at which k_{42} determined	C	16	MacFadyen (1963)

Table continued

TABLE IV *(continued)*

Symbol	Physical description	Units	Value	Reference
k_{44}	Oribatei assimilation fraction of mor	(pure number)	0.14	Berthet (1967)
k_{45}	Symphypleona assimilation fraction of mor	(pure number)	0.55	Assumed same as Poduromorpha
k_{46}	Poduromorpha assimilation fraction of mor	(pure number)	0.55	Healey (1967)
k_{47}	Entomobryomorpha assimilation fraction of mor	(pure number)	0.55	Assumed same as Poduromorpha
k_{48} k_{51} k_{54} k_{57} k_{60} k_{63} k_{66} k_{69}	Araneae ingestion rate of prey	g P ingested g A^{-1} g P^{-1} day^{-1}	0.359	
k_{49} k_{52} k_{55} k_{58} k_{61} k_{64} k_{67} k_{70}	Temperature at which Araneae ingestion rates determined	C	15	
k_{50} k_{53} k_{56} k_{59} k_{62} k_{65} k_{68} k_{71}	Araneae assimilation fraction of prey	(pure number)	0.93	Crossley and Shanks (1966)
k_{72} k_{75} k_{78} k_{81} k_{84} k_{87} k_{90} k_{93}	Mesostigmata ingestion rate of prey	g P ingested g M^{-1} g P^{-1} day^{-1}	0.364	

Table continued

TABLE IV *(continued)*

Symbol	Physical description	Units	Value	Reference
k_{73} k_{76} k_{79} k_{82} k_{85} k_{88} k_{91} k_{94}	Temperature at which Mesostigmata ingestion rates determined	C	15	
k_{74} k_{77} k_{80} k_{83} k_{86} k_{89} k_{92} k_{95}	Mesostigmata assimilation fraction of prey	(pure number)	0.47	Assumed same as Opiliones (Phillipson, 1960)
k_{96} k_{99} k_{102} k_{105} k_{108} k_{111} k_{114} k_{117}	Trombidiformes ingestion rate of prey	g P ingested g T^{-1} g P^{-1} day^{-1}	0.368	
k_{97} k_{100} k_{103} k_{106} k_{109} k_{112} k_{115} k_{118}	Temperature at which Trombidiformes ingestion rates determined	C	15	
k_{98} k_{101} k_{104} k_{107} k_{110} k_{113} k_{116} k_{119}	Trombidiformes assimilation fraction of prey	(pure number)	0.47	Assumed same as Opiliones (Phillipson, 1960)

Table continued

TABLE IV *(continued)*

Symbol	Physical description	Units	Value	Reference
k_{120}	Standard Formicidae ingestion rate of mor	g M g F^{-1} day^{-1}	0	Arbitrary
k_{121}	Temperature at which k_{120} determined	C	15	Arbitrary
k_{122}	Formicidae assimilation fraction of mor	(pure number)	0.55	Arbitrary
k_{123} k_{126} k_{129} k_{132} k_{135} k_{138} k_{141} k_{144}	Formicidae ingestion rate of prey	g P ingested g F^{-1} g P^{-1} day^{-1}	0.417	
k_{124} k_{127} k_{130} k_{133} k_{136} k_{139} k_{142} k_{145}	Temperature at which Formicidae ingestion rates determined	C	15	
k_{125} k_{128} k_{131} k_{134} k_{137} k_{140} k_{143} k_{146}	Formicidae assimilation fraction of prey	(pure number)	0.93	Assumed same as Araneae
k_{147}	Temperature sensitivity of Formicidae	C^{-1}	0.139	Assumed same as Poduromorpha
k_{148} k_{151} k_{154} k_{157} k_{160} k_{163} k_{166} k_{169}	Lithobiomorpha ingestion rate of prey	g P ingested g L^{-1} g P^{-1} day^{-1}	0.417	

Table continued

TABLE IV *(continued)*

Symbol	Physical description	Units	Value	Reference
k_{149} k_{152} k_{155} k_{158} k_{161} k_{164} k_{167} k_{170}	Temperature at which Lithobiomorpha ingestion rates determined	C	15	
k_{150} k_{153} k_{156} k_{159} k_{162} k_{165} k_{168} k_{171}	Lithobiomorpha assimilation fraction of prey	(pure number)	1.00	Crossley and Shanks (1966)
k_{172}	Temperature sensitivity of Lithobiomorpha	C^{-1}	0.139	Assumed same as Poduromorpha

converting them into their corresponding difference equations using Euler's method:

$$d\mathbf{x}/dt = \mathbf{f}(\mathbf{n}, \mathbf{x}, \mathbf{v}) \tag{3}$$

$$\Delta\mathbf{x}/\Delta t \doteq \mathbf{f}(\mathbf{n}, \mathbf{x}, \mathbf{v}) \tag{4}$$

$$\Delta\mathbf{x} \doteq \Delta t\mathbf{f}(\mathbf{n}, \mathbf{x}, \mathbf{v}), \tag{5}$$

where $\mathbf{f}(\mathbf{n}, \mathbf{x}, \mathbf{v})$ is the vector-valued function of the nondynamic state vector, the dynamic state vector, and the input vector, Δt is the time increment of the algorithm, and $\Delta\mathbf{x}$ is the resulting dynamic state vector increment. In the computer program, each dynamic state-variable increment is thus approximated by the product of the right side of the corresponding differential equation and a suitable time increment. At each step in the computation, state-variable increments are calculated from previous values of the dynamic state variables and current values of the others, and then added to the previous values of the dynamic state variables to approximate their next values

$$\mathbf{x}(t) \doteq \mathbf{x}(t - \Delta t) + \Delta t\mathbf{f}(\mathbf{n}(t), \mathbf{x}(t - \Delta t), \mathbf{v}(t)). \tag{6}$$

This process is repeated for the total time period over which a solution is desired.

Euler's method is very appealing to the mathematical neophyte because of its simplicity, but it is also very inaccurate. The error usually grows as the solution proceeds from the initial time, and is proportional to the time increment (Nielsen, 1964). The error can be reduced by using small time increments, but solutions at times distant from the initial time will still always be considerably in error. One alternative approach would be to use an analog rather than a digital computer to obtain solutions. In this case the solution is exact (within the errors introduced by the electronic components) since the analog computer operates in continuous time; however, it may by difficult to program the computer for some types of models. Another alternative is to use finite (based on the chosen time increment) rather than instantaneous rates in the formulation of the model. This would convert the differential equations into difference equations, and then a digital computer program could produce an exact solution to the model. However, the model would be more approximate. (If the computer program time increment were equal to the time increment used in the real-world measurements, then the calculation of rates would be greatly simplified. The finite rates could be calculated directly from the measurements. Otherwise, from the measurements based on one time increment must be calculated the instantaneous rates, and from these must be calculated the finite rates based on the other time increment.) An important drawback of this last alternative is that the theory of difference equations has been developed to a lesser degree than has the theory of differential equations.

The most practical alternative to the Euler method is to use one of the other standard methods of numerically approximating the solutions to differential equations (Nielsen, 1964; Scheid, 1968; Benyon, 1968), e.g., Taylor series, Runge–Kutta method, Milne method, Adams–Bashforth method, or Adams–Moulton method (see Chapter 1, Section VII.C). Of these, the fourth-order Runge–Kutta method is probably most practical for large systems, and is discussed later; the Milne method should be avoided because of its instability (Scheid, 1968). The Runge–Kutta method has been used for the pine–mor system, but discussion here is limited to the Euler method for the sake of simplicity.

In North America digital computer programs usually are written in Fortran, and thus I am assuming its use here. (Elements of Fortran are given in Chapter 1.) The first step is the dimensioning of variables. (Table V, card 042 as numbered at the extreme right.) The constants are treated as subscripted variables in the program, but, once read in, are never changed. One must also define a new set of variables, DX(I), which represents approximate increments of the dynamic state variables, i.e., Δx_i. (In transferring between a computer language and ordinary

mathematical terminology, one should be careful in the use of parentheses. They may signify subscripts, arguments of a function, multiplication, sets, explanatory statements, or nothing, depending on context.)

Next, any variable names implicitly typed incorrectly must be explicitly typed correctly. Thus, if one is using the v, n, x, k, dx notation, n and k must be explicitly typed "real" (card 043). The DO loop index, DAY, (see below) must be typed "integer" (044).

The constants must now be evaluated, and the initial state of the dynamic state variables fixed. This is accomplished by two pairs of READ and FORMAT statements, (046–7, 049–50). The evaluated constants and the initial state form the first and second types of data required by the program, and are placed after the program itself.

Before the DO loop, which calculates predicted states on the basis of the constants and initial state (and the input variables and equations), one must make certain preparations for the printout (predicted states) of the DO loop. The printout will normally consist of a column for the time variable, and several columns for selected state variables. These columns can be provided with headings by a pair of nonlist WRITE and Hollerith FORMAT statements (053–6). One must be careful that spacing of the headings matches that of the columns; either symbols or descriptive names could be used for column headings, but symbols will usually save space. At this point it is also useful to print the initial state, since the DO loop will not do this. Again, one must use the same format as that of the columns of predicted values of the selected state variables, plus print a zero in the time column by means of a Hollerith "field" (059–60).

The DO statement (064) is now written. The systems we are dealing with are continuous, state-determined systems, characterized by the state equation (DeRusso *et al.*, 1965, p. 328)

$$\mathbf{x}(t) = \mathbf{f}(\mathbf{x}(t_0), \mathbf{v}(t_0, t)), \tag{7}$$

where $\mathbf{x}(t)$ is the state vector, including both dynamic and nondynamic state variables. (For the analysis of the model, the nondynamic state variables are eliminated, so that the inconsistency disappears.) Equation (7) means that the state $\mathbf{x}$ at the end of the time interval, t_0 to t, is a function of the state at the beginning of the interval and the input $\mathbf{v}$ over this time interval. The equation represents conceptually the literal solution to our system of coupled (algebraic and) differential equations, i.e., our model. Since the literal solution is usually impossible or impractical to obtain, we obtain a numerical solution. This is done by the DO loop, by reading the input variables (066–7), calculating the nondynamic state variables (069–76), calculating the dynamic state-variable

TABLE V

A Sample Fortran Computer Program for the Pine-Mor Food Web Model

```
$PILER OPTIONS - NAME=  MAIN,OPT=00,LINECNT=50,SOURCE,EBCDIC,NOLIST,NODECK,LOAD,NOMAP
      C PINE-MOR FOOD WEB MODEL.                                                    001
      C N. E. KOWAL, INSTITUTE OF ECOLOGY, U. GA.                                   002
      C                                                                             003
      C MODEL CONTAINS 3 INPUT, 9 NONDYNAMIC STATE, AND 11  DYNAMIC STATE           004
      C   VARIABLES, PLUS 172 CONSTANTS.                                            005
      C      INPUT VARIABLES                                                        006
      C            V(1)   MEAN AIR TEMPERATURE                                     007
      C            V(2)   PRECIPITATION                                            008
      C            V(3)   PINE LITTERFALL                                          009
      C      NONDYNAMIC STATE VARIABLES                                            010
      C            N(1)   MOR TEMPERATURE                                          011
      C            N(2)   THROUGHFALL                                              012
      C            N(3)   STEMFLOW                                                 013
      C            N(4)   NET PRECIPITATION                                        014
      C            N(5)   POTENTIAL EVAPORATION FROM MOR                           015
      C            N(6)   ACTUAL EVAPORATION FROM MOR                              016
      C            N(7)   PRECIPITATION RETENTION                                  017
      C            N(8)   MOR MOISTURE FRACTION                                    018
      C            N(9)   MOR RESPIRATION RATE                                     019
      C      DYNAMIC STATE VARIABLES                                               020
      C            X(1)   MOR MOISTURE                                             021
      C            X(2)   MOR                                                      022
      C            X(3)   ARANEAE                                                  023
      C            X(4)   MESOSTIGMATA                                             024
      C            X(5)   TROMBIDIFORMES                                           025
      C            X(6)   ORIBATEI                                                 026
      C            X(7)   SYMPHYPLEONA                                             027
      C            X(8)   PODUROMORPHA                                             028
      C            X(9)   ENTOMOBRYOMORPHA                                         029
      C            X(10)  FORMICIDAE                                               030
      C            X(11)  LITHOBIOMORPHA                                           031
      C PROGRAM DATA REQUIREMENTS:                                                  032
      C      1) EVALUATED CONSTANTS: K(1)-K(172)                                    033
      C            CARDS 1-22(COLUMN 40)                                           034
      C            FORMAT 8F10.0                                                   035
      C      2) INITIAL STATE: X(1)-X(11) AT TIME ZERO                             036
      C            CARDS 23-24 (COLUMN 30)                                         037
      C            FORMAT 8F10.0                                                   038
      C      3) VALUES OF INPUT VARIABLES FOR PERIOD OF CALCULATION: V(1)-V(3)     039
      C            CARDS 25-(24&MAX DAY)                                           040
      C            FORMAT 3F10.0                                                   041
            DIMENSION V(3), N(9), X(11), K(172), DX(11)                           042
            REAL N, K                                                             043
            INTEGER DAY                                                           044
      C EVALUATION OF CONSTANTS.                                                  045
            READ (5,10) K                                                         046
         10 FORMAT (8F10.0)                                                       047
      C SETTING OF INITIAL STATE OF DYNAMIC STATE VARIABLES.                      048
            READ (5,20) X                                                         049
         20 FORMAT (8F10.0)                                                       050
      C PRINT COLUMN HEADINGS FOR PROGRAM OUTPUT. MUST CORRESPOND WITH SE-        051
      C    LECTED VARIABLES PRINTED OUT BY DO LOOP.                               052
            WRITE (6,30)                                                          053
         30 FORMAT (12IHI        DAY       X(1)       X(2)       X(3)       X(4)  054
           X   X(5)       X(6)       X(7)       X(8)       X(9)       X(10)      055
           X(11)                                                                  056
      C PRINT INITIAL STATES OF SELECTED DYNAMIC STATE VARIABLES. THESE MUST      057
      C    CORRESPOND WITH COLUMN HEADINGS.                                       058
            WRITE (6,35) X                                                        059
         35 FORMAT (11H          0, 1P11E10.3)                                    060
      C CALCULATION OF STATE VARIABLES FROM INITIAL STATE AND INPUT VARIABLES.    061
      C    DO LOOP PERFORMS NUMERICAL APPROXIMATION OF DYNAMIC STATE VARIABLES    062
      C    BY EULER'S METHOD.                                                     063
            DO 60 DAY=1,730,1                                                     064
      C VALUES OF INPUT VARIABLES FOR DAY "DAY".                                  065
            READ (5,40) V                                                         066
         40 FORMAT (3F10.0)                                                       067
      C EQUATIONS FOR NONDYNAMIC STATE VARIABLES, DURING DAY "DAY".               068
            N(1) = V(1)                                                           069
            N(2) = K(1)*V(2)                                                      070
            N(3) = K(2)*V(2)                                                      071
            N(4) = N(2) + N(3)                                                    072
            N(5) = K(3)*EXP(K(4)*N(1))                                            073
```

Table continued

TABLE V *(continued)*

```
      N(8) = X(1)/X(2)                                                    074
      N(6) = (N(4)-K(6))*N(5)/(K(5)-K(6))                                 075
      N(7) = (K(5)-N(8))*N(4)/(K(5)-K(6))                                 076
C NEXT TWO STATEMENTS PREVENT ACTUAL EVAPORATION (N(6)) FROM EXCEEDING    077
C  MOISTURE (X(1)), AND PRECIPITATION RETENTION (N(7)) FROM EXCEEDING     078
C  MOISTURE DEFICIT (K(5)*X(2)-X(1)). THESE MAY OCCUR BECAUSE OF THE      079
C  DISCRETE-TIME APPROXIMATION OF CONTINUOUS-TIME SOLUTIONS, ESPECIALLY   080
C  WHEN NOR (X(2)) IS LOW.                                                081
      IF(N(6).GT.X(1)) N(6)=X(1)                                          082
      IF(N(7).GT.(K(5)*X(2)-X(1))) N(7)=K(5)*X(2)-X(1)                    083
      N(9) = K(8)*EXP(K(7)*(N(1)-K(9)))*(N(8)-K(6))/(K(10)-K(6))          084
C EQUATIONS FOR DYNAMIC STATE VARIABLE INCREMENTS, DURING DAY "DAY".      085
      DX(1) = N(7) - N(6)                                                 086
C                                                                         087
      DX(2) = K(3) - N(9)*X(2) - K(11)*EXP(K(12)*(N(1)-K(13)))*X(6) -     088
     XK(14)*EXP(K(15)*(N(1)-K(16)))*X(7) - K(17)*EXP(K(18)*(N(1)-K(19)))  089
     X*X(8) - K(20)*EXP(K(21)*(N(1)-K(22)))*X(9) - K(120)*EXP(K(147)*(    090
     XN(1)-K(121)))*X(10)                                                 091
C                                                                         092
      DX(3) = K(48)*K(50)*EXP(K(23)*(N(1)-K(49)))*X(2)*X(4) + K(51)*K(53  093
     X1*EXP(K(23)*(N(1)-K(52)))*X(3)*X(5) + K(54)*K(56)*EXP(K(23)*(N(1)  094
     X - K(55)))*X(3)*X(6) + K(57)*K(59)*EXP(K(23)*(N(1)-K(58)))*X(3)*X(  095
     X7) + K(60)*K(62)*EXP(K(23)*(N(1)-K(61)))*X(3)*X(8) + K(63)*K(65)*  096
     XEXP(K(23)*(N(1)-K(64)))*X(3)*X(9) + K(66)*K(68)*EXP(K(23)*(N(1)-   097
     XK(67)))*X(3)*X(10) + K(69)*K(71)*EXP(K(23)*(N(1)-K(70)))*X(3)*X(1  098
     X) - K(26)*EXP(K(23)*(N(1)-K(27)))*X(3) - K(72)*EXP(K(24)*(N(1)-    099
     XK(73)))*X(3)*X(4) - K(96)*EXP(K(25)*(N(1)-K(97)))*X(3)*X(5) -      100
     XK(123)*EXP(K(147)*(N(1)-K(124)))*X(3)*X(10) - K(148)*EXP(K(172)*(   101
     XN(1)-K(149)))*X(3)*X(11)                                            102
C                                                                         103
      DX(4) = K(72)*K(74)*EXP(K(24)*(N(1)-K(73)))*X(4)*X(3) + K(75)*K(    104
     X77)*EXP(K(24)*(N(1)-K(76)))*X(4)*X(5) + K(78)*K(80)*EXP(K(24)*(N   105
     X(1)-K(79)))*X(4)*X(6) + K(81)*K(83)*EXP(K(24)*(N(1)-K(82)))*X(4)*  106
     XX(7) + K(94)*K(86)*EXP(K(24)*(N(1)-K(85)))*X(4)*X(8) + K(87)*K(89)  107
     X*EXP(K(24)*(N(1)-K(88)))*X(4)*X(9)+ K(90)*K(92)*EXP(K(24)*(N(1)-K(  108
     X91)))*X(4)*X(10) + K(93)*K(95)*EXP(K(24)*(N(1)-K(94)))*X(4)*X(11)   109
     X - K(28)*EXP(K(24)*(N(1)-K(29)))*X(4) - K(48)*EXP(K(23)*(N(1)-K(49  110
     X)))*X(4)*X(3) - K(99)*EXP(K(25)*(N(1)-K(100)))*X(4)*X(5) - K(126)*  111
     XEXP(K(147)*(N(1)-K(127)))*X(4)*X(10) - K(151)*EXP(K(172)*(N(1)-K    112
     X(152)))*X(4)*X(11)                                                  113
C                                                                         114
      DX(5) = K(96)*K(98)*EXP(K(25)*(N(1)-K(97)))*X(5)*X(3) + K(99)*K(10  115
     X1)*EXP(K(25)*(N(1)-K(100)))*X(5)*X(4) + K(102)*K(104)*EXP(K(25)*    116
     X(N(1)-K(103)))*X(5)*X(6) + K(105)*K(107)*EXP(K(25)*(N(1)-K(106)))*  117
     XX(5)*X(7) + K(108)*K(110)*EXP(K(25)*(N(1)-K(109)))*X(5)*X(8)        118
     X* K(111)*K(113)*EXP(K(25)*(N(1)-K(112)))*X(5)*X(9) + K(114)*K(116)  119
     X*EXP(K(25)*(N(1)-K(115)))*X(5)*X(10) + K(117)*K(119)*EXP(K(25)*(N   120
     X(1)-K(118)))*X(5)*X(11) - K(30)*EXP(K(25)*(N(1)-K(31)))*X(5) -      121
     XK(51)*EXP(K(23)*(N(1)-K(52)))*X(5)*X(3) - K(75)*EXP(K(24)*(N(1)-    122
     XK(76)))*X(5)*X(4) - K(129)*EXP(K(147)*(N(1)-K(130)))*X(5)*X(10)     123
     X- K(154)*EXP(K(172)*(N(1)-K(155)))*X(5)*X(11)                       124
C                                                                         125
      DX(6) = K(11)*K(44)*EXP(K(12)*(N(1)-K(13)))*X(6) - K(32)*EXP(K(12)  126
     X*(N(1)-K(33)))*X(6) - K(54)*EXP(K(23)*(N(1)-K(55)))*X(6)*X(3) -     127
     XK(78)*EXP(K(24)*(N(1)-K(79)))*X(6)*X(4) - K(102)*EXP(K(25)*(N(1)-K  128
     X(103)))*X(6)*X(5) - K(132)*EXP(K(147)*(N(1)-K(133)))*X(6)*X(10) -   129
     XK(157)*EXP(K(172)*(N(1)-K(158)))*X(6)*X(11)                         130
C                                                                         131
      DX(7) = K(14)*K(45)*EXP(K(15)*(N(1)-K(16)))*X(7) - K(34)*EXP(K(15)  132
     X*(N(1)-K(35)))*X(7) - K(57)*EXP(K(23)*(N(1)-K(58)))*X(7)*X(3) -     133
     XK(81)*EXP(K(24)*(N(1)-K(82)))*X(7)*X(4) - K(105)*EXP(K(25)*(N(1)-   134
     XK(106)))*X(7)*X(5) - K(135)*EXP(K(147)*(N(1)-K(136)))*X(7)*X(10) -  135
     X K(160)*EXP(K(172)*(N(1)-K(161)))*X(7)*X(11)                        136
C                                                                         137
      DX(8) = K(17)*K(46)*EXP(K(18)*(N(1)-K(19)))*X(8) - K(36)*EXP(K(18)  138
     X*(N(1)-K(37)))*X(8) - K(60)*EXP(K(23)*(N(1)-K(61)))*X(8)*X(3) -     139
     XK(84)*EXP(K(24)*(N(1)-K(85)))*X(8)*X(4) - K(108)*EXP(K(25)*(N(1)-   140
     XK(109)))*X(8)*X(5) - K(138)*EXP(K(147)*(N(1)-K(139)))*X(8)*X(10) -  141
     X K(163)*EXP(K(172)*(N(1)-K(164)))*X(8)*X(11)                        142
C                                                                         143
      DX(9) = K(20)*K(47)*EXP(K(21)*(N(1)-K(22)))*X(9) - K(38)*EXP(K(21)  144
     X*(N(1)-K(39)))*X(9) - K(63)*EXP(K(23)*(N(1)-K(64)))*X(9)*X(3) -     145
     XK(87)*EXP(K(24)*(N(1)-K(88)))*X(9)*X(4) - K(111)*EXP(K(25)*(N(1)-K  146
     X(112)))*X(9)*X(5) - K(141)*EXP(K(147)*(N(1)-K(142)))*X(9)*X(10) -   147
```

Table continued

TABLE V *(continued)*

```
      XK(166)*EXP(K(172)*(N(1)-K(167)))*X(9)*X(11)                          148
C                                                                           149
      DX(10) = K(120)*K(122)*EXP(K(147)*(N(1)-K(121)))*X(10) + K(123)*K(    150
     X(25)*EXP(K(147)*(N(1)-K(124)))*X(10)*X(3) + K(126)*K(128)*EXP(K(14    151
     X7)*(N(1)-K(127)))*X(10)*X(4) + K(129)*K(131)*EXP(K(147)*(N(1)-K(13    152
     X0)))*X(10)*X(5) + K(132)*K(134)*EXP(K(147)*(N(1)-K(133)))*X(10)*X(    153
     X6) + K(135)*K(137)*EXP(K(147)*(N(1)-K(136)))*X(10)*X(7) + K(138)*     154
     XK(140)*EXP(K(147)*(N(1)-K(139)))*X(10)*X(8) + K(141)*K(143)*EXP(K     155
     X(147)*(N(1)-K(142)))*X(10)*X(9) + K(144)*K(146)*EXP(K(147)*(N(1)-     156
     XK(145)))*X(10)*X(11) - K(40)*EXP(K(147)*(N(1)-K(41)))*X(10) - K(66    157
     X)*EXP(K(23)*(N(1)-K(67)))*X(10)*X(3) - K(90)*EXP(K(24)*(N(1)-K(91)    158
     X))*X(10)*X(4) - K(114)*EXP(K(25)*(N(1)-K(115)))*X(10)*X(5) - K(169    159
     X)*EXP(K(172)*(N(1)-K(170)))*X(10)*X(11)                               160
C                                                                           161
      DX(11) = K(148)*K(150)*EXP(K(172)*(N(1)-K(149)))*X(11)*X(3) + K(15    162
     X1)*K(153)*EXP(K(172)*(N(1)-K(152)))*X(11)*X(4) + K(154)*K(156)*       163
     XEXP(K(172)*(N(1)-K(155)))*X(11)*X(5) + K(157)*K(159)*EXP(K(172)*      164
     X(N(1)-K(158)))*X(11)*X(6) + K(160)*K(166)*EXP(K(172)*(N(1)-K(161))    165
     X)*X(11)*X(7) + K(163)*K(165)*EXP(K(172)*(N(1)-K(164)))*X(11)*X(8)     166
     X+ K(166)*K(168)*EXP(K(172)*(N(1)-K(167)))*X(11)*X(9) + K(169)*K(17    167
     X1)*EXP(K(172)*(N(1)-K(170)))*X(11)*X(10) - K(42)*EXP(K(172)*(N(1)-    168
     XK(43)))*X(11) - K(69)*EXP(K(23)*(N(1)-K(70)))*X(11)*X(3) - K(93)*     169
     XEXP(K(24)*(N(1)-K(94)))*X(11)*X(4) - K(117)*EXP(K(25)*(N(1)-K(118)    170
     X))*X(11)*X(5) - K(144)*EXP(K(147)*(N(1)-K(145)))*X(11)*X(10)          171
C EQUATIONS FOR DYNAMIC STATE VARIABLES, AT END OF DAY. "DAY".              172
      X(1) = X(1) + DX(1)                                                   173
      X(2) = X(2) + DX(2)                                                   174
      X(3) = X(3) + DX(3)                                                   175
      X(4) = X(4) + DX(4)                                                   176
      X(5) = X(5) + DX(5)                                                   177
      X(6) = X(6) + DX(6)                                                   178
      X(7) = X(7) + DX(7)                                                   179
      X(8) = X(8) + DX(8)                                                   180
      X(9) = X(9) + DX(9)                                                   181
      X(10) = X(10) + DX(10)                                                182
      X(11) = X(11) + DX(11)                                                183
C PRINT SELECTED VARIABLES. THESE MUST CORRESPOND WITH COLUMN HEADINGS.     184
      WRITE (6,50) DAY, X                                                   185
   50 FORMAT (1H , 110, 1P11E10.3)                                          186
   60 CONTINUE                                                              187
C PRINT V, N, AND K FOR CHECKING.                                           188
      WRITE (6,70)                                                          189
   70 FORMAT (17H1LAST VALUES OF V)                                         190
      WRITE (6,80) V                                                        191
   80 FORMAT (1H , 1P10F12.3)                                               192
      WRITE (6,90)                                                          193
   90 FORMAT (17H1LAST VALUES OF N)                                         194
      WRITE (6,80) N                                                        195
      WRITE (6,100)                                                         196
  100 FORMAT (12H1VALUES OF K)                                              197
      WRITE (6,80) K                                                        198
      STOP                                                                  199
      END                                                                   200
COMPILATION ******
```

increments (086–171), and calculating the dynamic state variables (173–83), for a sequence of time increments. The length of the total time interval of calculation is controlled by the DO statement.

(At this point, the reader may be wondering what happened to the outputs of the system, usually symbolized by **y**. If any outputs are deemed necessary in the model, e.g., precipitation runoff, they may usually be made simple algebraic functions of the state variables and input variables, and will present few problems. If they must be defined by differential equations, they can be considered to be dynamic state variables, and the problem disappears.)

The first act of the DO loop is to read the values of the input variables for each time increment. This is accomplished by a pair of READ and

FORMAT statements (066–7). These values form the third, and last, type of data required by the program, and it is important to have one set of values for each time increment. Each set of values, or input vector, should begin on a new card.

The algebraic equations for nondynamic state variables follow (069–76). Because of their nondynamic nature, these variables are not functions of their previous values, and can be calculated directly from the current values of the input variables and the dynamic state variables. One must be careful to arrange these equations in a sequence required by the manner of their coupling.

Equations for the dynamic state-variable increments are now written (086–171). They follow those for the nondynamic state variables, and are all written before the dynamic state variables themselves are evaluated. This arrangement is necessary because the current dynamic state variable increments are functions of the current values of the nondynamic state variables and the previous values of the dynamic state variables, as well as the current values of the input variables.

The dynamic state variables are then evaluated, simply by adding the current dynamic state variable increments to the previous values of the dynamic state variables (173–83). The results may be interpreted to be values of the dynamic state variables at the end of the current time interval, i.e., the $\mathbf{x}(t)$ of Eq. (7).

The last act within the DO loop is printing out the time variable (usually the index of the DO statement) and the values of the selected state variables. These must, of course, correspond to the column headings, and printing is achieved by a pair of WRITE and FORMAT statements (185–6). The use of an E format with a scale factor of one is desirable, since the number of significant digits can be controlled, the field lengths are uniform, and no space is wasted on long sequences of zeros. The DO loop is now completed, and may be closed by a CONTINUE statement (187).

The program is essentially complete at this point. However, it may be useful before ending to print out the last values of the input variables $\mathbf{v}$, the last values of the nondynamic state variables $\mathbf{n}$, and the values of the constants k_i. This (189–98) will facilitate finding mistakes and checking that input data has been properly read, as well as provide a convenient table of the constants. The program is now ended (199–200).

In using the program, the source deck must be followed by three types of data: the evaluated constants, the initial state, and values of the input variables for the period of calculation. Formats of the data cards must, of course, agree with those specified in the program, and each input vector must start on a new card because it is read within the DO

loop. If constant input is desired, there need be but one input vector, and it must be read before the DO loop.

The digital computer program is now complete, and can be used to obtain numerical solutions, or "transient responses," of the system, given a particular initial state and set of inputs. These numerical solutions are the states predicted by the hypothetical model, and may be tested against real-world measurements, in the process of system identification. Once a particularly formulated model has been accepted, the predicted states may be used in the process of system analysis, for theoretical or applied purposes.

The pine–mor program has been successfully run with both constant and variable inputs. For the constant input, mean annual values from Oak Ridge, Tennessee were used: 14.5 C mean air temperature (v_1), 3642.6 g m^{-2} day^{-1} precipitation (v_2), and 1.001 g m^{-2} day^{-1} ash-free *Pinus echinata* pine litterfall (v_3) (Bray and Gorham, 1964). Oak Ridge data were also used for the variable input: daily air temperature from a smoothed curve of monthly means, precipitation as randomly placed rainy days based on total precipitation and number of rainy days within each month, and pine litterfall based on uniform litterfall in all months except October, which has twice as much as each of the other months and whose litterfall follows a sinusoidal curve above the September–November base. The variable input data used are much less variable than real-world data would be, but give some idea of what a transient response to real-world data would be like, nonetheless.

TABLE VI
INITIAL STATE

Dynamic state variable		Initial value (g m^{-2})
x_1	Mor moisture	2239.7
x_2	Mor	2239.7
x_3	Araneae	0.0033
x_4	Mesostigmata	0.0073
x_5	Trombidiformes	0.0103
x_6	Oribatei	0.0881
x_7	Symphypleona	0.0059
x_8	Poduromorpha	0.0189
x_9	Entomobryomorpha	0.0640
x_{10}	Formicidae	0.0422
x_{11}	Lithobiomorpha	0.0421

The source of values used for the initial state (Table VI) was original measurements made on Oak Ridge material. The mor moisture fraction (n_8) was assumed to be 1.00, a typical field value.

Operation of the computer program with a constant input yields information on the system's behavior, possible equilibria (or "steady-states"), and stability. (Determination of the system's stability by observation of its transient response with no input, i.e., the stability of the unforced system in the engineering literature, is not valid here. This is because some of the input variables, i.e., temperature and precipitation, control fluxes of "energy" without entering the fluxes themselves. The concept of an "unforced system" is essentially a linear-system concept.)

When the pine–mor program was run (2 yr, daily calculations) with constant input, the following behavior occurred: Mor (x_2) decreased asymptotically toward a nonzero steady state, with mor moisture (x_1) following it (mor moisture fraction (n_8) remaining constant, near its upper limit (k_5)). Because of the structure of the equations, arthropod variables (x_3–x_{11}) are not affected by mor and mor moisture, and may be regarded as an independent subsystem; these assumptions (hypotheses) may have to be modified later in the process of system identification. The Acarina (mites, x_4–x_6) and Formicidae (ants, x_{10}) approached zero asymptotically. The Araneae (spiders, x_3) decreased with oscillations. The Collembola (x_7–x_9) displayed oscillations, but with no obvious trend. Likewise, the Lithobiomorpha (centipedes, x_{11}) displayed oscillations with no obvious trend, but of increasing amplitude and of the same frequency as Collembola, but out of phase. This transient response suggests that the system was developing into an oscillating predator–prey system of Lithobiomorpha and Collembola. The results with variable input were very similar, the major difference being in the periods of oscillations—an effect of temperature.

In order to obtain some idea of the amount of error introduced by using Euler's approximation, where the time differential dt is approximated by a time increment Δt of 1 day, the program was modified and rerun with the time increment equal to 0.1, 0.5, 2, and 10 days. The resulting state vectors for days 50 and 350 (together with the Runge–Kutta approximations, for comparison) are presented in Table VII. It is evident that the error increases with a larger time increment, and grows with time. For critical work a smaller time increment than one day would have to be used, or a better numerical approximation method used, e.g., the Runge–Kutta method (Chapter 1). The behavior described above for the Euler approximation was not qualitatively different from that for the Runge–Kutta approximation.

3. *System Identification*

The formulated mathematical model is a complex hypothesis, and the numerical solutions it produces are predictions of the hypothesis. The objective now is to produce a model whose predictions agree with real-world measurements at some satisfactory (arbitrary) level of statistical significance, by modifying the equation forms and constants. This is called "system identification" or the "identification problem" in engineering literature, but is simply the "scientific method" of empirical science.

The method is simple in concept, being an application of the state equation, Eq. (7), for dynamic (state-determined) systems. The predicted state ($\mathbf{x}(t)$) is calculated, using the digital computer program, from the (real-world) measured initial state ($\mathbf{x}(t_0)$) and the (real-world) measured inputs during the time interval of interest ($\mathbf{v}(t_0 , t)$). The predicted state is then compared with the (real-world) measured state. This is usually done for a sequence of time points within the total time interval of interest ($t_1 , t_2 ,..., t_n$). Data representing past measurements could be used as well as future measurements, if the model was constructed independently of the past measurements.

The predicted and measured states are compared with each other using the standard "hypothesis-testing" techniques of statistics, e.g., t-test and chi-square. This is where statistics makes a second major contribution to modeling (The first is "parameter estimation" in the evaluation of constants).

If predicted states agree with measured states at some satisfactory level of statistical significance, the real-world system may be considered "identified," and the model accepted, to be used in system analysis and applications. If such an agreement does not occur, then the model must be modified and predictions made until such agreement occurs. The modification is done by changing (1) the equation forms, and/or (2) values of the constants. Data used to test the model must always be independent of the data used to modify the model; thus a new set of measured states must usually be used in each cycle of modification and testing.

The last-mentioned requirement, i.e., that the set of data used to test a model be independent of the set of data used to formulate or modify the model, is a rather overpowering one. The measurement of states of dynamic ecological systems is usually extremely time- and energy-consuming. The labor involved can be reduced by originally formulating several alternative models, or multiple hypotheses (Platt, 1964), and testing all of these against the same set of measured states. The value of

TABLE VII

SOME APPROXIMATED STATES

	Dynamic state variable	Runge–Kutta approximation $\Delta t = 1$ day	Euler approximation for Δt (days)				
			0.1	0.5	1	2	10
State on day 50	x_1	$4.395 \cdot 10^3$	$4.395 \cdot 10^3$	$4.394 \cdot 10^3$	$4.394 \cdot 10^3$	$4.266 \cdot 10^3$	$3.432 \cdot 10^3$
	x_2	$2.039 \cdot 10^3$	$2.039 \cdot 10^3$	$2.039 \cdot 10^3$	$2.039 \cdot 10^3$	$2.048 \cdot 10^3$	$2.125 \cdot 10^3$
	x_3	$6.494 \cdot 10^{-3}$	$6.505 \cdot 10^{-3}$	$6.554 \cdot 10^{-3}$	$6.615 \cdot 10^{-3}$	$6.739 \cdot 10^{-3}$	$7.960 \cdot 10^{-3}$
	x_4	$2.705 \cdot 10^{-4}$	$2.680 \cdot 10^{-4}$	$2.577 \cdot 10^{-4}$	$2.450 \cdot 10^{-4}$	$2.196 \cdot 10^{-4}$	$2.878 \cdot 10^{-5}$
	x_5	$3.955 \cdot 10^{-4}$	$3.919 \cdot 10^{-4}$	$3.773 \cdot 10^{-4}$	$3.591 \cdot 10^{-4}$	$3.228 \cdot 10^{-4}$	$4.598 \cdot 10^{-5}$
	x_6	$5.305 \cdot 10^{-3}$	$5.266 \cdot 10^{-3}$	$5.105 \cdot 10^{-3}$	$4.905 \cdot 10^{-3}$	$4.501 \cdot 10^{-3}$	$1.150 \cdot 10^{-3}$
	x_7	$1.651 \cdot 10^{-3}$	$1.650 \cdot 10^{-3}$	$1.641 \cdot 10^{-3}$	$1.630 \cdot 10^{-3}$	$1.608 \cdot 10^{-3}$	$1.388 \cdot 10^{-3}$
	x_8	$5.290 \cdot 10^{-3}$	$5.284 \cdot 10^{-3}$	$5.257 \cdot 10^{-3}$	$5.223 \cdot 10^{-3}$	$5.152 \cdot 10^{-3}$	$4.446 \cdot 10^{-3}$
	x_9	$1.791 \cdot 10^{-2}$	$1.789 \cdot 10^{-2}$	$1.780 \cdot 10^{-2}$	$1.769 \cdot 10^{-2}$	$1.745 \cdot 10^{-2}$	$1.506 \cdot 10^{-2}$
	x_{10}	$2.845 \cdot 10^{-2}$	$2.853 \cdot 10^{-2}$	$2.882 \cdot 10^{-2}$	$2.920 \cdot 10^{-2}$	$3.000 \cdot 10^{-2}$	$3.900 \cdot 10^{-2}$
	x_{11}	$1.874 \cdot 10^{-1}$	$1.875 \cdot 10^{-1}$	$1.879 \cdot 10^{-1}$	$1.883 \cdot 10^{-1}$	$1.893 \cdot 10^{-1}$	$2.009 \cdot 10^{-1}$
State on day 350	x_1	$2.570 \cdot 10^3$	—	$2.609 \cdot 10^3$	$2.569 \cdot 10^3$	$2.510 \cdot 10^3$	$2.286 \cdot 10^3$
	x_2	$1.218 \cdot 10^3$	—	$1.212 \cdot 10^3$	$1.217 \cdot 10^3$	$1.275 \cdot 10^3$	$1.598 \cdot 10^3$
	x_3	$9.324 \cdot 10^{-4}$	—	$9.342 \cdot 10^{-4}$	$9.338 \cdot 10^{-4}$	$9.271 \cdot 10^{-4}$	$5.511 \cdot 10^{-4}$
	x_4	$1.973 \cdot 10^{-12}$	—	$1.420 \cdot 10^{-12}$	$1.006 \cdot 10^{-12}$	$4.780 \cdot 10^{-13}$	$2.822 \cdot 10^{-19}$
	x_5	$3.083 \cdot 10^{-12}$	—	$2.227 \cdot 10^{-12}$	$1.583 \cdot 10^{-12}$	$7.577 \cdot 10^{-13}$	$6.036 \cdot 10^{-19}$
	x_6	$1.506 \cdot 10^{-6}$	—	$1.417 \cdot 10^{-6}$	$1.329 \cdot 10^{-6}$	$1.157 \cdot 10^{-6}$	$4.311 \cdot 10^{-8}$
	x_7	$4.730 \cdot 10^{-3}$	—	$4.855 \cdot 10^{-3}$	$4.982 \cdot 10^{-3}$	$5.233 \cdot 10^{-3}$	$4.652 \cdot 10^{-3}$
	x_8	$1.515 \cdot 10^{-2}$	—	$1.555 \cdot 10^{-2}$	$1.596 \cdot 10^{-2}$	$1.676 \cdot 10^{-2}$	$1.490 \cdot 10^{-2}$
	x_9	$5.131 \cdot 10^{-2}$	—	$5.267 \cdot 10^{-2}$	$5.405 \cdot 10^{-2}$	$5.677 \cdot 10^{-2}$	$5.047 \cdot 10^{-2}$
	x_{10}	$4.476 \cdot 10^{-7}$	—	$4.033 \cdot 10^{-7}$	$3.614 \cdot 10^{-7}$	$2.848 \cdot 10^{-7}$	$9.595 \cdot 10^{-9}$
	x_{11}	$1.183 \cdot 10^{-1}$	—	$1.165 \cdot 10^{-1}$	$1.143 \cdot 10^{-1}$	$1.092 \cdot 10^{-1}$	$4.654 \cdot 10^{-2}$

this approach, of course, depends on the nature of the specific problem.

System identification has not yet been done for the pine–mor model. Thus, the model presently has the status only of an untested hypothesis.

B. Formulation as Sets of Ordinary Differential Equations

1. *Formulation*

Once the mathematical model has been satisfactorily formulated as a set of algebraic and ordinary differential equations, it is then ready to be analyzed, i.e., used to obtain predicted solutions and stability information. This can always be done by digital computer simulation (numerical approximation). However, since approximation is time-consuming and often very inaccurate, it is desirable to analyze the model by means of the theory of ordinary differential equations, i.e., the "qualitative theory" or "geometric theory" of ordinary differential equations. In order to make such an analysis, the algebraic equations must, of course, be eliminated; in so doing the nondynamic state variables are eliminated, leaving only the dynamic state variables.

Elimination of algebraic equations is extremely simple. It consists merely of substituting algebraic expressions for nondynamic state variables into differential equations for the dynamic state variables. This will often require a series of substitutions, where nondynamic state variables are functions of other nondynamic state variables; in some cases it might require algebraic solution of a system of algebraic equations. The net result is a system of ordinary differential equations of the form

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{v}). \tag{8}$$

Mathematically, the resulting systems of differential equations fall into two important classes, "autonomous systems" and "nonautonomous systems." Autonomous systems are of the general form

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}). \tag{9}$$

The independent variable, time, does not appear as an argument of any of the functions. These systems are often called "dynamical systems" (Birkoff, 1927; Nemytskii and Stepanov, 1960), and an extensive theory exists concerning them in classical physics.

If an autonomous system is linear, it possesses the form (homogeneous or unforced)

$$\dot{\mathbf{x}} = A\mathbf{x}, \tag{10}$$

or (nonhomogeneous or forced)

$$\dot{\mathbf{x}} = A\mathbf{x} + \mathbf{k}, \tag{11}$$

where A is a constant $n \times n$ matrix (n the number of state variables). Therefore, the linear differential equations have constant coefficients. If there is an input to the system, the vector of input variables $\mathbf{v}$ is a vector of constants $\mathbf{k}$, i.e., there is a constant input (forcing, disturbance, etc.). Many nonlinear and nonautonomous systems are approximated by this linear autonomous system because of its mathematical tractability.

Nonautonomous systems are of the general form

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, t). \tag{12}$$

The independent variable, time, appears as an argument of at least one of the functions. In an explanatory (causal) model, all of the effects of time would be through the vector of time-dependent input variables $\mathbf{v}$ so that Eq. (12) could be expressed as

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{v}). \tag{13}$$

This is the general form of our formulated model, Eq. (8).

If a nonautonomous system is linear, and an explanatory model, it has the form

$$\dot{\mathbf{x}} = A\mathbf{x} + \mathbf{f}(t), \tag{14}$$

or, equivalently, using our notation of $\mathbf{v}(t)$ for the input vector,

$$\dot{\mathbf{x}} = A\mathbf{x} + B\mathbf{v}(t), \tag{15}$$

where B is a constant $n \times m$ matrix, where m is the number of input variables. Therefore the linear differential equations have constant coefficients. In a nonexplanatory model the linear differential equations would have variable coefficients, i.e., the matrix A would be a function of time, and the equations could be homogeneous or nonhomogeneous. If the input is constant, Eq. (13) reduces to Eq. (9), an autonomous system.

It is useful to have an understanding of the different types of dynamic systems, since different methods are used in their analysis.

The system of ordinary differential equations representing the pine–mor food web is presented in Table VIII. It is nonautonomous, nonlinear, and "explanatory," and thus is of the form of Eq. (13).

TABLE VIII

EQUATIONS FOR STATE VARIABLES

$$\dot{x}_1 = \frac{k_5 - x_1/x_2}{k_5 - k_6}(k_1 v_2 + k_2 v_2) - \frac{x_1/x_2 - k_6}{k_5 - k_6}(k_3 \exp(k_4 v_1))$$

$$\begin{aligned}\dot{x}_2 = {} & v_3 - k_8 \exp(k_7(v_1 - k_9)) \left(\frac{x_1/x_2 - k_6}{k_{10} - k_6}\right) x_2 - k_{11} \exp(k_{12}(v_1 - k_{13}))\, x_6 \\ & - k_{14} \exp(k_{15}(v_1 - k_{16}))\, x_7 - k_{17} \exp(k_{18}(v_1 - k_{19}))\, x_8 \\ & - k_{20} \exp(k_{21}(v_1 - k_{22}))\, x_9 - k_{120} \exp(k_{147}(v_1 - k_{121}))\, x_{10}\end{aligned}$$

$$\begin{aligned}\dot{x}_3 = {} & k_{48}k_{50} \exp(k_{23}(v_1 - k_{49}))\, x_3x_4 + k_{51}k_{53} \exp(k_{23}(v_1 - k_{52}))\, x_3x_5 \\ & + k_{54}k_{56} \exp(k_{23}(v_1 - k_{55}))\, x_3x_6 + k_{57}k_{59} \exp(k_{23}(v_1 - k_{58}))\, x_3x_7 \\ & + k_{60}k_{62} \exp(k_{23}(v_1 - k_{61}))\, x_3x_8 + k_{63}k_{65} \exp(k_{23}(v_1 - k_{64}))\, x_3x_9 \\ & + k_{66}k_{68} \exp(k_{23}(v_1 - k_{67}))\, x_3x_{10} + k_{69}k_{71} \exp(k_{23}(v_1 - k_{70}))\, x_3x_{11} \\ & - k_{26} \exp(k_{23}(v_1 - k_{27}))\, x_3 - k_{72} \exp(k_{24}(v_1 - k_{73}))\, x_3x_4 \\ & - k_{96} \exp(k_{25}(v_1 - k_{97}))\, x_3x_5 - k_{123} \exp(k_{147}(v_1 - k_{124}))\, x_3x_{10} \\ & - k_{148} \exp(k_{172}(v_1 - k_{149}))\, x_3x_{11}\end{aligned}$$

$$\begin{aligned}\dot{x}_4 = {} & k_{72}k_{74} \exp(k_{24}(v_1 - k_{73}))\, x_4x_3 + k_{75}k_{77} \exp(k_{24}(v_1 - k_{76}))\, x_4x_5 \\ & + k_{78}k_{80} \exp(k_{24}(v_1 - k_{79}))\, x_4x_6 + k_{81}k_{83} \exp(k_{24}(v_1 - k_{82}))\, x_4x_7 \\ & + k_{84}k_{86} \exp(k_{24}(v_1 - k_{85}))\, x_4x_8 + k_{87}k_{89} \exp(k_{24}(v_1 - k_{88}))\, x_4x_9 \\ & + k_{90}k_{92} \exp(k_{24}(v_1 - k_{91}))\, x_4x_{10} + k_{93}k_{95} \exp(k_{24}(v_1 - k_{94}))\, x_4x_{11} \\ & - k_{28} \exp(k_{24}(v_1 - k_{29}))\, x_4 - k_{48} \exp(k_{23}(v_1 - k_{49}))\, x_4x_3 \\ & - k_{99} \exp(k_{25}(v_1 - k_{100}))\, x_4x_5 - k_{126} \exp(k_{147}(v_1 - k_{127}))\, x_4x_{10} \\ & - k_{151} \exp(k_{172}(v_1 - k_{152}))\, x_4x_{11}\end{aligned}$$

$$\begin{aligned}\dot{x}_5 = {} & k_{96}k_{98} \exp(k_{25}(v_1 - k_{97}))\, x_5x_3 + k_{99}k_{101} \exp(k_{25}(v_1 - k_{100}))\, x_5x_4 \\ & + k_{102}k_{104} \exp(k_{25}(v_1 - k_{103}))\, x_5x_6 + k_{105}k_{107} \exp(k_{25}(v_1 - k_{106}))\, x_5x_7 \\ & + k_{108}k_{110} \exp(k_{25}(v_1 - k_{109}))\, x_5x_8 + k_{111}k_{113} \exp(k_{25}(v_1 - k_{112}))\, x_5x_9 \\ & + k_{114}k_{116} \exp(k_{25}(v_1 - k_{115}))\, x_5x_{10} + k_{117}k_{119} \exp(k_{25}(v_1 - k_{118}))\, x_5x_{11} \\ & - k_{30} \exp(k_{25}(v_1 - k_{31}))\, x_5 - k_{51} \exp(k_{23}(v_1 - k_{52}))\, x_5x_3 \\ & - k_{75} \exp(k_{24}(v_1 - k_{76}))\, x_5x_4 - k_{129} \exp(k_{147}(v_1 - k_{130}))\, x_5x_{10} \\ & - k_{154} \exp(k_{172}(v_1 - k_{155}))\, x_5x_{11}\end{aligned}$$

$$\begin{aligned}\dot{x}_6 = {} & k_{11}k_{44} \exp(k_{12}(v_1 - k_{13}))\, x_6 - k_{32} \exp(k_{12}(v_1 - k_{33}))\, x_6 \\ & - k_{54} \exp(k_{23}(v_1 - k_{55}))\, x_6x_3 - k_{78} \exp(k_{24}(v_1 - k_{79}))\, x_6x_4 \\ & - k_{102} \exp(k_{25}(v_1 - k_{103}))\, x_6x_5 - k_{132} \exp(k_{147}(v_1 - k_{133}))\, x_6x_{10} \\ & - k_{157} \exp(k_{172}(v_1 - k_{158}))\, x_6x_{11}\end{aligned}$$

$$\begin{aligned}\dot{x}_7 = {} & k_{14}k_{45} \exp(k_{15}(v_1 - k_{16}))\, x_7 - k_{34} \exp(k_{15}(v_1 - k_{35}))\, x_7 \\ & - k_{57} \exp(k_{23}(v_1 - k_{58}))\, x_7x_3 - k_{81} \exp(k_{24}(v_1 - k_{82}))\, x_7x_4 \\ & - k_{105} \exp(k_{25}(v_1 - k_{106}))\, x_7x_5 - k_{135} \exp(k_{147}(v_1 - k_{136}))\, x_7x_{10} \\ & - k_{160} \exp(k_{172}(v_1 - k_{161}))\, x_7x_{11}\end{aligned}$$

TABLE VIII *(continued)*

$$\dot{x}_8 = k_{17}k_{46}\exp(k_{18}(v_1 - k_{19}))\,x_8 - k_{36}\exp(k_{18}(v_1 - k_{37}))\,x_8 - k_{60}\exp(k_{23}(v_1 - k_{61}))\,x_8x_3 - k_{84}\exp(k_{24}(v_1 - k_{85}))\,x_8x_4 - k_{108}\exp(k_{25}(v_1 - k_{109}))\,x_8x_5 - k_{138}\exp(k_{147}(v_1 - k_{139}))\,x_8x_{10} - k_{163}\exp(k_{172}(v_1 - k_{164}))\,x_8x_{11}$$

$$\dot{x}_9 = k_{20}k_{47}\exp(k_{21}(v_1 - k_{22}))\,x_9 - k_{38}\exp(k_{21}(v_1 - k_{39}))\,x_9 - k_{63}\exp(k_{23}(v_1 - k_{64}))\,x_9x_3 - k_{87}\exp(k_{24}(v_1 - k_{88}))\,x_9x_4 - k_{111}\exp(k_{25}(v_1 - k_{112}))\,x_9x_5 - k_{141}\exp(k_{147}(v_1 - k_{142}))\,x_9x_{10} - k_{166}\exp(k_{172}(v_1 - k_{167}))\,x_9x_{11}$$

$$\dot{x}_{10} = k_{120}k_{122}\exp(k_{147}(v_1 - k_{121}))\,x_{10} + k_{123}k_{125}\exp(k_{147}(v_1 - k_{124}))\,x_{10}x_3 + k_{126}k_{128}\exp(k_{147}(v_1 - k_{127}))\,x_{10}x_4 + k_{129}k_{131}\exp(k_{147}(v_1 - k_{130}))\,x_{10}x_5 + k_{132}k_{134}\exp(k_{147}(v_1 - k_{133}))\,x_{10}x_6 + k_{135}k_{137}\exp(k_{147}(v_1 - k_{136}))\,x_{10}x_7 + k_{138}k_{140}\exp(k_{147}(v_1 - k_{139}))\,x_{10}x_8 + k_{141}k_{143}\exp(k_{147}(v_1 - k_{142}))\,x_{10}x_9 + k_{144}k_{146}\exp(k_{147}(v_1 - k_{145}))\,x_{10}x_{11} - k_{40}\exp(k_{147}(v_1 - k_{41}))\,x_{10} - k_{66}\exp(k_{23}(v_1 - k_{67}))\,x_{10}x_3 - k_{90}\exp(k_{24}(v_1 - k_{91}))\,x_{10}x_4 - k_{114}\exp(k_{25}(v_1 - k_{115}))\,x_{10}x_5 - k_{169}\exp(k_{172}(v_1 - k_{170}))\,x_{10}x_{11}$$

$$\dot{x}_{11} = k_{148}k_{150}\exp(k_{172}(v_1 - k_{149}))\,x_{11}x_3 + k_{151}k_{153}\exp(k_{172}(v_1 - k_{152}))\,x_{11}x_4 + k_{154}k_{156}\exp(k_{172}(v_1 - k_{155}))\,x_{11}x_5 + k_{157}k_{159}\exp(k_{172}(v_1 - k_{158}))\,x_{11}x_6 + k_{160}k_{162}\exp(k_{172}(v_1 - k_{161}))\,x_{11}x_7 + k_{163}k_{165}\exp(k_{172}(v_1 - k_{164}))\,x_{11}x_8 + k_{166}k_{168}\exp(k_{172}(v_1 - k_{167}))\,x_{11}x_9 + k_{169}k_{171}\exp(k_{172}(v_1 - k_{170}))\,x_{11}x_{10} - k_{42}\exp(k_{172}(v_1 - k_{43}))\,x_{11} - k_{69}\exp(k_{23}(v_1 - k_{70}))\,x_{11}x_3 - k_{93}\exp(k_{24}(v_1 - k_{94}))\,x_{11}x_4 - k_{117}\exp(k_{25}(v_1 - k_{118}))\,x_{11}x_5 - k_{144}\exp(k_{147}(v_1 - k_{145}))\,x_{11}x_{10}$$

2. *Analog Computer Simulation*

Once the model has been formulated as a set of ordinary differential equations, numerical solutions can often be computed by the process of analog computer simulation (e.g., Chapters 1 and 9). This is only feasible with rather simple models, but in these cases is extremely useful since the solutions are exact (within the errors introduced by electronic components).

This concludes the discussion of formulating mathematical models of dynamic ecological systems. A general view of the process of formulation, or "system identification," and the subsequent "system analysis" is given in Fig. 3. The problem of system identification consists of hypothesizing equations, measuring physical and biological constants, and the cyclic testing and modification of the system of equations until it is in an acceptable form. Thus, it is primarily a biological problem.

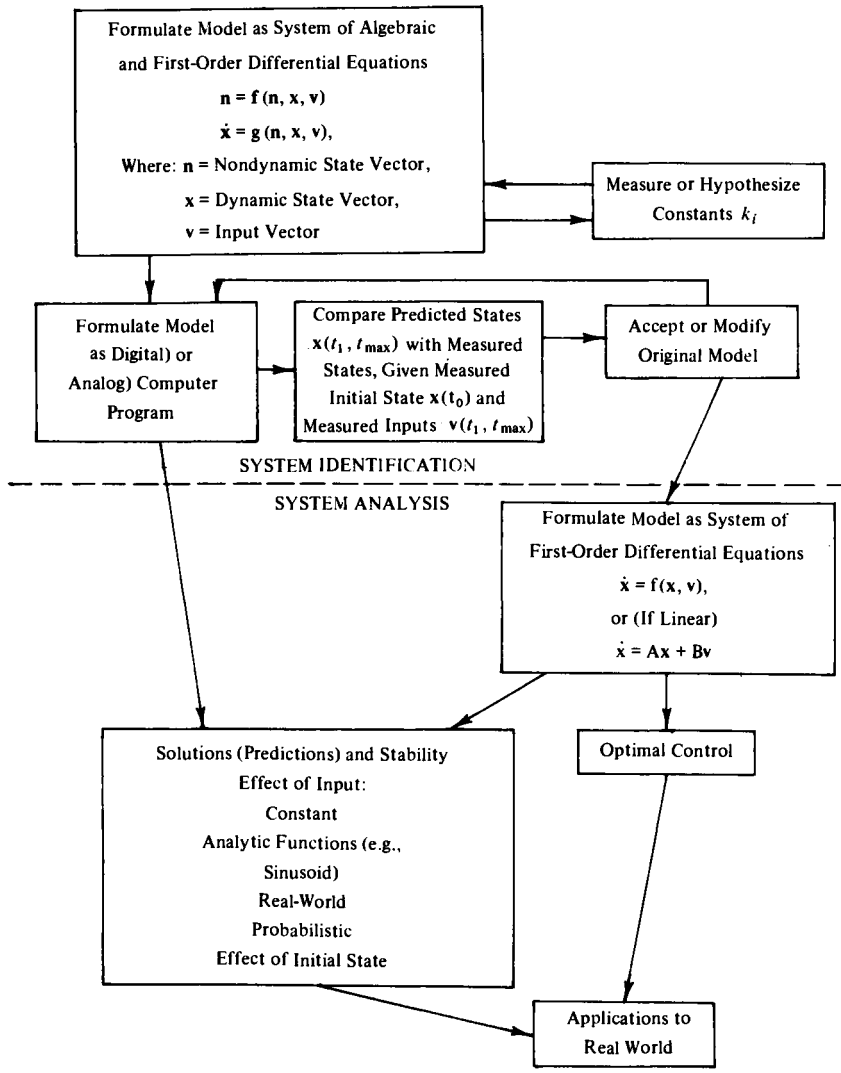

FIG. 3. System identification and system analysis.

On the other hand, system analysis is primarily a mathematical problem. It consists of starting with a mathematical model which has been accepted on biological grounds, and obtaining solutions and stability information from the model. These may be obtained analytically, but more commonly are obtained by some technique of numerical approximation. The information so obtained may then be used to make real-world predictions,

given real-world inputs, or may be used to select particular controllable input values which will produce an optimum behavior of the real-world system, i.e., optimal control. These are extremely important practical applications of the mathematical approach to biology, and perhaps its main justification.

In the third section of this chapter is presented a brief survey of mathematical techniques available for the analysis of continuous dynamic systems.

III. Analysis of Models of Dynamic Ecological Systems

The previous discussion describes formulation of an acceptable mathematical model in the form of a set of coupled first-order differential equations which define relationships among input variables and state variables. This is done by a process of system identification, in particular by cycles of hypothesis formation, direct measurement, and testing. This process lies in the realm of biology; it is the traditional method of empirical science.

Once the model has been accepted on biological grounds, it can be used for theoretical or applied purposes, in particular, for prediction and optimal control. This constitutes the subject of analysis of mathematical models, and lies primarily in the realm of mathematics. Of course, applications of mathematical conclusions to the real world lie again in the realm of biology.

We consider first the predictions, i.e., obtaining of solutions and solution behavior, especially stability, from the differential equations. In advanced works this is often called the "qualitative theory" or "geometric theory" of differential equations. Most of the material in such works is not useful to ecologists, who are usually concerned with complex multivariable systems; only material which seems immediately practical will be discussed here. We then will consider the subjects of optimal control and system optimization. These are of extreme practical importance, but because of their mathematical difficulty are treated very superficially.

This chapter is concerned only with continuous dynamic systems, and treats them with sets of coupled, first-order, ordinary differential equations in the state-variable form. (Any n-order ordinary differential equation can be reduced to a set of n first-order ordinary differential equations (Coddington, 1961).) Other approaches to such systems are possible, and this one should be justified. As an alternative to the state variable approach (i.e., the use of input and state variables or input, state, and output variables, the last algebraically defined on the input

and state variables), one could use the input–output approach. In the latter approach one uses only input and output variables. The system itself is viewed as a "black box," which converts inputs into outputs; no hypotheses are made on the structure of the system. For extremely simple systems this approach works quite well, but for most practical ecological systems, which are nonlinear and multivariable (multiple inputs and multiple outputs), this approach can only yield mathematically intractable and intellectually unsatisfying models. Indeed, most of the time we are primarily interested in the structure of the system, e.g., feeding rates and competition, rather than just the inputs, e.g., solar energy and precipitation, and the outputs, e.g., runoff and nutrient loss.

As an alternative to the differential equation approach, one could use the transfer function approach (e.g., Chapter 4). In the latter approach one expresses the relationship between an output (or state variable) and an input by a transfer function rather than a differential equation. A transfer function is the Laplace transform of the deviation of a system output (or state variable) from equilibrium divided by the Laplace transform of the deviation of a system input from equilibrium. In multivariable systems a matrix of transfer functions is used to express the relationships between individual outputs (or state variables) and each input. The advantage of the transfer function approach is that it substitutes algebraic equations for linear differential equations, greatly facilitating their solution. However, the transfer function approach is practical only for linear systems, and, even then, when the system is multivariable the use of transfer functions is cumbersome. Since most practical ecological models will turn out to be nonlinear, it may be unwise to place much emphasis on the transfer function approach.

Traditional engineering has placed great emphasis on the combination of input–output and transfer function approaches, and physiologically oriented biologists have eagerly adopted this combination in the last decade (Grodins, 1963; Milsum, 1966; Milhorn, 1966). It seems unlikely, however, that these approaches will prove very useful in solving ecological problems, for reasons cited above. Moreover, almost all modern literature on ordinary differential equations and optimal control is based on sets of first-order ordinary differential equations.

A. Solutions and Solution Behavior

1. *Deterministic Systems and Inputs*

a. *Linear Systems.* Linear systems are those which are defined by linear differential equations. Since analytical solutions are often easily found for these systems, and an extensive literature exists on the subject,

they are very attactive when the real-world problem can be satisfactorily represented linearly. However most practical ecological problems cannot satisfactorily be so represented, and doing so can lead to large differences between predicted solutions and stability, and real-world measurements. Gumowski and Mira (1968, pp. 3–7) have brought attention to the ill effects of the excessive concentration on linear systems in the field of engineering; their argument is valid for ecology as well. Nevertheless, linear system theory is useful in many cases, has been well developed (Zadeh and Desoer, 1963), and is a prerequisite to the understanding of nonlinear theory.

(i) *Solutions.* Linear systems are defined by equations of five basic types: the autonomous systems represented by Eqs. (10) and (11), nonautonomous systems as represented by Eq. (14), and

$$\dot{\mathbf{x}} = A(t)\,\mathbf{x}, \tag{16}$$

$$\dot{\mathbf{x}} = A(t)\,\mathbf{x} + \mathbf{f}(t). \tag{17}$$

As before, $\mathbf{x}$ is an n-dimensional state vector, A is an $n \times n$ constant matrix, $\mathbf{k}$ is an n-dimensional constant vector, $\mathbf{f}(t)$ is an n-dimensional vector-valued function of time, and $A(t)$ is an $n \times n$ time-varying matrix. Equation (17) is the general case from which the others may be derived; (11) and (14) are the equations in which we are usually interested. Input to the system is represented by $\mathbf{k}$ or $\mathbf{f}(t)$; the former is used when input is constant and the latter when input is time varying. Both are the equivalents of $B\mathbf{v}(t)$ in Eq. (15). The latter formulation is necessitated by the fact that in ecological problems we usually must deal with several different input variables. When the input variables are constant, $B\mathbf{v}(t) = \mathbf{k}$; when at least one input variable is time varying, $B\mathbf{v}(t) = \mathbf{f}(t)$.

Note that the difference between autonomous and nonautonomous systems is not whether they have an input, but whether the time-derivative of the state vector is an explicit function of time. Practical nonautonomous systems are extremely difficult to solve, and are usually approximated by Eq. (11). Equations (16) and (17) are linear equations with time-varying (or "variable," as opposed to "constant") coefficients. They represent what I have been calling "nonexplanatory" or "noncausal" models, and thus do not properly concern us here. Their solutions are almost always obtained by numerical approximation, and they are discussed by DeRusso *et al.* (1965, pp. 362–394) and Schwarz and Friedland (1965, pp. 114–118). Thus, for most ecological problems the linear mathematical model is of the form of Eq. (15).

The solution, or "transient response" (so called because the system responds to an input, as the system approaches steady state), of the

first-order vector differential equation (15) is analogous to solution of the corresponding first-order scalar differential equation

$$\dot{x} = ax + bv(t). \tag{18}$$

The solution to (18) is

$$x(t) = e^{at}x(0) + e^{at}\int_0^t e^{-a\tau}bv(\tau)\,d\tau. \tag{19}$$

Of course, in the differential equations literature (e.g., Coddington, 1961) $f(t)$ is used rather than $bv(t)$. Similarly, the solution to the vector equation (15) is

$$\mathbf{x}(t) = e^{At}\mathbf{x}(0) + e^{At}\int_0^t e^{-A\tau}B\mathbf{v}(\tau)\,d\tau. \tag{20}$$

The second right-hand term of (20), with the first exponential moved into the integral,

$$\int_0^t e^{A(t-\tau)}B\mathbf{v}(\tau)\,d\tau, \tag{21}$$

represents the effect of the input on the solution. In engineering literature this expression is called the "convolution integral." (When the matrix A is time varying, thus $A(t)$, it is the more general "superposition integral.") The first right-hand term of (20) represents the effect of the initial state, $\mathbf{x}(0)$.

When the input is time varying, evaluation of the convolution integral is usually extremely difficult, and thus exact solutions are rather rare. On the other hand, when the input is constant, the convolution integral simplifies nicely, yielding the solution

$$\mathbf{x}(t) = e^{At}\mathbf{x}(0) + (e^{At} - I)\,A^{-1}\mathbf{k}, \tag{22}$$

where I is the n-dimensional unit (or identity) matrix, and $\mathbf{k} = B\mathbf{v}$. (This is done by integrating the infinite series expression for the matrix exponential in (20) and substituting (cf. DeRusso *et al.*, 1965, p. 287).) A convenient digital computer program, MATEXP, for obtaining numerical solutions to the constant input form of (15) using (22) (Ball and Adams, 1967) was discussed in Chapter 1.

When the input is time varying, an approximate numerical solution to (15) can be obtained by using (22) in short time-steps, during each of which the input is made constant. This also can be done with the Ball and Adams (1967) program.

While the above discussion covers the most straightforward method of obtaining the solution, or transient response, of the mathematical model (15), the engineering literature abounds with other methods and concepts. Figure 4 represents an attempt to bring these together to indicate their relationships with one another. In particular, the figure shows the intimate relationship between the differential equation (to the left) and the transfer function (to the right) approaches.

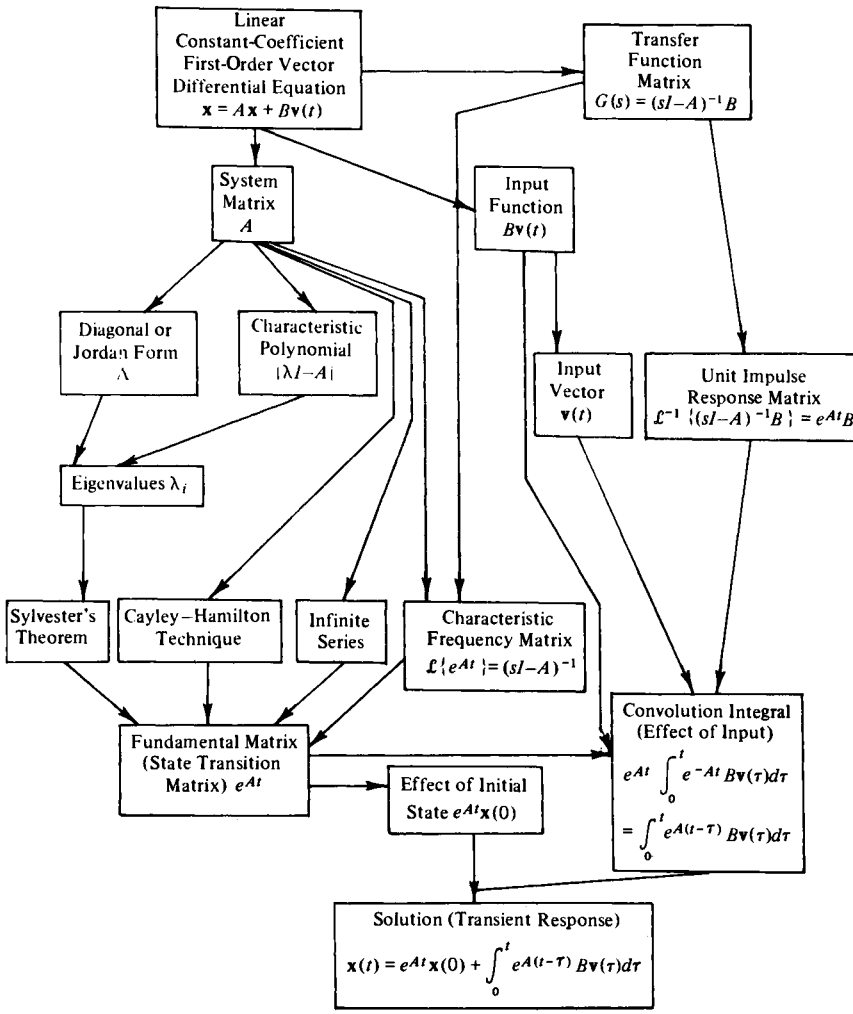

FIG. 4. Linear system transient analysis.

Note that the effect of the input is calculated by means of the convolution integral whether one uses the basic differential equation approach or the more specialized transfer function approach. An important difference between these two approaches is that the transfer function approach does not take into account the initial state (or "initial conditions"). This is because the transfer function approach derives from electrical engineering experience, where the initial state is usually either zero or equilibrium (in which case deviations from equilibrium are of interest, and equilibrium is defined to be zero). Since the initial state in most ecological systems rarely is zero (actually, the zero vector) or known to be equilibrium, and in view of earlier arguments, this approach is not to be recommended.

Note also that there are at least four different methods of obtaining the fundamental matrix (state transition matrix) e^{At} (a matrix exponential). The infinite series (Taylor series) expansion is best suited to the digital computer, and is the method used by Ball and Adams (1967). If one is interested in questions of stability, then he will want to use Sylvester's theorem after calculating the eigenvalues (characteristic values, characteristic roots, latent roots) λ_i of the system matrix A. The eigenvalues of the differential equation approach are equal to the "poles" s_i of the transfer function approach.

The analogy between solutions to vector and scalar differential equations has been made. Perhaps a comment on the analogy between the vector and scalar transfer function is in order. The transfer function of the scalar differential equation (18) is $b/(s - a)$, or $(s - a)^{-1}b$. The transfer function matrix of the vector differential equation (15) is the comparable $(sI - A)^{-1}B$. Further discussion of the concepts appearing in Fig. 4 may be found in the texts by De Russo *et al.*, (1965) and Schwarz and Friedland (1965), among others.

A particular type of solution, of some potential in ecology, is the "frequency response." In frequency analysis the system is assumed to be in a stable equilibrium, with a constant equilibrium input vector and a constant equilibrium state vector. (Thus it is sometimes called "steady-state analysis.") The frequency response describes the deviations of the state vector from equilibrium in response to a sinusoidal deviation of one input variable from equilibrium. The response of the state vector is a sinusoidal deviation from its equilibrium, with a particular gain (in general different for each state variable) and phase angle (also in general different for each variable). (The gain is the ratio of the amplitude of the response to the amplitude of the input; the phase angle is the phase shift.) In linear systems (to which frequency analysis is usually limited), the frequency of the response is the same as the frequency of the input

signal. The input sinusoidal deviation is completely characterized by its frequency.

Actual calculation of the frequency response involves the transfer function and elementary complex algebra. Further explanation of the method, and a digital computer program for calculating the frequency response of multivariable systems may be found in Kerlin and Lucius (1966). A frequency-response analysis of magnesium cycling in a tropical moist forest is presented in Volume II, Chapter 3 of this work.

(ii) *Stability.* (a) *Definitions of stability (linear and nonlinear).* The situation often arises that we are interested not in particular numerical solutions to a mathematical model, but in qualitative behavior of the model, and in particular whether the system will "blow up" in time. Thus, we become interested in system stability. The stability concept, particularly concerning ecological systems, means many different things to different people. However since we are dealing with differential equations in the state-variable form, our options are considerably limited.

To obtain a convenient intuitive feel for stability, we introduce a geometric interpretation of the state of a system. At any given time the state of a system is represented by the value of its n-dimensional state vector $\mathbf{x}$. Thus, at any given time the state can be represented as a point in the n-dimensional vector space, "state space" or "phase space," each of whose axes represents the scale of values for one of the n state variables x_i. A solution to the system describes the "trajectory" (or "motion") in state space of the state vector with passage of time, from a particular initial state (where the state vector is at "time zero"). An "equilibrium state" ("steady state," "equilibrium point," "critical point," "singular point") $\mathbf{x}_e$ is any state in which the system remains indefinitely with the passage of time, i.e., at which $\dot{\mathbf{x}} = \mathbf{0}$. Stability is usually defined with reference to the equilibrium states.

In autonomous linear systems the equilibrium state is unique, i.e., there is but one. For systems without an input, Eq. (10), it is the origin or zero vector $\mathbf{0}$; for systems with a constant input, Eq. (11), it is the vector $-A^{-1}\mathbf{k}$. Nonautonomous linear systems, Eqs. (14), (16), and (17), in general do not have equilibrium states (as defined above). Nonlinear systems may have no, one, or several equilibrium states.

The distance between two points $(\mathbf{x}_1, \mathbf{x}_2)$ in state space is measured by the Euclidean "norm," $|\mathbf{x}_2 - \mathbf{x}_1|$. Thus, one may consider the concept of a "neighborhood" (or "open ball") of an equilibrium state $\mathbf{x}_e$. A neighborhood is the set of all points which lie less than a fixed distance ϵ from $\mathbf{x}_e$, i.e., all points for which $|\mathbf{x} - \mathbf{x}_e| < \epsilon$.

We are now in a position to define stability, as it is usually treated

in engineering and differential equations, i.e., in the "Lyapunov sense." An equilibrium state is "stable" if an initial state within a small neighborhood of the equilibrium state results in a trajectory which remains within another small neighborhood of that equilibrium state. The initial state is thus a perturbation from the equilibrium state, e.g., the result of some sudden disturbance to an ecological system in equilibrium. An equilibrium state is "asymptotically stable" if (1) it is stable, and (2) the initial state within a small neighborhood of the equilibrium state results in a trajectory which approaches the equilibrium state as time approaches infinity (De Russo *et al.*, 1965, pp. 503–504). Obviously the latter is a much stronger type of stability.

This concept of stability is a local one, i.e., applicable only within a small neighborhood of each equilibrium state. This restriction leads to problems in nonlinear systems. But in linear systems things work out nicely, since the "neighborhood" constitutes the whole state space! Thus, stability of a linear system is a property of the system itself, rather than of any particular equilibrium state (DeRusso *et al.*, 1965, p. 501). Moreover, if a linear system is autonomous it has only one equilibrium state.

(b) *Ecological significance of stability (linear and nonlinear).* It is clear from the previous definitions that stability is a property of the model, stability being operationally defined (on the model) in a particular way. This indicates that stability is a variable, in this case with only two values, + and −. The same is true of asymptotic stability; likewise with real-world ecological systems. Stability is a variable which, in order to have any practical meaning, must be operationally defined, i.e., must be associated with a set of instructions on how to measure it. There are infinitely many possible measures of stability, each of them defining a different variable, or concept; there is no such thing as "real" or "true" stability any more than there is a "real green" or "true short". One defines stability to suit one's purposes, e.g., the definitions of MacArthur (1955) and of Hairston *et al.* (1968).

Once one has a satisfactory definition of the variable, "stability," then he may hypothesize and test relationships between this stability and other operationally defined variables, e.g., diversity or species number. This is fair game, and may prove to be useful in ecology. Hairston *et al.* have tested a hypothesized relationship between their "stability" and a variable which is MacArthur's "stability." Their negative results say nothing about the validity of MacArthur's definition, since definitions are not testable, no matter how psychologically unsatisfying they are. Their results do question the relationship between stability and diversity, however. (This discussion is not to lead to the conclusion that I feel

that one operational definition of a variable is as good as another. I am only discussing the logical status of the definitions. On grounds of practical utility and esthetics, different definitions of variables are not equally good.) [The subject of stability in ecological systems has been recently discussed in a Brookhaven Symposium in Biology (1969).]

Getting back to the mathematical model and Lyapunov stability (a special type of stability), the claim might be made that testing of a system (or individual equilibria) for stability may well not be relevant. This is because the process of system identification earlier would have resulted in a model which yielded acceptable state variable behavior for the time period of interest (the domain of the model). Whether the system blew up beyond this time period might not be of concern. However, it might be feasible to analyze hypothetical models *before* system identification, and use only those models proved stable for infinite time. These models would be more appealing in some ways, but the selection process might inhibit flexibility in choosing biologically meaningful and realistic hypotheses. For example, some ecological phenomena might be described by models not stable over a long period of time, such as the dynamics of a plankton bloom described by a model with a short time domain.

Perhaps the major potential of stability analysis is in the design of, or modification of, ecosystems for practical purposes, e.g., agriculture and silviculture, pollution control, and satellites. Given an acceptable (on the basis of past experience) form for a mathematical model, one could select values of its parameters (constants) which would result in the model possessing stability of a desired type.

(c) *Stability criteria.* For linear systems the question of whether a system possesses Lyapunov stability is answered in a straightforward manner. The analysis centers on the autonomous system without any input,

$$\dot{\mathbf{x}} = A\mathbf{x}. \tag{23}$$

From the $n \times n$ system matrix A can be calculated n eigenvalues; these are equivalent to the poles which derive from the transfer function approach (they are calculated the same way, and used for the same purposes). The calculation is most easily done by one of the existing digital computer packaged programs (IBM Share Program 1578; Parlett, 1962). In general the eigenvalues are complex, i.e., they have a real part and an imaginary part. If all of the eigenvalues have negative real parts, the system (23) is asymptotically stable. If some of the eigenvalues have zero real parts (and are not repeated, i.e., are distinct, which is the usual case), and the rest have negative real parts, the

system (23) is stable. Otherwise, the system (23) is unstable. These criteria are intuitively reasonable when one realizes that the solution to Eq. (23) consists of exponential terms, in which the eigenvalues are the exponents. The nature of the imaginary parts of the eigenvalues does not affect the stability criteria; their presence, i.e., their nonzero values, only means that the solution is periodic.

Before the widespread use of large digital computers, numerous alternatives to the difficult calculation of eigenvalues were used by engineers in stability analysis of linear systems. None of these furnishes any more stability information than does the calculation of eigenvalues. Among the more important of these methods are the Routh–Hurwitz method and its Lienard–Chipart simplification, and several graphical methods, e.g., the Nyquist method, the root–locus method, and the Mikhailov method (Schwarz and Friedland, 1965, pp. 399–433).

When one wishes to compare the relative stability of several systems, the concept of "degree of stability" is very useful. This is defined as the absolute value of the least negative real part of the eigenvalues, of an asymptotically stable system. It is a measure of the speed at which the state vector returns to equilibrium after a perturbation. The degree of stability is to be used with caution, however, since the speed of return to equilibrium is affected by the eigenvectors, as well as the eigenvalues.

So far, the discussion has been limited to the autonomous system without any input, Eq. (23). This is because the stability of the fixed system with input, i.e.,

$$\dot{\mathbf{x}} = A\mathbf{x} + B\mathbf{v}(t), \tag{24}$$

depends upon the stability of the system without input. In other words, the stability depends upon the nature of the constant system matrix A. If the input is constant, we have the autonomous system (11); if the input is time-varying, we have the nonautonomous system (14). In either case, if the input is bounded (never becomes infinite), the system with input is stable if the system without input is asymptotically stable (Schwarz and Friedland, 1965, pp. 382–384).

When one is dealing with time-varying systems, i.e., Eqs. (16) and (17), the situation is much more difficult. In this case, stability must be tested for by Lyapunov's "direct" (or "second") method (Schwarz and Friedland, 1965, pp. 390–394). This method is used primarily in testing nonlinear systems for stability, and is discussed below.

b. *Nonlinear Systems.* (i) *Solutions.* Nonlinear systems are of two basic types, autonomous systems,

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}), \tag{25}$$

which would include those without any input (and rarely of ecological interest) and those with constant input, and nonautonomous systems,

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, t), \tag{26}$$

which would include those with time-varying input. When we are dealing with "explanatory" or "causal" models, all effects of time are through the input vector $\mathbf{v}$. Thus, our mathematical model is usually of the form

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{v}), \tag{27}$$

but can be converted to the form of Eq. (26) for purposes of analysis, since $\mathbf{v}$ is a function of time. (Where $\mathbf{v}$ is in the form of a table of numerical values or of noncontinuous functions, this conversion will probably not be fruitful. This is the situation with most practical ecological models.)

Although exact literal solutions of Eq. (26) are usually not possible to obtain, the theory of differential equations provides us with an extremely important existence and uniqueness theorem (Sanchez, 1968, p. 8–10). (Much of mathematics is concerned with the subject of "existence and uniqueness," which is simply proving that a mathematical structure having a particular property exists, and that it is unique, even if the form of that structure is not known.) The theorem states that given Eq. (26) and that f_i and the partial derivatives, $\partial f_i/\partial x_j$, $i, j = 1, 2, \ldots, n$, are continuous, then for every initial state, $\mathbf{x}(t_0)$, and initial time t_0, there exists a unique solution $\mathbf{x}(t)$ to Eq. (26).

In most continuous dynamic systems, the hypotheses of the theorems are satisfied. If in a model the partial derivatives are not continuous, a solution would still exist, but it might not be unique.

The theorem justifies analysis of the behavior, particularly stability, of a solution, given particular initial conditions, even though we are unable to obtain the exact solution. Perhaps more important, uniqueness justifies our obtaining the approximate solution by numerical approximation, which would lead to trouble if two or more solutions existed (since we would calculate only one of them).

Since most ecological models are of high order and rather complex, exact literal solutions are usually not possible to obtain, and numerical approximation must be resorted to. As stated previously, a particularly convenient numerical approximation technique for systems of first-order ordinary differential equations is the fourth-order Runge–Kutta method.

The Runge–Kutta method approximates solutions by time increments, as does the Euler method. The fourth-order Runge–Kutta approximation for the scalar differential equation

$$\dot{x} = f(x, t), \tag{28}$$

with the initial values x_0 and t_0, and time increment Δt, is obtained in the following manner (see also Chapter 1):

$$\begin{aligned} k_1 &= \Delta t f(x_0, t_0) \\ k_2 &= \Delta t f(x_0 + \tfrac{1}{2}k_1, t_0 + \tfrac{1}{2}\Delta t) \\ k_3 &= \Delta t f(x_0 + \tfrac{1}{2}k_2, t_0 + \tfrac{1}{2}\Delta t) \\ k_4 &= \Delta t f(x_0 + k_3, t_0 + \Delta t) \end{aligned} \tag{29}$$

$$\Delta x \doteq \tfrac{1}{6}(k_1 + 2k_2 + 2k_3 + k_4) \tag{30}$$

$$x \doteq x_0 + \Delta x, \tag{31}$$

where x is the approximated value of the dependent variable at the end of the time increment Δt.

We wish to make use of the approximation in the vector case, and where all effects of time are through the input vector, i.e.,

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{v}). \tag{32}$$

The values of the input variables are assumed to remain constant during each calculation increment; this assumption is usually matched by the restricted availability of input data. To obtain the numerical approximation by use of a Fortran program, it is convenient to use a subroutine to calculate values of the function **f**, since this is done four times within each calculation increment (each time with a different argument). Each calculation increment is done by one run through a large DO loop, just as with the Euler method described previously.

One possible Fortran implementation within the large DO loop is the following (each equation actually represents a series of statements performed by a DO loop or subroutine as indicated):

$\mathbf{rx} = \mathbf{x}$	(DO Loop)
$\mathbf{k0} = \mathbf{f}(\mathbf{x}, \mathbf{v})$	(Subroutine)
$\mathbf{k1} = \mathbf{k0}$	(DO Loop)
$\mathbf{x} = \mathbf{rx} + \frac{1}{2}\mathbf{k1}$	(DO Loop)
$\mathbf{k0} = \mathbf{f}(\mathbf{x}, \mathbf{v})$	(Subroutine)
$\mathbf{k2} = \mathbf{k0}$	(DO Loop)
$\mathbf{x} = \mathbf{rx} + \frac{1}{2}\mathbf{k2}$	(DO Loop)
$\mathbf{k0} = \mathbf{f}(\mathbf{x}, \mathbf{v})$	(Subroutine)
$\mathbf{k3} = \mathbf{k0}$	(DO Loop)
$\mathbf{x} = \mathbf{rx} + \mathbf{k3}$	(DO Loop)
$\mathbf{k0} = \mathbf{f}(\mathbf{x}, \mathbf{v})$	(Subroutine)
$\mathbf{k4} = \mathbf{k0}$	(DO Loop)
$\mathbf{dx} = \frac{1}{6}(\mathbf{k1} + 2\mathbf{k2} + 2\mathbf{k3} + \mathbf{k4})$	(DO Loop)
$\mathbf{x} = \mathbf{rx} + \mathbf{dx}$	(DO Loop),

where **rx**, **k0**, **k1**, **k2**, **k3**,**k4**, and **dx** are vectors of the same dimension as **x**. (The "*k* variables" should be typed "real.") If the time increment is not unity, then **f**(**x**, **v**) in the subroutine must be multiplied by it. There may be more efficient implementations of the Runge–Kutta method to obtain approximate numerical solutions of Eq. (32) but the structure of this one is particularly clear.

(ii) *Stability.* (a) *Linear versus nonlinear systems* (DeRusso *et al.*, 1965, pp. 501–502). As was mentioned previously, the stability of fixed nonautonomous linear systems depends upon the stability of the corresponding autonomous linear systems. Autonomous linear systems have but one equilibrium state, and the neighborhood of this equilibrium state, for which stability is defined, includes the whole state space. Thus, for fixed linear systems stability is a property of the system itself, and not just of a particular equilibrium state. The perturbation (or new initial state) may lie anywhere in the state space.

Stability in nonlinear systems is a different matter. Nonlinear systems may have several equilibrium states, each with its own stability properties within its own neighborhood. Some equilibrium states may be asymptotically stable, some stable, and some unstable. Thus, behavior of the solution depends upon the location of the perturbation in the state space, i.e., the initial state vector value. This is why the behavior of nonlinear systems depends upon their initial states. From a particular initial state the trajectory may move through state space to one equilibrium state, to another equilibrium state, to infinity, or even into a "cycle" (which is the trajectory of a periodic or oscillating solution), depending upon the value of the initial state.

(b) *Autonomous systems.* We are concerned here with the stability of systems of the form of Eq. (25), i.e., systems with no input or with constant input. As is true (to a lesser extent) in linear systems, the theory of nonautonomous systems has been developed to a much lower degree than that of autonomous systems. Consequently, most available tools deal with autonomous systems. This is unfortunate, since most practical ecological problems are formulated as nonautonomous systems.

Phase plane analysis. When the system consits of only two state variables, the behavior of the system may be graphically analyzed by direct observation of the trajectories (after they have been calculated and plotted) in state space (or "phase space"). In this case, the state space is 2-dimensional, and thus a state plane (or "phase plane"), and the analysis termed "phase plane analysis." (The term "phase" comes from the phase angle of the polar coordinate analysis of second-order systems in engineering.)

The distinction between a "trajectory" and a "solution" should be

kept in mind. A solution of an n-dimensional system is an integral curve in $(n + 1)$-space, a space with n axes for the n state variables and one axis for time. The exact position of the integral curve depends upon the position of the fixed point, usually the initial state and initial time, through which the curve passes. A trajectory (or "motion") of an n-dimensional system is a curve in n-space, state space. The exact position of the trajectory, likewise, depends upon the position of the fixed point, usually the initial state (LaSalle and Lefschetz, 1961, p. 24). Each trajectory is a parametric curve that may represent several solutions, depending upon the time associated with each point of the trajectory (Sanchez, 1968, p. 70).

The behavior of trajectories near each equilibrium state determines the stability near that equilibrium state. If trajectories continuously approach an equilibrium state, that equilibrium is asymptotically stable. If they continuously diverge, the equilibrium is unstable. And if they remain within a small neighborhood, but do not approach the equilibrium, it is just stable.

Trajectory behavior near equilibrium states can be classified into several basic types. A "center" is a set of concentric cycles (closed curves) around the equilibrium, and indicates that the equilibrium possesses stability, but not asymptotic stability. A "stable focus" is a set of converging spirals, indicating asymptotic stability. (Note: the direction of a trajectory is always that of increasing time.) An "unstable focus" is a set of diverging spirals. A "stable node" is a set of converging radii, indicating asymptotic stability. An "unstable node" is a set of diverging radii. A "saddle point" is a set of radii converging in some areas and diverging in others, indicating instability. Finally, a "limit cycle" is an isolated cycle around an equilibrium. By "isolated" is meant that trajectory behavior inside and outside of the limit cycle is not in the form of other cycles. If the trajectories on both sides of the limit cycle converge to the limit cycle, the limit cycle is stable (and the enclosed equilibrium is an unstable focus or node). If the trajectories on both sides of the limit cycle diverge from the limit cycle, the limit cycle is unstable (and the enclosed equilibrium is a stable focus or node). If the trajectories are convergent on one side and divergent on the other (two possibilities), the limit cycle is "semistable."

Interesting as it is, phase plane analysis is practically limited to autonomous 2-dimensional systems, and thus will probably find little use in the analysis of complex ecological systems. The reader may find more details on the subject (including methods for the calculation of the trajectories) in the text by DeRusso *et al.* (1965, pp. 470–498).

The traditional graphical analysis of predator–prey and competition

models is an ecological example of phase plane analysis (e.g., Slobodkin, 1961). Another example comes from the pine–mor food web model. The solutions for Collembola and Lithobiomorpha are periodic (oscillating) curves of increasing amplitude; the Lithobiomorpha maxima follow the Collembola maxima. This behavior could be interpreted in the phase plane, defined by a horizontal Collembola axis and a vertical Lithobiomorpha axis, as a trajectory forming an unstable counterclockwise focus around an unstable equilibrium. (Of course in the complete state space of the model this trajectory would be rather difficult to visualize.) This is an example of the common unstable predator–prey cycle.

Variational equations (perturbation equations, linearization). Within a small neighborhood of an equilibrium state, a nonlinear system behaves similarly to a corresponding linear system. Thus, stability within the neighborhood of equilibrium for the nonlinear system can be estimated from stability of the corresponding linear system (a different one for each equilibrium). The ith linear system corresponding to the ith equilibrium state of the nonlinear system (25) is calculated by expanding the components of $\mathbf{f}(\mathbf{x})$ in a Taylor series about the ith equilibrium state, and ignoring the high-order terms of the expansion. This results in the homogeneous, constant-coefficient, linear system,

$$\frac{d}{dt}(\mathbf{x} - \mathbf{x}_{e_i}) = J(\mathbf{x}_{e_i})(\mathbf{x} - \mathbf{x}_{e_i}), \tag{33}$$

where $J(\mathbf{x}_{e_i})$ is the Jacobian matrix of $\mathbf{f}(\mathbf{x})$, evaluated at the ith equilibrium state $\mathbf{x}_{e_i}$ (DeRusso *et al.*, 1965, pp. 479–488).

The Jacobian matrix is a constant $n \times n$ matrix. Thus its eigenvalues may be computed, and used for stability judgements. A simpler alternative to the calculation of the eigenvalues of the Jacobian matrix has been developed by Krasovskii (Kalman and Bertram, 1960). Krasovskii proved that if the matrix $-(J + J^T)$, where J^T is the transpose of J, is positive definite (see below), then the linear approximation is asymptotically stable.

The analysis of stability based on the linear approximation is valid only within an infinitesimal neighborhood about an equilibrium state. If the perturbation is outside this neighborhood, the resulting trajectory may be stable or unstable, but the linear analysis tells us nothing, not even the size of the neighborhood. Thus, stability analysis by the variational equations is often not practical (LaSalle and Lefschetz, 1961, p. 57, Gumowski and Mira, 1968, pp. 10–11).

Lyapunov's direct (second) method (DeRusso *et al.*, 1965, pp. 498–527; LaSalle and Lefschetz, 1961). Most nonlinear stability analyses in engineering are based upon the methods originally published by Lyapunov in 1892 (Lyapunov, 1907). An intuitive understanding of the ideas underlying the method can be gained by considering a function defined on the state variables of the system, and physically representing the energy of the system (in ecological systems the function might be thought to represent biomass). If the time rate of change of energy is negative for every possible state except for one equilibrium state, then the energy will continually decrease until it reaches its minimum at the equilibrium state. The system, in this case, is intuitively felt to be stable (in particular, asymptotically stable).

Usually there is no simple physical interpretation for the function, "energy," and an arbitrary mathematical scalar function of the state variables is used in the analysis. This function is a "Lyapunov V-function" or, simply, a "Lyapunov function." Unfortunately, there are no general methods for defining Lyapunov functions, and this is a major limitation of the method.

In stability analysis it is much more convenient to deal with stability of the state space origin than with other equilibrium points (states). Thus, in the analysis it is usually understood that the state space origin has been translocated to the point representing the equilibrium state under consideration. This amounts to replacing the state variables with their corresponding perturbation variables, and all states henceforth represent perturbations from a particular equilibrium state. This is exactly what was done in the previous section on the variational equations. This entails no special assumptions; it is simply a shift of axes for the sake of simplification.

Before stating Lyapunov's theorems it is necessary to make a few definitions. The function $V(\mathbf{x})$ is "semidefinite" in a neighborhood about the origin if it is continuous and has continuous first partial derivatives, and if it has the same sign throughout the neighborhood, except where it is zero. Thus $V(\mathbf{x})$ can be positive semidefinite or negative semidefinite. The function $V(\mathbf{x})$ is "definite" in a neighborhood about the origin if it is continuous and has continuous first partial derivatives, and if it has the same sign throughout the neighborhood, and is nowhere zero, except possibly at the origin. Therefore, $V(\mathbf{x})$ can be positive definite or negative definite. The time derivative of $V(\mathbf{x})$, $\dot{V}(\mathbf{x})$, is defined in the normal fashion for scalar functions of vectors

$$\dot{V}(\mathbf{x}) = \frac{\partial V}{\partial x_1}\dot{x}_1 + \frac{\partial V}{\partial x_2}\dot{x}_2 + \cdots + \frac{\partial V}{\partial x_n}\dot{x}_n\,, \tag{34}$$

or, in terms of the inner ("dot," "scalar") product with the gradient of $V(\mathbf{x})$

$$\dot{V}(\mathbf{x}) = \text{grad } V(\mathbf{x}) \cdot \dot{\mathbf{x}} = \text{grad } V(\mathbf{x}) \cdot \mathbf{f}(\mathbf{x}), \tag{35}$$

assuming the system to be described by Eq. (25). Then $\dot{V}(\mathbf{x})$ can be evaluated directly from $V(\mathbf{x})$ and Eq. (25), without obtaining solutions of Eq. (25).

We are now in a position to state the Lyapunov theorems. It must be kept in mind that the state variables now represent perturbations from a particular equilibrium, and that the stability is with reference to that equilibrium.

Given the system described by Eq. (25), the equilibrium is stable if it is possible to determine a definite $V(\mathbf{x})$, such that $V(\mathbf{0}) = 0$ and $\dot{V}(\mathbf{x})$ is semidefinite of sign opposite to $V(\mathbf{x})$. Such a $V(\mathbf{x})$ is a Lyapunov function. The Lyapunov theorem for asymptotic stability is similar. Given the system described by Eq. (25), the equilibrium is asymptotically stable if it is possible to determine a definite $V(\mathbf{x})$, such that $V(\mathbf{0}) = 0$ and $\dot{V}(\mathbf{x})$ is definite of sign opposite to $V(\mathbf{x})$. The Lyapunov function is usually defined so that it is positive; thus $\dot{V}(\mathbf{x})$ is negative or zero. Thinking of the Lyapunov function as "energy" again, the theorems state that for the trajectory resulting from a perturbation within a neighborhood of an equilibrium, if the "energy" does not exceed its original finite value then the equilibrium is stable, and if the "energy" approaches zero then the equilibrium is asymptotically stable.

As with the variational equations, conclusions about stability from the Lyapunov theorems are valid only when the perturbation lies within a small neighborhood of the equilibrium, i.e., the stability is local. What one usually wants in practical problems is asymptotic stability "in the large," i.e., asymptotic stability no matter where in state space the initial perturbation lies. This often is true of linear systems, and occurs in nonlinear systems if the following condition is satisfied. If the system described by Eq. (25) is asymptotically stable, and if $V(\mathbf{x})$ approaches infinity as the norm of $\mathbf{x}$, $|\mathbf{x}|$, approaches infinity, then the equilibrium is asymptotically stable in the large.

As mentioned previously, there are no general methods for defining Lyapunov functions; it is partly a matter of experience. Several specific methods have been developed, however, and an introduction to the literature may be found in DeRusso *et al.* (1965, pp. 524–527).

First canonic form of Lur'e and Popov's method (DeRusso *et al.*, 1965, pp. 513–517; LaSalle and Lefschetz, 1961, pp. 75–105). These are methods useful where the nonlinear system can be manipulated into

an almost linear form, and thus apply only to a narrow class of nonlinear systems.

Practical stability (total stability). Up to now we have been dealing with the stability of trajectories resulting from a single perturbation, i.e., an impulse shifting the state away from equilibrium. The system has been assumed to be undisturbed following the initial perturbation. In real-world systems this situation is extremely unlikely; perturbations are likely to be acting constantly. A number of theorems have been developed to deal with constantly acting perturbations (DeRusso *et al.*, 1965, pp. 518–519; LaSalle and Lefschetz, 1961, pp. 121–126). They conclude that the trajectory remains near the equilibrium if it is not too far away intially, and if the perturbations are not too large.

Since the perturbations are acting constantly on these autonomous systems, it is possible that they might be reformulated and considered as nonautonomous systems, and handled as such. However, this would require knowledge of the mathematical form of the perturbation.

(c) *Nonautonomous systems.* We are concerned here with the stability of systems of the form of Eq. (26), i.e., systems with time-varying input. As was mentioned previously, the theory of nonautonomous systems has been developed to a much lower degree than that of autonomous systems, and most practical ecological problems are formulated as nonautonomous systems.

Lyapunov's direct (second) method. With a slight modification of the requirements of the Lyapunov function (now $V(\mathbf{x}, t)$), and of the asymptotic stability theorem, Lyapunov's method may be used for nonautonomous systems (DeRusso *et al.*, 1965, pp. 527–529). Unfortunately, the definition of Lyapunov functions for nonautonomous systems is even more difficult than for autonomous systems, and thus the method has proved to be of limited usefulness.

Eventual stability (DeRusso *et al.*, 1965, pp. 529–531). The concepts of stability used in the discussion heretofore were in the Lyapunov sense, i.e., they were concerned with the system trajectory following a perturbation from a particular equilibrium state. However, in many (perhaps most) ecological systems the input is time-varying in such a way that no equilibrium state exists, and thus the Lyapunov concepts cannot be used. (This also puts into question much discussion in the ecological literature which assumes the existence of an equilibrium or steady state, e.g., in the calculation of many rates.)

Lyapunov's direct method has been extended to such systems by LaSalle and Rath (1963) to produce the concept of "eventual stability," which, in general, states that if a system behaves properly for a sufficiently long time, it can be expected to behave properly in the future.

In conclusion, it should be obvious that for most complex, nonlinear, practical, ecological systems, stability analysis will probably not prove to be very useful. This is partly because in empirical ecology we shall often be dealing with systems satisfactorily identified and thus stability may be irrelevant [see (b) Ecological significance of stability, p. 176], and partly because the tools are not available. The major use of stability analysis might be in ecological design problems, where it finds its major use in engineering.

The reader seeking further discussion of the analysis of deterministic systems is referred to the excellent text by DeRusso *et al.* (1965), from which I have here drawn heavily.

2. *Probabilistic (Stochastic, Random) Systems or Inputs*

Heretofore we have been concerned with deterministic mathematical models, i.e., the values of input variables, of initial state variables, and of constants were assumed to be known exactly. Thus, predictions generated by the model were exact, or deterministic. These assumptions are wildly unrealistic if one is using the model to help solve practical problems.

Since the values used for input variables, initial state variables, and constants of the model are derived from physical measurements, each value is actually an element of a probability distribution. This is because of the nature of measurement, and not necessarily because of the nature of the real world (whose nature we cannot know anyway). Therefore, in generating predictions from the model, instead of entering specific values for variables and constants we should be entering probability distributions. The predictions generated by the model in this case will be probability distributions, rather than exact values.

This would be realistic, but unfortunately it is extremely difficult to do. In many practical systems it will probably be impossible to do without resorting to Monte Carlo techniques, which are very time-consuming on the computer.

The special case of probabilistic inputs ("random signals," "noise") to linear deterministic systems has been particularly well analyzed because of its applications in electrical engineering and other areas (Schwarz and Friedland, 1965). For the probability theory background to this work, see the excellent text by Papoulis (1965).

The case of probabilistic systems (probabilistic operators) has been developed for linear systems by Adomian (1963, 1970), and has great potential for dynamic ecological systems. The model allows a "stochastic filter" whose parameters are randomly varying in time, or a differential

equation with randomly time-varying constants, as well as the simpler cases of probabilistic inputs or boundary conditions (e.g., initial state) (Syski, 1967). Both cases can be represented by a "stochastic operator," and "stochastic Green's functions" can be found for the various statistics of interest, e.g., the covariance function of the output or solution process. Sibul (1968) has extended Adomian's formulation into a state space formulation particularly adaptable to control applications.

The general probabilistic operator model opens a fertile new field for consideration of sophisticated modeling of randomly varying phenomena, for statistical optimization of stochastic systems, and for a new approach to nonlinear stochastic systems. This field, the combination of nonlinear differential equations and stochastic processes, is a very active area of modern research in optimization theory (Bellman and Kalaba, 1964).

B. Optimal Control and System Optimization

In the analysis of models of dynamic ecological systems we are interested in two essentially different objectives: (1) prediction of system behavior (solutions and solution behavior, e.g., stability), and (2) control of system behavior. For example, given a fish pond with known inputs and an acceptable mathematical model, we might wish not only to predict fish production, but also to maximize fish production by controlling the inputs. Or, given an agricultural pest common on field crops, and several possible predators and competitors, we might wish to select that combination of organisms which would minimize the pest or maximize crop production. (The first example would be an "optimal control" problem; the second, a "system optimization" problem.) Since the control of system behavior requires use of the calculus of variations, or some derivative of it, this is a much more difficult problem than just prediction.

We are dealing here with optimization, or "extremal," problems, i.e., finding maxima or minima of functions or functionals (functions of functions). "Optimal control" is the optimization of system input to the desired system behavior; "system optimization" is the optimization of system structure (equation forms and parameters) and, perhaps, input to the desired system behavior. Stated in this way, system optimization is the "design problem" of engineering, i.e., how to construct the best system from components with known properties. If the "desired system behavior" actually represents real-world data, measured from an existing real-world system, then system optimization is equivalent to what we have been calling "system identification," i.e., the mathematical empirical description of a phenomenon based on measurements and (usually)

hypothetical equation forms. Curve-fitting or parameter-estimation ("measurement") of statistics is a special case of system identification, when the systems are very simple.

Stated in the mathematical notation developed previously, optimization consists of minimizing a functional of the general form

$$\int_{t_0}^{t_1} g(\mathbf{x}(t), \mathbf{v}(t), t)\, dt, \tag{36}$$

where (t_0, t_1) is the total time interval of interest. The functional (36) is called the "optimization criterion," "error index," "performance criterion," etc. Ecological examples might be pest productivity, production of pollutant, food production (in which case the functional would be formulated with a minus sign, resulting in a maximization), or a function of some desired final state, in which case it would be of the general form $h(\mathbf{x}(t_1))$. In most real control problems only some of the input variables are controllable, and the rest are uncontrollable (the "disturbances"). For example, in a model of an agricultural field one might consider as input variables only fertilizer, temperature, and precipitation (assuming no irrigation); the first would be controllable, and the others not. In the standard formulation of the optimization criterion the input vector $\mathbf{v}(t)$ includes only the controllable input variables.

Along with a particular formulation of the optimization criterion, several types of constraints exist, their type and formulation depending upon the particular problem. These constraints may be on the input variables (both controllable and uncontrollable), the system itself (the mathematical model of coupled differential equations), or the state variables.

In the optimal control problem, the optimization criterion is minimized by finding the optimal control (optimum controllable input, "optimum control signal") $\mathbf{v}(t_0, t_1)$ subject to the constraints represented by the previously accepted mathematical model of the system,

$$\dot{\mathbf{x}}(t) = f(\mathbf{x}(t), \mathbf{v}(t), t), \tag{37}$$

the initial state $\mathbf{x}(t_0)$, and the values of the uncontrollable input variables for the time interval (t_0, t_1). As in the formulation of (36), $\mathbf{v}(t)$ represents only controllable input variables, the uncontrollable input variables being incorporated into Eq. (37) as time-dependent disturbance functions.

The system optimization problem, as mentioned above, really takes on

two forms, system design and system identification. In the design problem, the optimization criterion is minimized by finding the optimum mathematical model (theoretical design) and, perhaps, optimal control, subject to constraints represented by the values of uncontrollable input variables for the time interval (t_0 , t_1) and, often, the forms of the model equations. In the identification problem, the optimization criterion is minimized by finding the optimum mathematical model, subject to constraints represented by values of the controllable and uncontrollable input variables for the time interval (t_0 , t_1), the values of the state variables $\mathbf{x}(t_0 , t_1)$, and, usually, the equation forms of the model.

In any of these optimization problems additional constraints are usually made in the form of upper and lower limits on values of the controllable input variables and the state variables. The lower limits for most of these variables in ecological systems, for example, would be zero.

The system optimization problem is most commonly encountered in ecology as a parameter optimization problem in system identification. This is simply fitting of the hypothetical model equations to observed behavior. When the optimization criterion is a quadratic functional (as it usually is), parameter optimization is equivalent to parameter estimation by least squares in statistics. Given several complete sets of data [i.e., for the period (t_0 , t_1)] for the input and state variables, one may attempt to estimate values of all the parameters, or constants, simultaneously (that is, those parameters which are not, together with the equation forms, part of the hypothesis). This is really an elaborate form of curve fitting and, as with curve fitting, one of the main problems with parameter identification is that of uniqueness. When one is trying simultaneously to estimate more than a certain maximum number of constants (and the number may be very small), several widely different combinations of estimates will yield local minimum sums of squares of deviations (Kerlin, 1968). In this case, the only practical alternative is parameter identification from simpler systems, perhaps so simple that the process is called "direct measurement." (It should be kept in mind that measurement is a form of estimation, and estimation is an optimization procedure, usually done by minimizing a sum-of-squares function.)

Other common types of system optimization problems are impulse–response or transfer-function optimization for linear systems, and equation-form optimization for nonlinear systems (Harris and Lapidus, 1967).

The actual solution of optimal control and system optimization problems requires the digital computer application of some rather elaborate mathematical techniques. These techniques are all closely

related to the classical calculus of variations; they are Bellman's "dynamic programming," Pontryagin's "maximum principle," and the "direct methods" (Gumowski and Mira, 1968; Gelfand and Fomin, 1963; Elsgolc, 1962) of the calculus of variations.

Although the mathematical theory of optimal control and system optimization is only in its infancy and already very difficult, it is destined to play an extremely important role in ecology in the future, because of the pressing needs to control and design real-world ecological systems. However, the theory of optimal control and system optimization is concerned with optimization only of mathematical models. In very few areas of ecology has formulation and testing of mathematical models resulted in models whose correspondence with the real world is satisfactory enough to be used in optimization applications. To attempt to do so prematurely could result in disaster.

Before closing, something should be said about the subject of "sensitivity analysis" (Tomović, 1963). The sensitivity of system solutions to small changes in components of the system (mathematical model) is usually expressed as partial derivatives of state variables with respect to system components, the partials being either absolute or normalized. When formulating a model for design purposes, it is very important to keep these values as small as possible, i.e., a successful practical design must be relatively insensitive to small variations in its components (Gumowski and Mira, 1968, pp. 11–12). This is because values of a model's components are not known exactly, nor is the range of the input or the initial state. Sensitivities to the following have proved important in design problems (Gumowski and Mira, 1968, pp. 11–35): parameter variations, equation forms (leading into the fascinating subject of "structural stability" or "inertness" (Peixoto, 1967; Thom, 1968)), time delays, discretization (the representation of the differential equations by difference equations), noise (probabilistic input), and initial state. When formulating a model for identification purposes, the sensitivities, of course, depend upon the observed behavior. The mathematical expressions for sensitivities find great use in the techniques of optimal control and system optimization, particularly for linear systems.

For serious study of the theory of optimal control and system optimization the reader is referred to texts by Merriam (1964), Fel'dbaum (1965), and Pontryagin *et al.* (1962), and to the series of three volumes by Bellman (1967). The subject of optimal control and system optimization of general (not restricted to linear) stochastic systems is an extremely difficult one; an introduction to the subject, as well as a treatment of the linear case, may be found in the text of Pugachev (1965).

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PART II

ONE-SPECIES MODELS

Population dynamics has always been as important concern in ecology. It may be said fairly that, if there now exist natural affinities between mathematics and ecological science generally, this is the clear result of both early and continuing efforts to mathematize populations. The chapters of this section illustrate three different approaches to population modeling. But perhaps their main significance in the context of this book is in representing *experimental* systems ecology. This is a side of the subject that is hardly underway beyond the stage of simple two-species interactions, except in rudimentary (from the systems standpoint) manipulations of artificial ecosystems like microcosms, agriculture plots, or experimental ponds and streams, and a few natural units such as old fields and watersheds. Outside the framework of one or two species, connections between experimental results and systems models have so far been tenuous and tentative indeed.

Chapter 3 presents a thoroughgoing mathematical analysis of microbial (*Chlorella*, *Selenastrum*) dynamics in both continuous and batch cultures. The modeling is mechanistic, seeking to reconstruct whole-system dynamics from detailed understanding of the parts, with impressive success. The experimental work has a definite systems analysis component, particularly in the use of step and pulse inputs into the cultures. This comes very close, at least in principle, to the engineers' use of "singularity functions" (impulses, steps, ramps, etc.) in transient analysis, or sinusoids in frequency analysis. Dr.Williams develops two types of complementary models, dealing with what he terms "extensive" and "intensive" population properties. He seeks to interact these models heuristically in a process of theory construction referred to as "anacalypsis." In his closing discussion of Hutchinson's (1961. *Am. Nat.* **95**, 137) "paradox of the plankton," he makes a convincing argument for the importance of instantaneous dynamics of competitive advantage in the partitioning of biotopes that leads to stable, multispecies equilibria.

Chapter 4 is a bioenergetics study of the terrestrial isopod *Armadillidium*, utilizing concepts from control theory and the transfer function technique of classical dynamic analysis. Dr. Hubbell's perspective is a hierarchical view of the natural world in which lower-level laws account for properties of systems at lower levels of organization. These properties constrain what is possible at higher levels, and the more restricted set of the actual is generated by higher-level laws. The widespread notion of organisms as passive energy partitioners is criticized, and from the contrary view a focus upon control aspects of energy processing is developed. Biological control systems and characteristics of the cybernetic control model are contrasted, illustrating little general comparability of components. Since "control" inevitably presumes—in some sense—objectives to be met or optimized, two methods of estimating set points experimentally are identified: an "optimum environment" method, and a "perturbation" method.

Three models of energy regulation by *Armadillidium* are formulated, two linear and one nonlinear. "Linearity" is restricted to mean the additivity component of the superposition principle (additivity *and* homogeneity) by which linear dynamic systems are usually defined, and it is pointed out that the algebraic equation for a line defines a *nonlinear* input–output relation. This is useful because ecologists usually confuse what is meant by a "linear system."

Chapter 9 of this volume, and the chapters in Part IV, of Volume II, all of which deal with linear dynamics, will serve further to clarify the definition. In the context of Laplace transform transfer functions, Dr. Hubbell develops his models, incorporating such standard transient analysis techniques as step, impulse, and pulse testing, and of opening feedback loops to determine whole-system transfer functions.

This sort of work, along with other attempts of ecologists to employ classical systems analysis methods, has been criticized by some on the frontiers of systems science as archaic and obsolete. So it may be in engineering, but not in ecology. It seems quite reasonable that ecologists should explore "old" territory for new insights. It is not old to them, and what better systematic entries into modern approaches are there than paths already well-worn by predecessors? Dr. Hubbell's chapter, in this instance, stands as an important contribution to the orderly development of new perspectives and new progress in systems ecology.

Chapter 5 presents an analysis, based on interaction of laboratory experiments and the digital computer, of factors pertinent in predator-prey relations of a freshwater fish, *Micropterus*. The emphasis is on habitat complexity and its implications for predator efficiency viewed in terms of energetics. The work is patterned after Holling's (1963. *Mem. Entomol. Soc. Can.* **32**, 22) experimental components analysis approach, in which detailed mechanistic submodels are combined to produce a static representation of factors accounting for the overall predation process.

Both "routine" and "active" aspects of the fish's respiratory metabolism are modeled, and a computerized sensitivity analysis of the routine metabolism performed to identify parameters of greatest significance. An energy model is then constructed, incorporating both routine and active aspects, and used to investigate consequences of cover density in the predator's environment. Movie films of feeding experiments, analyzed by computer, provide the basis for conclusions about the stabilizing effect of cover upon the prey–predator interaction.

3

Dynamics of Microbial Populations

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I. Introduction

A. Rationale for Microbial Population Studies

Detailed studies of single-species microbial population dynamics are important to ecology both to gain understanding of population behavior as an end in itself, and also as a means of approaching the analysis of large, complex ecosystems. In the latter context, there seem to be three main reasons for the importance of microbial dynamics to ecological systems research:

(1) Microorganisms comprise a major fraction of the earth's biomass. To the extent that this is true for any ecological system, the dynamics of that system must be largely microbial dynamics. Also, the turnover rate of microorganisms is generally greater than that of higher organisms. Since the flux through a system equals the product of its mass times its turnover rate, it should be clear that microorganisms, with high biomass *and* high turnover rates, must be overwhelmingly important to energy or material fluxes in an ecological system. Energetically, at least, higher animals are little more than a minority ghetto in the total community.

(2) The relative simplicity of microbial systems allows us to approach most closely the ideal of a complete quantitative description of population behavior. As implied above, it is scientifically satisfying to understand microbial dynamics for its own sake. But also, being aware of the remarkable conceptual advances made in genetics and molecular biology *via* the use of microbial "model" systems, it behooves us as ecologists to explore the extent to which the study of microbial systems can provide us with a basic, fundamental dynamics, to which we can add the complicating factors present in higher organisms. The basic question I am raising is whether, say, territoriality is the fundamental population control mechanism of higher animals, or whether it is a secondary factor modifying the action of some more universal and fundamental

dynamic principles. The elucidation of such principles, if they exist, may be easiest through study of simple microbial systems. Perhaps we ecologists should begin a search for our own "*Escherichia coli.*"

(3) Detailed knowledge of single-species dynamics is essential for optimal modeling of complex ecosystems. However, in an ecosystem model we clearly cannot include all possible detailed information for every species; as Levins (1966) points out, such a "naive, brute force approach" leads to both computational and conceptual intractability. What, then, is the value of single-species details? Even though the species will be represented in a highly simplified fashion in a large model system, only by having prior knowledge of the details can we ensure that the simplifications we choose will be most appropriate. Our task in simplifying is to obtain a maximum of realistic prediction with a minimum of complexity. Beginning with the detailed model, we can consciously and rationally eliminate the minor second-order effects while preserving the important first-order effects. Otherwise, simplifying would be mere guesswork.

Further, it is not necessarily true that theory complexity increases in proportion to the quantity of empirical information accounted for. A great wealth of empirically relevant detail may be predicted, if we are fortunate, by a very simple theory. Such is, of course, the goal of all theory construction. We usually obtain the greatest predictive power by proposing new entities or relationships between entities, an aspect of theory construction we can call *anacalypsis* (ανακαλυψις: discovery, invention). In this chapter I hope to show that, by addition of a single new variable to standard population equations, we can predict many more general properties of microbial populations than we could before. By opening up a wider variety of empirical phenomena against which to test the model, not only is the anacalyptic model potentially more fruitful, but also more vulnerable to rejection. The vulnerability of the anacalyptic model is a property to be cherished.

B. An Approach to Microbial Populations

The first section of this chapter will describe the results of experimental studies on the population dynamics of unicellular green algae, both in continuous (chemostat) culture and unrenewed (batch) culture. Included will be observations on oscillations, lags, and synchronous growth. Measured variables include cell number, biomass, chlorophyll, limiting nutrient concentration, and cell size distributions. Environmental variables studied include turnover rate, temperature, carbon dioxide concentration, and photoperiod.

In subsequent sections I shall describe an approach to microbial population theory. The models thus generated seem to have general applicability to most microbial populations. As an overall philosophy of population modeling, I shall take the approach that an understanding of the control of single cell growth and division will entail a prediction of the population dynamics of the organisms. If we know the behavior of individuals, we can deduce the behavior of the population.

Two complementary models are developed. The first entails the prediction of time-dependent behavior of *extensive* population variables: total biomass, numbers, nutrient, etc. The second entails the prediction of time-independent properties of *intensive* population variables: distributions of age, size, etc., within the population. (An example of an extensive model is the time-honored logistic equation, while an example of an intensive model is a life table.) Ultimately any complete theory must combine both intensive and extensive properties within a single framework. At present, however, any such amalgamation of the two approaches seems to me unmanageable without an immense "brute force" computer program. Such a computer program I believe would be premature and nonanacalyptic.

II. Experimental Studies on Algal Populations

I report here the results of population studies of algae grown under very precise conditions of batch and chemostat culture. The experiments have been designed such that both steady state and transient population behavior could be studied. The approach is along lines used in control systems analysis (e.g., Harris, 1961), in the hope that insight might be gained by recognizing the feedback nature of population control. Most of the interesting processes occurring, however, are almost certainly nonlinear, such that analysis in terms of linear control systems does not seem to be the simplest or most straightforward method. However, the experimental design is quite adaptable to a variety of theoretical approaches.

I believe the chemostat (Novick and Szilard, 1950) is the best laboratory idealization of nature for population studies. It is a dynamic system with continuous energy and material inputs and outputs, thus modeling the open system character and temporal continuity of nature. The input and removal of nutrient analogs the continuous turnover of nutrients in nature. The washout of organisms is formally equivalent to non-age specific death, predation, or emigration which always occur in nature.

A. METHODS

A much more detailed description of methods will be found in Williams (1965).

1. *General Culture Procedures*

Two green algae of the order Chlorococcales were used: *Selenastrum gracile* Reinsch and *Chlorella pyrenoidosa* Chick. Both were purchased from the Indiana University Culture Collection of Algae (Starr, 1960). Both were grown on a modification of Chu No. 10 culture medium (Chu, 1942). The Chu medium was used because its composition and concentrations are more ecologically realistic than many frequently used, highly concentrated media. The composition of Chu No. 10, as modified, is given in Table I. Nitrate is the limiting nutrient. All media were

TABLE I
MODIFIED CHU NO. 10 CULTURE MEDIUM

Compound	Concentration (mg/liter)
$Ca(NO_3)_2 \cdot 4H_2O$ [a]	59.2 (500 μM NO_3^-)
K_2HPO_4	10.0
Na_2CO_3	20.0
$MgSO_4 \cdot 7H_2O$	25.0
$Na_2SiO_3 \cdot 9H_2O$	58.0
$FeCl_3$ [a]	0.5
Disodium versenate[a]	10.0
Trelease trace element solution[a]	0.5 cc

[a] Denotes change from formulation of Chu (1942).

sterilized by filtration through a Selas 03 Filter Candle or a Millipore GS Filter.

Chlorella was purchased axenic, and was maintained thus. *Selenastrum* was purchased contaminated. It was rid of its contamination by approximately three weeks' growth in a chemostat using the inorganic medium described above. The chemostat may be potentially useful to axenize many autotrophs which have proved refractory to other methods.

2. *The Chemostat*

The chemostat system developed was capable of highly precise, reliable, long-term use. The culture vessel was approximately a standard

design (Novick and Szilard, 1950), but containing 130 cc of culture. It was illuminated by a 22-W-circular fluorescent bulb, providing almost uniform illumination over the entire cylindrical surface of the vessel. Incident intensity was approximately 6.5 klx, saturating but not inhibitory to growth.

Temperature was controlled to ± 0.05 C. Mixing and gas exchange were accomplished by bubbling humidified air (or air + 1% CO_2) through each culture at 500 cc/min.

Flow rate in early experiments was controlled by the method of Kubitschek (1954), impeding flow from a constant head Mariotte bottle with a capillary tube. This was accurate to $\pm 1.5\%$. Most experiments had more precise flow control ($\pm 0.5\%$) by use of a peristaltic pump (Harvard Apparatus).

3. *Assay Techniques*

A maximum sample of 2 to 3 cc could be removed without perturbing the culture. In early experiments, cell number was estimated by hæmacytometer counts. High accuracy ($\pm 2\%$) was possible with a modified filling technique (Williams, 1965). In most experiments, a Coulter Counter Model B was used with a 50 μ aperture. Routine accuracy was $\pm 0.5\%$.

Size distributions were made with the Coulter Size Plotter, graphing between 30 and 50 size classes for a total of about 30,000 cells/distribution. At least three replicates were run per sample.

Grown in essentially fresh water osmotic concentrations, the cells plasmolyzed when added to the 0.9% NaCl normally used for counting and sizing in the Coulter Counter. This was solved by an empirically

TABLE II

IMPROVED COULTER COUNTER FLUID

Compound	g/liter
NaCl	5.0
PVP[a]	35.0
Na_2HPO_4	0.32
NaH_2PO_4	0.04
NaOH	0.08

[a] PVP is Polyvinylpyrollidone ("Plasdone C," $\overline{MW}$ = 40,000, Antara Chemicals, Gracelli, N.J.).

developed counting fluid (Table II) containing polyvinylpyrollidone. In addition to preventing plasmolysis, the fluid's high density and viscosity improve counting accuracy by (i) impeding the settling out of cells and (ii) slowing passage of cells through the aperture, thereby preventing the pulse truncation and size distortions resulting from normal counter methods (Kubitschek, 1964).

Dry weights were determined from 2 cc of culture filtered onto a tared 13-mm Ultrathin Millipore Filter, washed, desiccated, and weighed on a quartz cantilever microbalance. There was a linear correlation coefficient of 0.982 ($DF = 28$; $t = 743.2$, $P \ll 0.001$) between dry weight and total cell volume over a variety of experimental conditions involving mean cell dry weights of 4 to 40 $\mu\mu$g/cell. This is shown in Fig. 1. Since there is thus no evidence for density differences between cells, cell volume data (from the Coulter Counter) and cell mass are equivalent, and will be used interchangeably.

Selenastrum pigments were extracted in 80% acetone, while the more

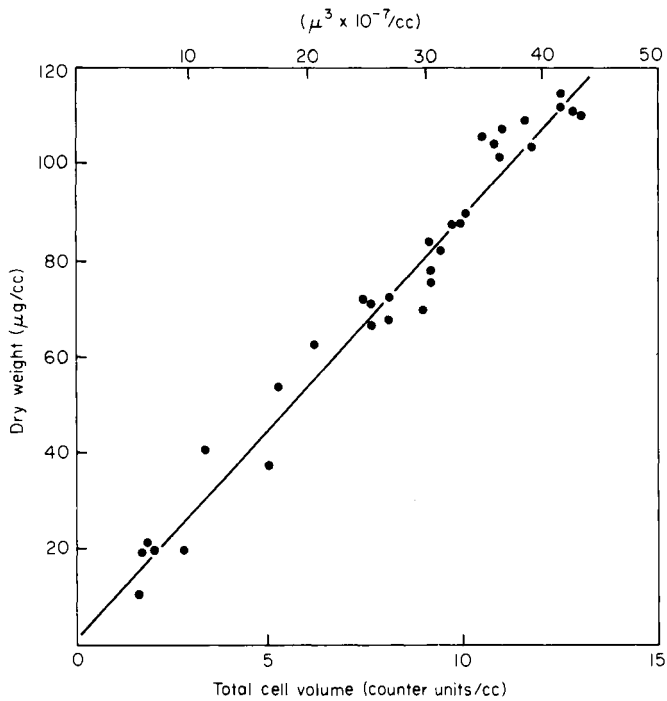

FIG. 1. Total cell volume from Coulter Counter data versus dry weight: Coulter Counter volume is a good measure of biomass.

refractory *Chlorella* pigments were extracted in absolute methanol. Chlorophyll was estimated at 670 nm, and carotenoids at 480 nm. Accuracy was $\pm 1\%$.

A semi-micro modification of the phenoldisulfonic acid method was developed (Williams, 1965) for nitrate assay. Sensitivity was ± 1 mμ mole nitrate/sample.

4. *Data Presentation*

Each experimental population furnishes information on a variety of subjects; hence subject matter and not the individual experiment will be the unit of organization. More complete presentation of the data is in Williams (1965).

B. Precision of Steady State Regulation

When studying causes of natural population fluctuations it is important to know whether populations will fluctuate in the absence of environmental fluctuations. In this section we examine the organisms' ability to maintain a steady state under constant environmental conditions. The results relating to steady state precision fall empirically into two classes: short-term and long-term precision. The two questions are not logically disjunct, but they must be so treated at present by virtue of the experimental design. I will show that regulation is quite precise over periods up to 15 generations, but that over longer periods of time there are occasional unexplained and very gradual trends in the population parameters.

1. *Short-Term Precision*

I choose a maximum of 14 generations as an arbitrary but convenient time limit, during which enough measurement can be made to assure a steady state, but during which any long-term trends will be insignificant.

Note that the question concerns *capability* of population regulatory mechanisms; hence only those populations are treated for which it was clear that no significant environmental fluctuations occurred.

Three measures are used. First is the coefficient of variation ($S_x/\bar{X}$). Although intuitively comprehensible, the coefficient of variation does not take account of the time-sequential nature of the data.

The second measure I shall call the *coefficient of sequential variation.* It is derived (Williams, 1965) from the mean square successive difference

($\partial_x{}^2$) of von Neumann *et al.* (1941). The coefficient of sequential variation ($\partial_x/\bar{X}$) I define as

$$\frac{\partial_x}{\bar{X}} = \left(\frac{\sum_{i=1}^{n-1} \left(\frac{X_i}{\bar{X}} - \frac{X_{i+1}}{\bar{X}} \right)^2}{(n-1)} \right)^{1/2}, \tag{1}$$

where i enumerates the variates X chronologically.

The third measure is a measure of randomness in sequential variation based on the above: Since $\partial_x{}^2 = 2S_x{}^2$ for random sequences, and since the two functions are statistically independent, $\Delta_x = 1 - \partial_x{}^2/2S_x{}^2$ should be normally distributed about a mean of zero when the sequence is random. Deviations of Δ_x from zero are thus a test of nonrandomness (Young, 1941).

Table III presents the results from seven steady state populations. The variability of steady states is quite small, ranging from a coefficient of variation of 0.0174 to one of 0.0593; most fall on the low side of this range. The variability is, however, greater than that of any environmental or sampling parameter. There is zero correlation between the three variables (Williams, 1965).

While most of the biomass and chlorophyll measurements appear random, most of the cell number measurements appear nonrandom. Since the chemostat is nutrient (i.e., biomass) limited, and since cell division is much more of a discrete (or "digital") process than cell growth, the results presage a general character of cell populations, that cell division is only loosely coupled to cell growth. Cell number may be thought of as an oscillator (cf. "cell cycle") set in motion by small random fluctuations in biomass growth. The loosely coupled nature of the division process will be discussed at length later on.

2. *Long-Term Precision*

There is little systematically collected data on long-term changes in supposedly steady state populations. No experiments were specifically designed to study such changes. Nevertheless, there is evidence for their occasional occurrence.

Two simple measures are adequate here. The first is R_x, the ratio of the averages of the last few values in the time sequence to the average of the first few values. Thus $R_x > 1$ shows an increase with time; $R_x < 1$ shows a decrease. The second measure is $r_x = 100R_x\tau_2/t$, where τ_2 is the doubling time interval studied; r_x measures the average percentage change per generation. The results are shown in Table IV.

Of the few significant long-term trends, it is difficult to see any

TABLE III

COEFFICIENTS OF VARIATION ($S_x/\bar{X}$), COEFFICIENTS OF SUCCESSIVE VARIATION ($\partial_x/\bar{X}$), AND A MEASURE OF NONRANDOMNESS (Δ_x) FOR SEVERAL POPULATIONS

Culture designation	Duration (hr)	Number of samples	Cell number (N)			Biomass (M)			Total chlorophyll (ϕ)		
			$S_n/\bar{N}$	$\partial_n/\bar{N}$	Δ_n	$S_m/\bar{M}$	$\partial_m/\bar{M}$	Δ_m	$S_\phi/\bar{\phi}$	$\partial_\phi/\bar{\phi}$	Δ_ϕ
Selenastrum											
IV	190	10	.0373	.0373	0.50[a]	—	—	—	—	—	—
IV_2	293	12	.0296	.0406	0.16	—	—	—	—	—	—
IV_4	240	12	.0593	.103	−0.49[a]	.0246	.0347	0.01	.0480	.0738	−0.173
Chlorella											
VI_1 (a)	239	11	.0175	.0271	−0.19[c]	.0384	.0516	0.096	.0354	.0458	0.354
VI_2 (a)	239	11	.0174	.0172	0.49[a]	.0298	.0386	0.164	.0384	.0504	0.270
VI_1 (b)	252	14	.0225	.0142	0.83[b]	.0353	.0309	0.614[b]	.0226	.0346	−0.170
VI_2 (b)	252	14	.0230	.0216	0.56[b]	.0313	.0210	0.665[b]	.0249	.0357	−0.012

[a] Nonrandom, $0.05 > P > 0.01$.
[b] Nonrandom, $P < 0.01$.
[c] If one possibly (but unprovably) erroneous measurement is removed, $\Delta_n = 0.545$, $0.05 > P > 0.01$.

pattern: the presence or absence of trends, their direction, and their magnitudes, seem to be at best sporadic. No instrumental changes can be invoked to explain the trends (Williams, 1965).

Mutation accumulation should be minimal in an autotrophic organism on inorganic medium, but it is possible that the trends result from

TABLE IV

LONG-TERM POPULATION CHANGES, EXPRESSED AS THE RATIO OF FINAL TO INITIAL VALUES (R_x) AND THE PERCENT CHANGE PER GENERATION (r_x)

Population	Interval t (hr)	τ_2 (hr)	R_n	r_n (%)	R_m	r_m (%)	R_ϕ	r_ϕ (%)
Selenastrum								
IV_2	1033	20.0	1.211[b]	0.41	—		—	
IV_4	938	20.6	1.024		0.75[b]	−0.55	0.87[b]	−0.29
Chlorella								
VI_1	252	18.0	0.946		1.046		0.912[a]	−0.63
VI_2	198	18.0	1.030		0.995		0.945	
VI_1 (a)	322	18.0	1.015		1.114[b]	0.64	—	
VI_2 (a)	322	18.1	0.987		1.078		—	
VI_1 (b)	308	36.6	0.990		0.982		0.975	
VI_2 (b)	308	36.6	0.942[a]	−0.69	0.924[b]	−0.90	0.965[a]	−0.42

[a] Results of t-test between initial and final means show value to be significantly different, $P \leqslant 0.05$.

[b] Results of t-test between initial and final means show value to be significantly different, $P \leqslant 0.01$.

accumulation of a number of small polygenic changes. Since these organisms are almost certainly asexual, such polygene accumulation would be quite slow to achieve equilibrium. This slowness is in distinction to the normally discussed major gene situation in the chemostat, where selection is accelerated (Moser, 1958). However, since the trends are so sporadic and slight, it would be difficult to study them systematically.

C. STEADY STATE DEPENDENCE ON TURNOVER RATE

In order for a steady state to occur in a chemostat, the specific growth rate ($dX/X\,dt$) must exactly equal the turnover (dilution) rate of the instrument. Consequently, as the turnover rate increases, we expect a greater nutrient requirement per cell in order to achieve faster growth.

Hence we expect a smaller population at higher turnover rates. The theory predicting these relationships is well known (Herbert *et al.*, 1956). However, that theory utilizes only one measure of population density, thus making the implicit assumption that organisms are chemically or physiologically identical, regardless of growth rate. I shall show that this assumption is incorrect; the model (for extensive properties) developed later in this chapter is designed explicitly to handle changes in physiological state of organisms.

Figure 2 shows the relationship to steady state turnover rate of three

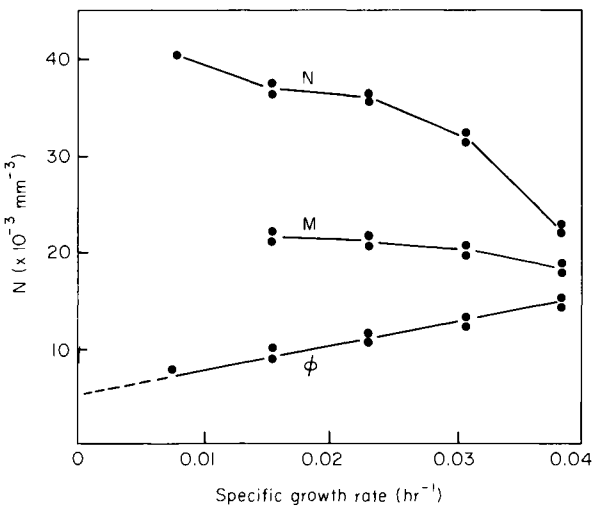

FIG. 2. Steady state specific growth rate versus total numbers (N), biomass (M), and chlorophyll (ϕ) for *Chlorella*. Ordinate scaled for cell number. Biomass and chlorophyll in arbitrary units. (Note different slopes as discussed in text.)

extensive properties of *Chlorella*: cell number (N), biomass (M), and total chlorophyll (ϕ). Both cell number and biomass decline with increasing turnover rate, but they do so with different slopes. Total chlorophyll, on the other hand, actually *increases* as the biomass and number decline. The corresponding measures of average cell mass (M/N), chlorophyll per cell (ϕ/N), and chlorophyll per unit mass (ϕ/M) are shown in Fig. 3. A few data points are added from batch culture, to show the great range over which cell mass (and volume) may vary.

We shall see that increased cell mass with higher growth rate is a generalization for most microorganisms; it is a result of increases primarily in the cell's synthetic machinery. Note the strong increase in total chlorophyll, an important part of this synthetic machinery.

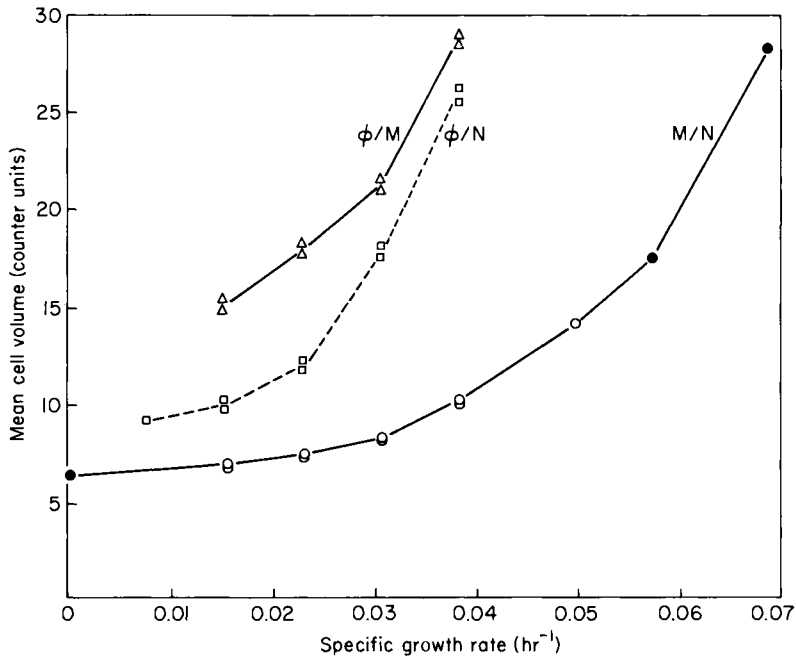

FIG. 3. Average cell size (M/N), average chlorophyll per cell (ϕ/N) and per unit mass (ϕ/M) versus specific growth rate (turnover rate). ●: batch culture, ○: chemostat.

Note also in Fig. 2 that the slope of cell number is steeper than that of biomass; if we extrapolate to the right, cell number will be expected to reach zero before biomass. The washout or extinction point of course occurs when cell division cannot keep up, regardless of the potential for biomass growth. We shall see in other contexts also that cell division is a critical rate-limiting and lag-producing step. There is further discussion of this in Section III on the extensive model.

The relation of chlorophyll to productivity is of the form

$$\overline{\frac{dM}{M\,dt}} = K(\bar{\phi} - \bar{\phi}_0), \tag{2}$$

where $\bar{\phi}_0$ is the intercept value of total chlorophyll ($\bar{\phi}$) at zero growth rate. Since chlorophyll is part of that synthetic machinery which increases at high growth rates, extrapolation to zero growth should define that amount of chlorophyll required for maintenance metabolism. If this is so, maintenance chlorophyll is anywhere from 30 to 70% of the chlorophyll measured in the experiments reported.

D. Effects of Temperature and CO_2

In addition to the effects of turnover rate (and hence nutrient limitation), it is of interest to investigate the effects of nonlimiting factors on steady state behavior. Although not directly involved in the regulation of the organisms' biomass, nonlimiting factors may interact in a manner profoundly affecting the character of the population. Two such nonlimiting factors, temperature and CO_2, will be discussed briefly here. I shall show, in the model section, that temperature effects can be adequately explained by effects on the kinetics of nutrient uptake and incorporation. The CO_2 effects are more problematical.

1. *Temperature Effects*

The chemostat provides a unique method for studying temperature effects, in that the same steady state growth rate may be maintained independent of temperature. We shall see that this provides a unique analytical tool for the analysis of temperature effects: If two mutually dependent processes have different temperature optima, we should be able to dissociate the processes by maintaining a constant specific growth rate in the chemostat.

Figure 4 shows the steady state values of cell number, biomass, and chlorophyll over a very narrow temperature range, 22–25 C. (These preliminary experiments were hampered by the limited range of a homemade contact thermometer controller.) Even over this three-degree

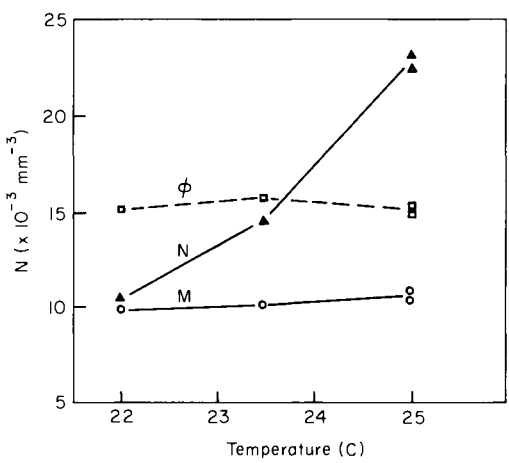

Fig. 4. Steady state cell number (N), biomass (M), and chlorophyll (ϕ) over a three-degree temperature range. Cells at 22 C are twice as large as those at 25 C.

range, the results are striking. Very small changes in total chlorophyll and biomass are accompanied by very large changes in cell number; cells at 25 C are approximately one-half the size of cells at 22 C.

More recently in my laboratory, Maurice Blaug (1970) has extended these measurements over a wider temperature range. His results are shown schematically in Fig. 5, pending publication of his detailed

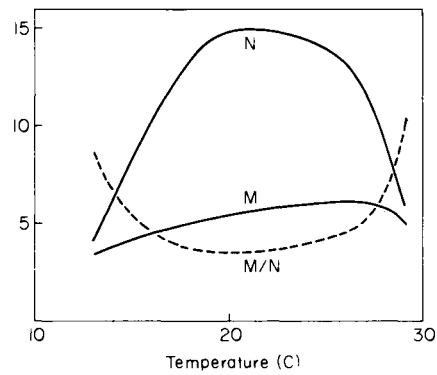

FIG. 5. Schematic representation of Maurice Blaug's results on *Chlorella*, showing steady state number, biomass, and average cell size versus temperature.

findings. There are distinct maxima for cell number and total biomass, corresponding to a minimum in cell size. Thus, at the same growth rate, large cells may occur either at high or low temperatures. Minimum cell size presumably occurs at the temperature optimum. Similar results have been reported for *Tetrahymena* cell size versus temperature in batch culture (Zeuthen, 1964).

By changing cell size with temperature, we have again demonstrated that there is only loose coupling between the growth and division processes. The lack of significant change in total chlorophyll is interpreted to mean that the linear relationship of total chlorophyll to specific production rate ($dM/M\,dt$) is relatively temperature independent. This might be expected if the light reaction rate, which is relatively temperature independent, were controlling the amount of chlorophyll present. Further discussion of temperature occurs in the description of the extensive model.

2. CO_2 *Effects*

With nitrogen as the growth limiting nutrient, one might expect the addition of extra carbon to the nutrient supply to have no effect. On the

other hand, if more photosynthesis occurs with added CO_2, one might expect excess carbohydrate to accumulate, causing an increase in total biomass. Neither of these alternatives, however, occurs. The data are shown in Table V. Total biomass is not significantly affected by added

TABLE V

EFFECTS OF CO_2 ON THE STEADY STATE

Population	w	CO_2	$\bar{M}$	$\bar{N}$	$\bar{\phi}$	M/N	ϕ/M	ϕ/N
VI_1 (a)	5.00	air + 1%	123.9	18,810	.0483	13.18	3.90	2.57
VI_2 (a)	4.98	air + 1%	126.0	19,170	.0492	13.14	3.90	2.57
VII_1 (a)	4.98	air	111.3	22,920	.0750	9.75	6.74	3.27
VII_2 (a)	4.98	air	122.2	23,760	.0752	10.28	6.70	3.17
VI_1 (b)	2.46	air + 1%	135.5	32,630	.0419	8.30	3.09	1.28
VI_2 (b)	2.46	air + 1%	136.0	33,040	.0417	8.24	3.07	1.26
VII_1 (c)	2.99	air	131.3	36,670	.0572	7.16	4.36	1.56
VII_2 (c)	2.98	air	136.3	35,680	.0576	7.64	4.23	1.61
VII_1 (d)	1.97	air	132.2	36,640	.0460	7.22	3.48	1.26
VII_2 (d)	1.97	air	139.6	36,440	.0475	7.64	3.40	1.30

CO_2; this rules out carbohydrate accumulation. The added CO_2, nonetheless, causes a decided decrease both in cell number and total chlorophyll; cells grown in high CO_2 are larger and contain less chlorophyll. Since the total population biomass is virtually unchanged by CO_2, and since nitrogen is rate-limiting, there has been no significant change in carbon/nitrogen ratio, hence no carbohydrate accumulation.

This argument has more generality. For any condition where the total biomass remains constant and cell size changes (temperature, CO_2, and the transient cases to be discussed), it follows that the relative proportions of all of the major elements (carbon, nitrogen, oxygen, etc.) in the organism are the same for all cell sizes regardless of cell size change. In this context, recall also that there was no evidence of any specific gravity changes over a wide range of cell sizes (Fig. 1). In a nitrogen limiting chemostat, cell composition seems very well controlled. This is contrary to some previous reports (Fogg, 1965) based on experiments done under very different conditions in batch culture.

In the presence of high CO_2, it seems plausible that less chlorophyll would be required to maintain the same rate of carbon fixation. *Chlorella* thus seems to have a control mechanism that allows maintenance of just enough chlorophyll to maintain the steady state photosynthetic rate. Recall also that total population chlorophyll was a linearly increasing

function of steady state growth rate (Fig. 2). As a generality, we may propose the controlled production of just the right amount of synthetic machinery to maintain the environmentally appropriate growth rate. This generalization is a theorem of the model presented for extensive properties, and further illustrates the looseness of coupling between cell growth and division.

E. Unused Limiting Nutrient

The amount of unused nutrient remaining in the culture container during a steady state must be just that amount required in the medium to maintain the steady state growth rate. If it were higher, the population would increase; if it were lower, the population would decrease.

Using the original Monod or Novick and Szilard chemostat theories (1950), we can predict from the biomass data that nitrate concentrations in the steady state cultures should be of the order of 0.2 to 1.0 μg(N)/cc (15–75 μM) over all experiments (Williams, 1965).

Despite the fact that the assay technique was refined to a sensitivity of ± 0.014 μg(N)/cc (± 1 μM), actual nitrate levels were so low that it was impossible to obtain good quantitative estimates. All samples measured between 0.01 to 0.04 μg(N)/cc (0.75–3 μM), right at the sensitivity limits of the technique.

However, there is enough accuracy to warrant the following important conclusion: The average steady state nutrient concentration is 20–100 times lower than that predicted by the basic theory of growth dynamics (Herbert *et al.*, 1956). Despite the uncertainty of the values, 20–100 fold is certainly a very real difference. Almost no growth is observed in batch cultures with 3 μM nitrate (Williams, unpublished).

I suggested earlier (Williams, 1965) that this discrepancy might be accounted for by the existence of a nitrate pool within the cells. Other experiments (Ketchum, 1939) have demonstrated a very rapid uptake of nutrient following starvation, along with the ability to use that nutrient for growth later when removed from the nutrient. Recent data by Caperon (1968) provide similar indirect evidence for an internal nitrate pool in *Isochrysis*, by showing a constancy of nitrate over a wide range of growth rates.

Ideas similar to this have been invoked to explain high growth rates in apparently nutrient-poor natural waters (Rhode, 1948). *Thus, in an open natural system, measurement of nutrient concentrations may not provide an adequate predictor of growth potential.*

The role of intracellular nutrient pools in population control is explored in the extensive model developed in the next section.

F. Transient Population Behavior

In principle, the transient behavior of populations should provide the most unambiguous reflection of operative control mechanisms (Harris, 1961). It is here, for example, that we might expect the clearest expression of looseness of coupling between cell growth and division. But, for successful transient experiments environmental conditions must be very well controlled and biological states must be precisely measurable. Transient studies thus entail considerable technical difficulty. Chemostat use can eliminate many of these difficulties: With clearly defined steady states as initial conditions, the responses of populations to systematic perturbations can be followed until new steady states are reached. This is a powerful approach familiar to systems engineers.

Only a few of the clearer experimental results will be shown here. The treatment of some aspects of the transients is frankly descriptive, for no satisfactory model has been developed to predict observed oscillatory behavior. Further results of these experiments can be seen in Williams (1965).

We shall subdivide transient phenomena as follows:

(1) Batch culture: always transient
(2) New chemostat inocula: transients approaching a steady state
(3) Chemostat perturbations: steady state–transient–steady state
    (a) step function perturbations
        (i) nutrient concentration
        (ii) flow rate
    (b) square wave perturbations
        (i) flow rate
        (ii) temperature

These experiments have been done on both *Chlorella* and *Selenastrum*.

1. *Batch Culture*

Batch cultures are closed systems in which inocula are allowed to grow, with no nutrient addition, until nutrient exhaustion causes growth cessation. Figure 6 shows the usual cycle of events for *Chlorella* as it passes from "lag" phase to "exponential" phase to "stationary" phase. Cell numbers, total biomass, and average cell size are shown. Figure 7 shows a similar batch culture growth curve for *Selenastrum* showing cell number, total chlorophyll, and chlorophyll per cell.

Note that the lag phase is a lag merely in cell division. While cell number remains constant for a time following inoculation, both biomass and chlorophyll show large increases, 4-fold and 8-fold, respectively.

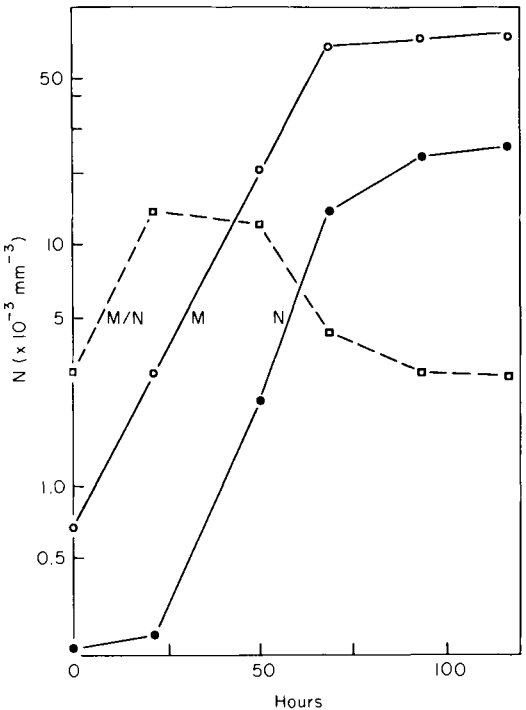

FIG. 6. Batch culture growth cycle for *Chlorella*, inoculated with stationary cells. Note lag in numbers but not biomass, as well as cyclic return of cells to original minimum size upon entering stationary phase. *M*: biomass, *N*: cell numbers, *M*/*N*: average cell biomass.

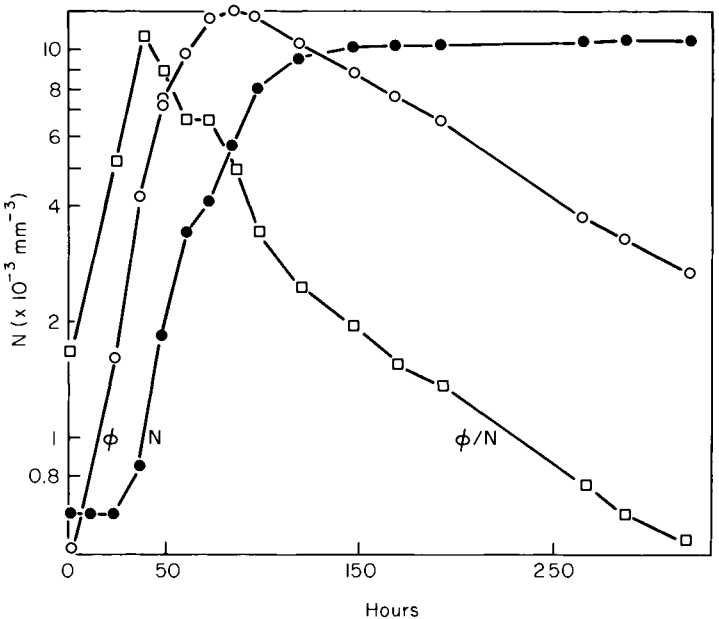

FIG. 7. Batch culture growth cycle for *Selenastrum*. Note initial rapid increase in chlorophyll during lag, and continued decay of chlorophyll in stationary phase. *N*: cell number, ϕ: total chlorophyll, ϕ/*N*: chlorophyll per cell.

Certainly the cell synthetic machinery is not lagging. Following the lag phase, cells divide and the population numbers increase exponentially for a time, along with biomass and chlorophyll. When nitrate becomes limiting, the biomass and chlorophyll stop increasing, but cell division continues, producing smaller cells with less chlorophyll in stationary phase. (Chlorophyll continues to decline continuously because of photodecomposition.)

Referring to Fig. 3 for comparison, we see that the cycle of events in batch culture is simply a particular transient reflection of the changes in cell properties with turnover or growth rate which we have already seen in steady state conditions. Thus, lag and stationary phases are simply an antisymmetric pair of extremes on the continuum of cell property changes with turnover rate. Therefore, a single explanation will account for all of these, as will be shown with the extensive model. Nowhere else is the complete uncoupling of growth and division more clearly illustrated than in batch cultures.

2. *New Chemostat Inocula*

Because of lag phase, there is a tendency for new inocula to be washed out of a chemostat before division begins. For this reason, the most reliable method of starting up a chemostat is to establish a large, rapidly growing batch culture population before turning on the nutrient flow-through. This procedure makes transient analysis difficult, since conditions are difficult to define precisely.

The sudden switching on of nutrient flow is likely to produce oscillations in cell number, while biomass and chlorophyll respond generally without oscillation. This is illustrated for *Selenastrum* and *Chlorella* in Figs. 8 and 9, respectively. By contrast, a nonoscillating approach to the steady state is achieved when flow is turned on at the time of inoculation with already rapidly growing *Chlorella* (Fig. 10).

Otherwise, the approach of a new inoculum to a steady state in the chemostat shows strong similarities to the batch culture cycle, with a decline in cell size and chlorophyll content as the steady state is approached, illustrating further that the lag and stationary phases are merely special cases of the physiological differences between organisms at different growth rates.

3. *Chemostat Perturbations*

Several examples are shown here of steady state–transient–steady state perturbation experiments. Other examples may be found in Williams (1965).

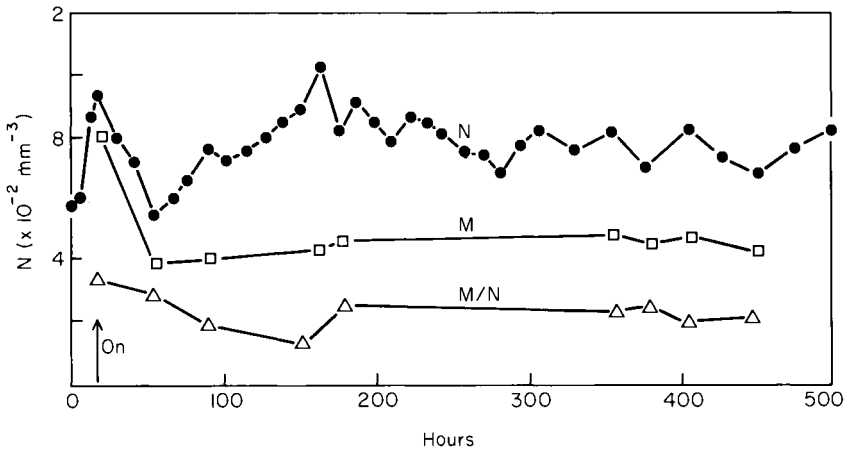

FIG. 8. New inoculum of *Selenastrum* in chemostat. Flow is turned on at arrow. *M/N*: average cell volume (in this case measured optically), *M*: biomass, *N*: cell number. Note irregular (?) oscillations.

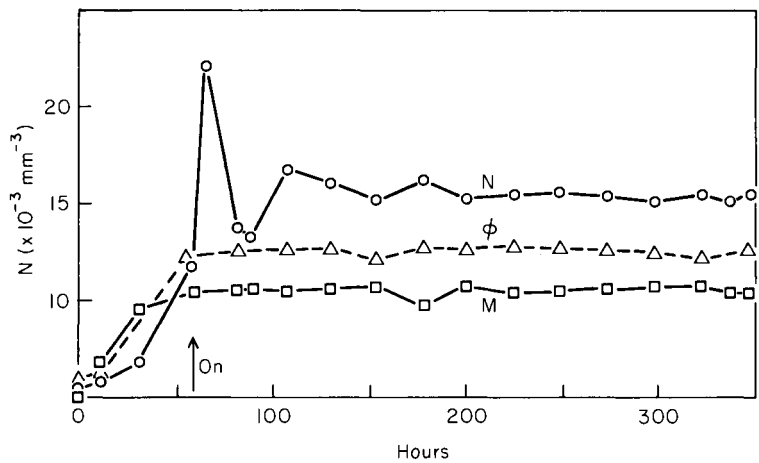

FIG. 9. New inoculum of *Chlorella* in chemostat. Flow is turned on at arrow. Note large, damped oscillations in cell number compared to uniform behavior of biomass. *N*: cell number, ϕ: chlorophyll, *M*: biomass.

a. *Step Function Perturbations.* A step function is defined as an instantaneous change of a constant parameter to a new constant value. I shall show one example of each for step function changes of limiting nutrient concentration and of flow rate.

(i) *Nutrient Concentration.* A *Selenastrum* culture is shown in Fig. 11 which has been stepped instantaneously from 100 μM nitrate

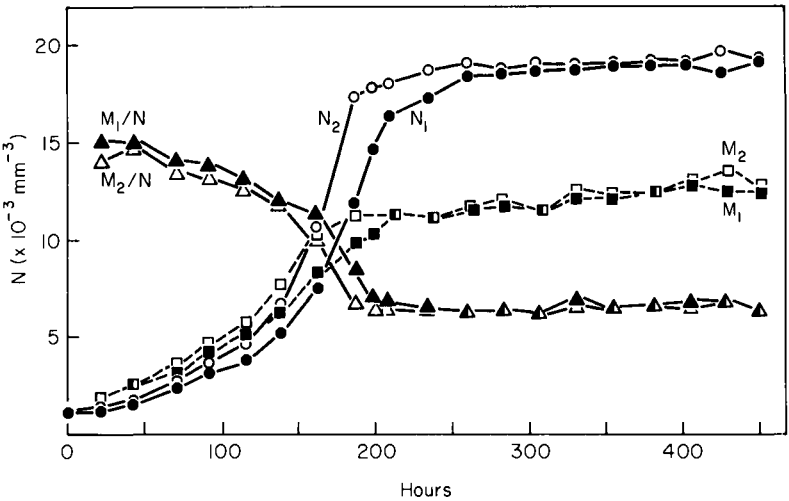

FIG. 10. New inoculum of two replicate *Chlorella* populations in chemostat, starting with already rapidly growing cells. Note smoothness of approach to steady state compared to Fig. 9. N: cell number, M: biomass, M/N: average cell volume. Subscripts (1, 2) identify the two populations.

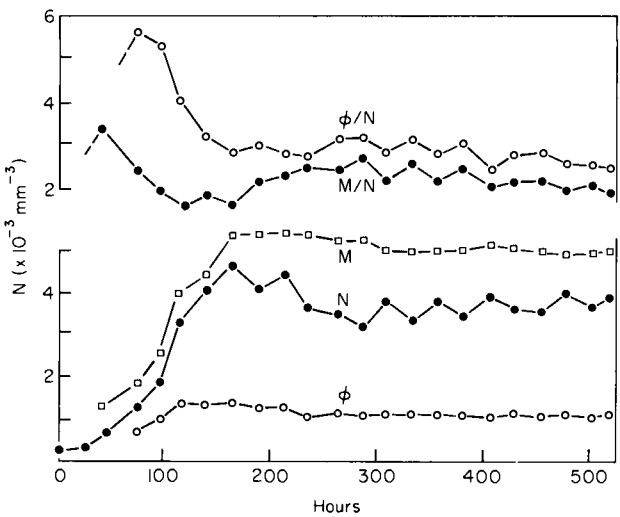

FIG. 11. Step function increase of nitrate concentration from 100 to 500 μM, for *Selenastrum* in chemostat. Note decreases in cell size and chlorophyll per cell as higher nutrient concentration is exhausted, and oscillatory behavior of cell number.

to 500 μM. This is not an ideal example in that preshift variables other than cell number were not measured. The initial and final cell sizes and chlorophyll should be identical because the flow rate and hence steady state growth rate remain constant throughout. Nevertheless, we can follow the response after the cells have increased size and chlorophyll content because of higher nutrient level. All three variables increase to new steady state standing crop values in response to the higher input nutrient concentrations. As the growth rate decreases to the steady state value, cell size and chlorophyll decline accordingly to values which should be identical to the initial conditions.

(ii) *Flow Rate.* In contrast to the above, a step function change in flow rate sets a new steady state growth rate, and hence leads to new cell size and chlorophyll contents. Except for cell number, changes in standing crop values are minimal. An example is shown in Fig. 12

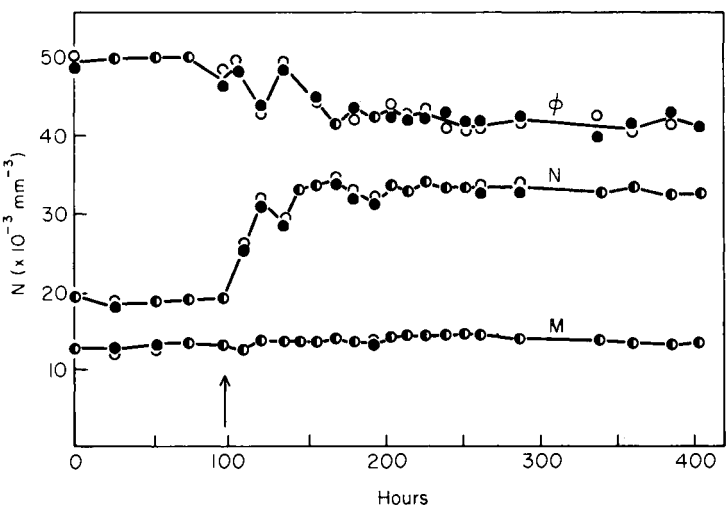

FIG. 12. Step function decrease to 50% flow rate for two replicate *Chlorella* populations. Notice large change in cell number compared to almost negligible change in biomass, causing about a 45% decrease in cell size.

showing a *Chlorella* population responding to a halving of flow rate. Since cell number increases significantly, and total biomass and chlorophyll change little, cell size and chlorophyll content decrease strikingly. The increase in cell number is the result of a lag in cell division response; cells continue to divide at the same rate as previously, but not being washed out as fast, until the new steady state cell number is achieved. This is a further example of the dissociation of growth and division

control processes. Oscillatory behavior, expecially in cell number, is present in both of the above experiments.

Other examples are in work by Williams (1965); this type of experiment corresponds to Caperon's (1969) "first experiment," measuring cell number of *Isochrysis*.

b. *Square Wave Perturbations.* A square wave perturbation is defined as an instantaneous shift of a parameter to a new constant value, held for a defined period of time (usually short) and then returned to its original value. I shall show one example each for square wave changes of flow rate and of temperature.

(i) *Flow Rate.* An example of a square wave cessation of flow rate is shown for *Selenastrum* in Fig. 13. Cells continue to divide at the same

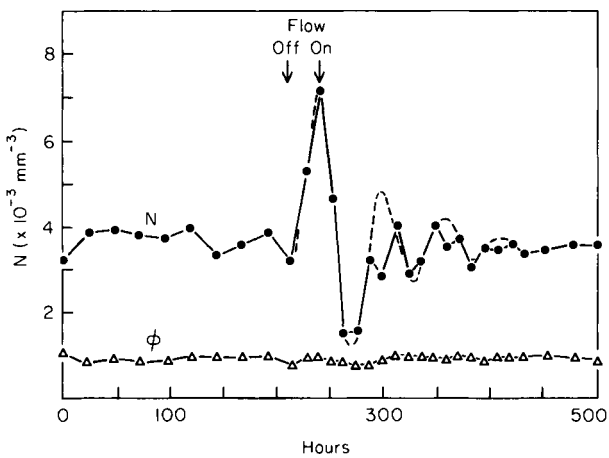

FIG. 13. Square wave cessation of flow rate for one day in a chemostat population of *Selenastrum*. Note constancy of chlorophyll compared to cell number. Dashed line is a damped sinusoid curve; discrepancies where maxima should be are the "notched peaks"; see text and Fig. 14.

rate, but since they are no longer washed out, increase in number. Chlorophyll standing crop remains constant, drastically reducing the chlorophyll content per cell. Although it is not shown quantitatively, cell size became much smaller; there was almost certainly little or no change in standing crop biomass.

When nutrient flow is turned on again, there is a sharp decline in cell number, with a corresponding increase in cell size, but no significant change in total chlorophyll (visually, this and other cultures look greenest at cell number minima). There is an oscillatory return to the original

cell number steady state value. This corresponds to Caperon's (1969) "second experiment" with *Isochrysis*, where there are overshoots, but no obvious oscillations.

The dashed line following the cell number trajectory is a damped sinusoid; the fit is everywhere excellent except at the maxima which show what I have called a "notched peak" (Williams, 1965). *Selenastrum* populations have subpopulations of cells dividing into two and four daughter cells (autospores) under the conditions used. Since oscillation of cell number implies at least a partial synchrony of cell division, one can show that a synchronization of the subpopulations will produce a higher harmonic to the fundamental frequency illustrated by the dashed line. The effect of this higher harmonic is to produce the "notched peak" effect. An example is shown in Fig. 14, and further details of

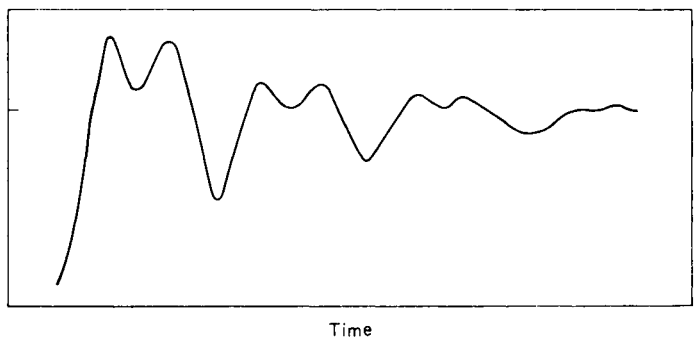

FIG. 14. The combination of two harmonics, representing division synchrony of subpopulations producing two and four daughter cells, resulting in the "notched peak" effect. Compare with Fig. 13.

the argument appear in my thesis (Williams, 1965). The argument must be regarded as at best semi-quantitative.

(ii) *Temperature.* Because of the drastic effects of temperature on cell size and other population measures, it is of interest to see the effects of a temperature pulse on the population behavior. One example is shown in Fig. 15 of a square wave temperature perturbation, admittedly accidental, from 22 to 27 C. The unique aspect of this perturbation is that, unlike other populations observed, cell number oscillations showed no sign of damping out for the almost 300 hr observed after the perturbation. Again qualitatively, cells were very small and very pale at the maxima and very large and very green at the minima, indicating much less, if any, response of biomass and total chlorophyll. Mr. Blaug is just completing an extensive study of temperature effects (1970). In

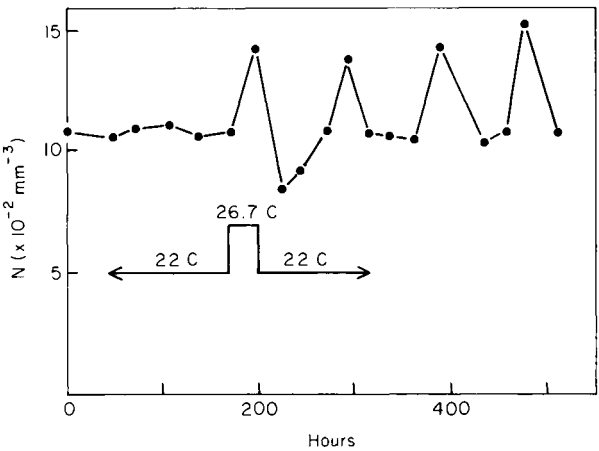

FIG. 15. Sustained oscillation following a square wave temperature shock to a *Selenastrum* population.

general, it seems that the effects of temperature perturbation are much more persistent than effects of nutrient and flow rate perturbation.

G. OSCILLATIONS

A generalization of the above studies is that oscillations occur primarily if not exclusively in cell number; biomass and chlorophyll generally approach a steady state monotonically. Observed amplitudes of oscillation range up to $\pm 75\%$ of the steady state cell numbers.

While we might expect a relationship between oscillation amplitude and the rate of approach to a steady state, this is not very satisfactory. Figure 16 shows the amplitude of initial over- (under) shoot as a function of the difference between growth rate and washout rate, i.e., the rate of approach. While there is some correlation, it is by no means a precise one.

On the other hand, there is an excellent and surprising relationship between period of oscillation (expressed as fractions of a generation time) and rate of approach, shown in Fig. 17. Except for population crashes in which cell disintegration occurred (Williams, 1965), the relationship is a remarkably precise straight line. This implies that the period of oscillation is a constant, regardless of culture conditions, and more remarkably, regardless of whether it is *Selenastrum* or *Chlorella*. Over all experiments, the oscillation period is 62.3 ± 7.1 hr. Also remarkable is the fact that the period is greater than most generation times.

I shall attempt to explain this bit of numerology in the following way.

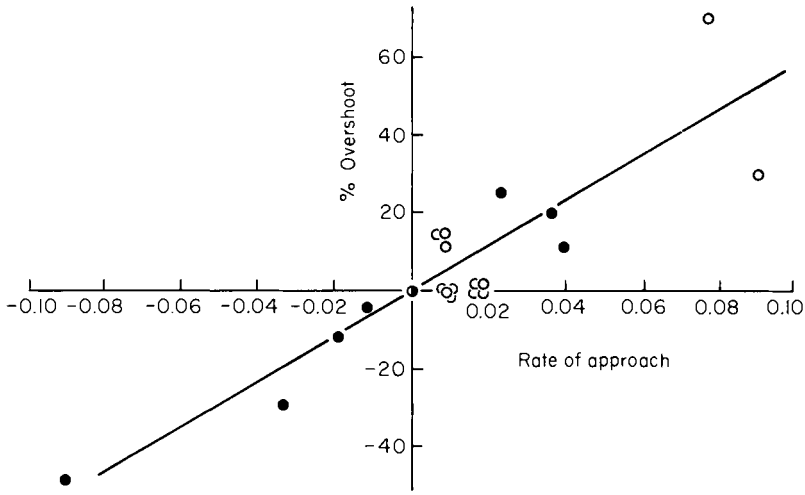

FIG. 16. Initial amplitude of oscillation versus rate of approach to a steady state for both *Chlorella* and *Selenastrum* cell number. ○: *Chlorella*, ●: *Selenastrum*.

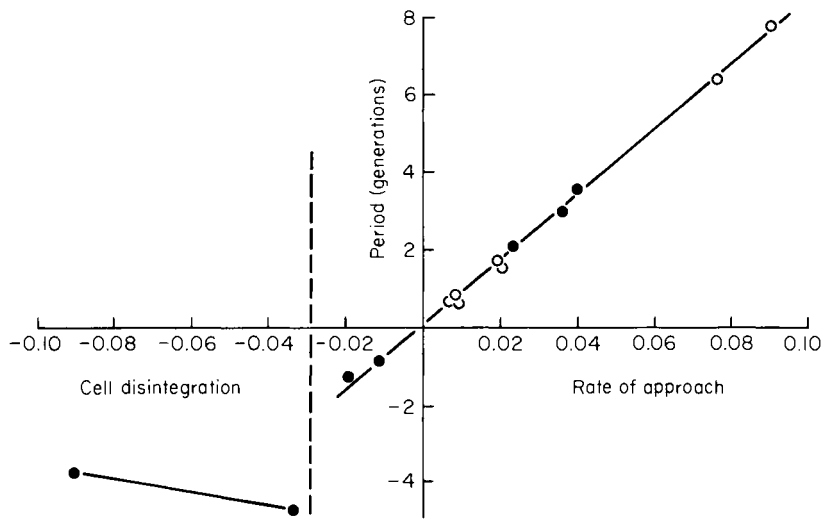

FIG. 17. Period of oscillation versus rate of approach to steady state. Period is expressed per generation time. Constant frequency is implied, unless cells disintegrate during extreme population crashes. ○: *Chlorella*, ●: *Selenastrum*.

Since I have shown cell division and growth to be loosely coupled, and since I have shown growth or mass increase to be temporally prior

to division response, this implies that there is a time lag in division response.

Hutchinson (1948) and Wangersky and Cunningham (1956, 1957) developed a general population model based on an abstract time lag built into the logistic equation. Their most complete form of the model is (1957)

$$\frac{dN(t)}{N(t)\,dt} = \frac{A}{K}\,[K - N(t - \tau)], \tag{3}$$

where K is the steady state number, $N(t)$ and $N(t - \tau)$ are numbers of organisms at times t and $t - \tau$, respectively, and A is a specific rate of approach to the steady state, which is a complicated form of another lag and an age structure, including a density-independent mortality term. Since the age structure in A is a linear transformation of the microbial age density functions to be developed in the next section, and since the washout from a chemostat is a density and age independent "mortality," we may accept the validity of the model for chemostat purposes. Empirically, the value of A is just the rate of approach calculated above (division rate minus washout rate).

The authors show that when oscillations occur in the above model, the oscillation period will be approximately 4.4τ. Thus the time lag for these populations will be $62.3/4.4 = \tau = 14.1$ hr. The minimum generation time of both *Chlorella* and *Selenastrum* under the conditions used is just about 14 hr (Williams, 1965). Thus we conclude tentatively that the response lag of a cell *is* its minimum generation time. Conversely, the minimum generation time is a simple expression of the time lag under steady state conditions. The response lag may be thus the minimum time required for the genome to replicate (Donachie, 1968; Donachie *et al.*, 1968).

H. Cell Size Distributions

It is impossible to pick out a cell from a population and measure its age. We can, however, measure age-dependent properties of cells: the simplest of these is cell size (volume or dry mass). The overall behavior of a population is the result of the distributions of ages and sizes of cells comprising the population, since chemical composition and physiological condition will be functions of age and size.

In this section I shall show the appearance of size distributions as measured by the Coulter Counter (see Section II.A) from steady state *Chlorella* cultures.

Figure 18 is an example of such distributions from two populations,

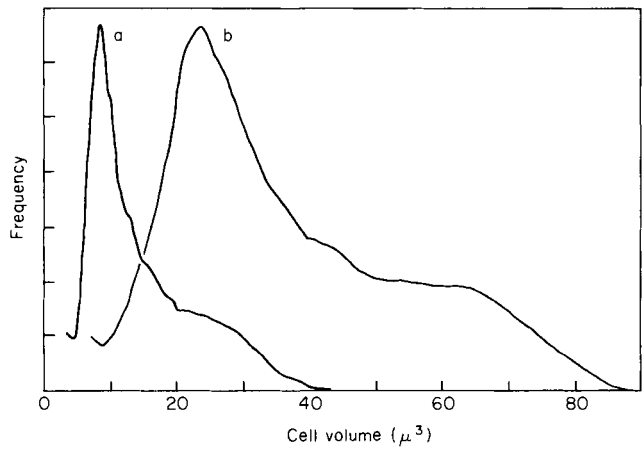

FIG. 18. Frequency of cells versus cell size for two steady state *Chlorella* populations. Note "plateau" on right of each, and note geometric similarity of the two.

one with large and the other with small cells. The distributions are remarkable in that there is an extensive "plateau" region on the right of each distribution. This plateau is absent from size distributions which have been reported for other cells (e.g., Kubitschek, 1969; Bell and Anderson, 1967; Scherbaum and Rasch, 1957).

The other feature of the two distributions shown in Fig. 18 is that they are remarkably similar in shape, despite the absolute differences in cell sizes. Figure 19 shows eight different size distributions from different experimental conditions (flow rate, temperature, CO_2), all scaled for equal means and areas. The similarity of shape is obvious. From the similarity of shape we can conclude that there are no differences in interdivision cell growth (and hence growth control) under different experimental conditions. When I develop the intensive model in a later section, I shall show how the size distributions may be accurately predicted, and how they allow us to deduce the growth curves of individual cells.

I. PHOTOPERIOD SYNCHRONIZED POPULATION

Photosynthetic cells have been shown to be easily entrained into repetitively synchronous divisions by growing them in a photoperiod (Tamiya, 1964; James, 1964; Bernstein, 1960; Howell, *et al.*, 1967). I report growth of *Selenastrum* synchronized by photoperiod in a chemostat.

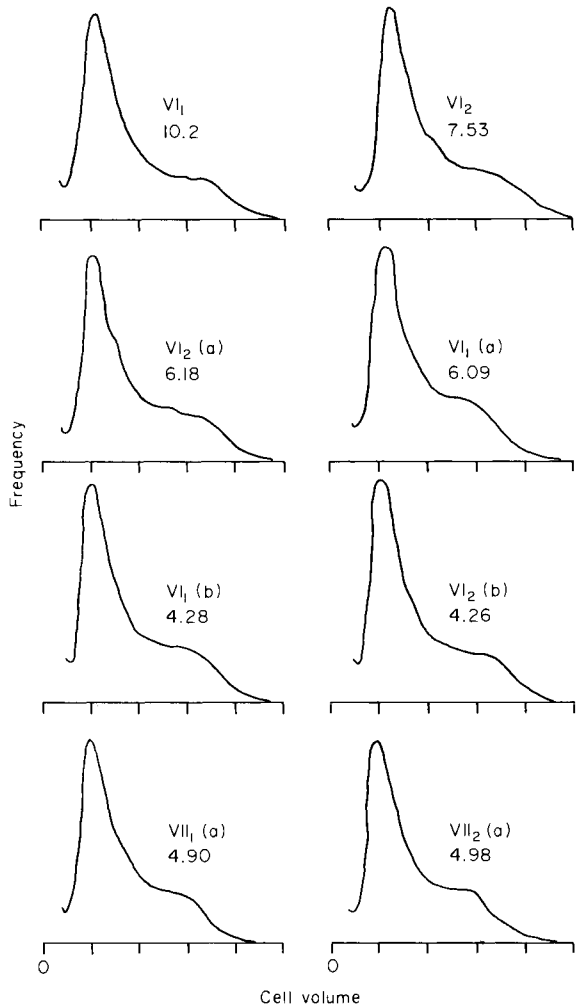

FIG. 19. Eight steady state size distributions from different conditions of growth rate, temperature, and CO_2, normalized for equal means and areas. Numbers at right of each are mean cell sizes. Note geometric similarity of all.

Existence in an open system with a photoperiod is in fact the natural state of existence for organisms. At any rate, when cells are synchronized, they must be all approximately the same age at the same time, and the sizes of cells should give us a direct measure of interdivision growth patterns.

Figure 20 shows the approach of *Selenastrum* to a steady state of

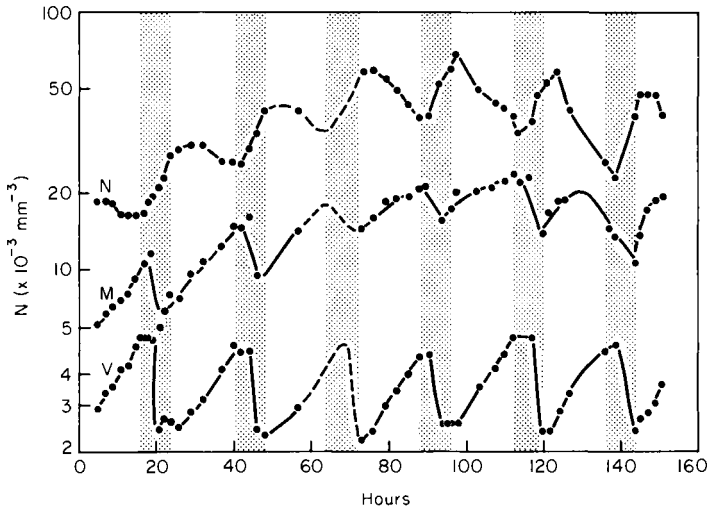

FIG. 20. Photoperiod entrained growth and division synchrony in a chemostat culture of *Selenastrum*. Here V is modal cell volume for $D = 2$ cells; see Fig. 21.

synchronous oscillation. Illumination was on a 16-hr light: 8-hr dark cycle. Unfortunately, this experiment was plagued by use of a highly erratic piston pump rather than the usual precise peristaltic pump. Hence the oscillations of cell number are not as uniform as might have been otherwise. But cell growth and division, as represented by the modal cell volumes in the size distributions, behaves in precisely periodic fashion.

Figure 21 shows a typical sequence of cell size distributions from neonatal to ripe to neonatal cells, and also shows a non-synchronous size distribution for comparison. During division, we can resolve two modes, representing the large ripe cells and the small neonatal cells just being formed. Apparent growth of cells seems to vary between approximately exponential and approximately linear, probably because of the erratic pumping of nutrient. Under these conditions of light entrainment, we can clearly confirm the existence of subpopulations of cells dividing into two and four daughters, represented by the distribution peaks.

J. SUMMARY OF EXPERIMENTAL STUDIES

Methodology and results are reported from studies on the growth dynamics of *Chlorella* and *Selenastrum* in (usually) precisely controlled chemostat cultures. Populations were accurately assayed for cell number,

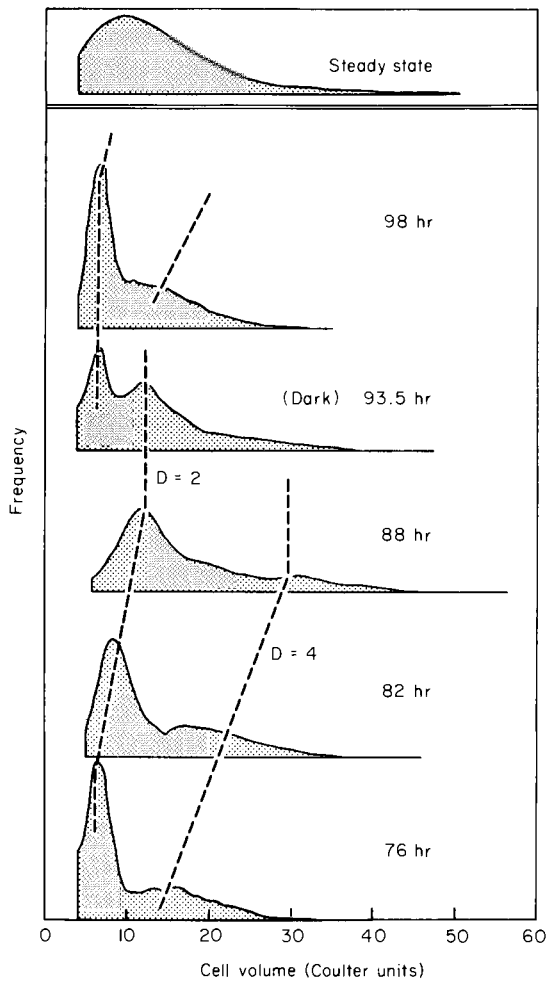

FIG. 21. Partial sequence of *Selenastrum* size distributions over one cycle of synchronous growth (bottom to top). Dashed lines follow modes of cells dividing into two ($D = 2$) and four ($D = 4$) daughter cells. Steady state size distribution at top for comparison.

cell size and size distributions, chlorophyll, and (less accurately) unused limiting nutrient (nitrate).

Steady state regulation of all population variables was quite precise over periods of less than 15 generations (doubling times). Coefficients of variation were as low as 0.0175. The small steady state fluctuations in

cell number are nonrandom, probably reflecting the discrete nature of the cell division cycle, and a loose coupling of cell division to the cell growth process. Total biomass and chlorophyll variabilities were also small, but generally random.

Over longer periods there were occasional upward or downward trends, which remain unexplained. A trend in one population variable was unrelated to the presence or absence of a trend in any other variable in the same population. All trends were less than 1% per generation.

Not only population size but cellular characteristics are functions of steady state turnover rates. Population numbers and biomass decline with increasing flow rates, as predicted by the simple chemostat theory. But they do so with very different slopes, contrary to the theory. Consequently, average cell size is a positively accelerating, increasing function of specific growth rate. Cell size changes represent the uncoupling of cell growth and division processes, and larger cells are the result of more synthetic machinery at higher growth rates.

Completely contrary to the basic theory is the increase of total population chlorophyll with increasing growth rate; while numbers and biomass decline, chlorophyll increases. Extrapolation to zero growth rate partitions the chlorophyll into that required for maintenance and that required for growth.

A temperature increase of 3 C causes a doubling of steady state cell number, but no significant change in total biomass or chlorophyll. Cell size is thus halved over only a 3 C range.

Elevated CO_2 causes more than a 30% decrease in cell number and total chlorophyll but no change in total biomass. Larger cells are not the result of accumulation of carbon compounds at high CO_2 levels.

The unused limiting nutrient concentration is 20–100 times lower than that predicted by the simple chemostat theory. This is explained by accumulation of cellular metabolite pools.

Transient population behavior was studied under conditions of batch culture, new chemostat inocula, and perturbations of steady state chemostats. Generally, biomass and chlorophyll appear critically damped, approaching a steady state monotonically, while cell number can oscillate violently under certain conditions. The transient data indicate a loose coupling between growth and division, and a time lag between response of mass growth and cell division. The oscillation period is a constant, indicating a division time lag which is equal to the minimum generation time.

Cell size distributions are presented which differ from most previous observations in the presence of a large "plateau" on the right side. The distributions are geometrically similar, regardless of cell size or

environmental condition, indicating a constancy in the cell control and growth processes.

Preliminary results of photoperiod synchronized populations are presented for the open system chemostat, and its relevance to natural systems emphasized.

III. The Model for Extensive Properties

In this section and the next I develop two model systems, one devoted to a population's *extensive* properties, the other to its *intensive* properties. Although the terms "extensive" and "intensive" do not have here exactly their usual physical definitions, the spirit is identical. Extensive properties refer to overall measures of population size, such as numbers, biomass, and amount of nutrient available, as well as derived measures such as average mass per cell. Intensive properties refer to frequency distributions of age, size, and chemical components *within* a given population. Both approaches are based on my conviction that a knowledge of physiological and reproductive behavior in the individual allows us simply to deduce the behavior of the population.

Qualitatively, many of the experimental observations reported above are not unique to green algae; most have been reported for at least one other organism. I have argued elsewhere (Williams, 1967) that there are a very large number of dynamical features universal to all cell populations, whether they be bacteria, algae, protozoa, or even mammalian cells in culture. Through elucidation of these universal features, it is my hope that we can approach the fundamental dynamical principles of populations.

Thus the models are broadly based, and I have consciously attempted to avoid reference to details concerning any particular taxonomic group. I begin with the model for extensive properties.

Much of the extensive model is already published, but with a cell-biological emphasis (Williams, 1967). I repeat it here for ecological emphasis, and greater accessibility to ecologists. Some new predictions have been derived, which are included here.

As a basis against which to test the population model, I list what I believe is a minimal set of universal features of microbial population behavior:

(i) "lag phase," during which biomass increases, but numbers do not;

(ii) an approximately "exponential phase," during which all population variables increase at about the same rate;

(iii) "stationary phase," during which the population no longer increases, but remains viable at a minimum cell size;

(iv) greater cell size at higher specific growth rates, i.e., at higher nutrient levels;

(v) different chemical composition at different growth rates and nutrient levels; especially, higher contents of synthetic machinery at higher growth rates;

(vi) absence of lag phase when a population is started with already rapidly growing cells;

(vii) ability of a population to increase in number after the removal of all nutrients; ability of starved cells to absorb nutrient for use in division at a later time;

(viii) differences in response lag of different population variables following an environmental change; a temporal precedence of biomass response over number response;

(ix) overall shapes of population growth and response curves, measuring more than one variable, and under various conditions;

(x) positive sister–sister cell correlations in size and generation time;

(xi) environmentally entrained population growth and reproductive synchrony;

(xii) cell and population changes as a function of temperature.

I shall present partial documentation for the ubiquity of these microbial population features as I proceed. I believe also that most or all of these principles can be applied to populations of higher organisms with little or no modification except changes in wording.

I begin with the notion of a cell, and derive the population behavior from it.

A. General Model of a Cell

We start with the obvious functional differences between the growth and replicative processes, to postulate the existence of two separately measurable portions of the cell, one for each process. Hence there is one fundamental assumption: *The cell comprises two basic portions, a synthetic portion* (s) *and a structural/genetic portion* (n). Stipulative assumptions are:

(i) The synthetic portion (s) increases by uptake of externally available nutrient (c);

(ii) The structural/genetic portion (n) increases in turn from materials in the synthetic portion;

(iii) The total cell mass $m = s + n$.

An important stipulation is:

(iv) *cell division into D equal daughter cells occurs if and only if the n-portion has become D times its initial size.*

For most cells, $D = 2$ and division will occur when the n-portion has doubled; for algae such as studied above, D may be 2, 4, 8,..., depending on environmental conditions (Fritsch, 1961; Morimura, 1959).

Since the necessary and sufficient condition for cell division is a D-fold increase of n, it follows that the size of the s-portion, and hence the overall size of the cell at division, is not uniquely determined. Size differences between cells are determined by variations in s which will be a function of nutrient conditions through the cell cycle as well as a function of its initial (neonatal) value s_0 . If a dividing cell apportions each component systematically to its daughter cells, then s_0 is a function of the state of a cell's immediate ancestor. Therefore, the model provides for cell size and composition being determined by both nutrient conditions and ancestral history.

The synthetic portion may be interpreted as the raw materials and synthetic machinery of the cell (soluble pools, precursor material, synthetic enzymes, chlorophyll, ribosomes, and other RNA's). The structural/genetic portion may be interpreted as the genome along with structures and materials necessary to maintain a minimal intact and viable cell (cell wall and membranes, any self-replicating cytoplasmic inclusions, and the genome (DNA) with its associated structures, especially protein). This interpretation is more fully discussed in my earlier paper (Williams, 1967).

It remains only to specify the exact functions by which the cell and environmental components interact, consistent with the above assumptions. This is done simply by assuming that:

(v) reaction rates are proportional to quantities present, and are bimolecular.

Hence,

$$ds/dt = k_1cm - k_2sn, \tag{4}$$

and

$$dn/dt = k_2sn. \tag{5}$$

Since $m = s + n$, the overall cell growth rate is

$$dm/dt = k_1cm. \tag{6}$$

Clearly, since cell growth is a function of an external nutrient dynamics

yet to be specified, and since overall growth sheds no light on the s–n interactions, empirical observation of individual cells will provide little or no information with which to test this model. We thus create populations of such model cells, to provide testable consequences.

B. Populations of Model Cells

To have a population we must have an environment, and consequently we must specify a nutrient dynamics. For present purposes, I shall make the simplest possible assumption of an open system environment, namely:

(vi) there is a constant input to the environment of nutrient with concentration C_0 at rate k_0 ; there is a constant output from the environment of unused nutrient (C) and organisms* at rate k_0 .

This assumption effectively defines a chemostat, but it is also nearly true of a stable natural environment (e.g. Silver Springs: Odum, 1957). Clearly, the definition of a particular environment is arbitrary, and may be done in any manner conforming to experimental or field conditions. We use the well-defined chemostat because its simplicity makes it easy to study implications of the model.

To study the population behavior of these model cells, we sum over the individual s and n components. Thus, if cell division is approximately asynchronous, the extensive variables of the population may be represented by the following equations, shown schematically in Fig. 22.

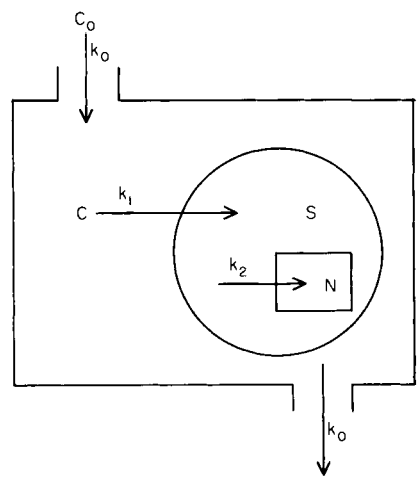

FIG. 22. Diagrammatic representation of population constructed of model cells in the assumed open system environment. C_0 : input nutrient concentration; C: unused nutrient in environment; S: synthetic portion of population; N: structural/genetic portion of population equivalent to cell number.

* Again, output of organisms may correspond to mortality, predation, or emigration.

$$dC/dt = k_0(C_0 - C) - k_1CM, \tag{7}$$

$$dS/dt = k_1CM - k_2SN - k_0S, \tag{8}$$

and

$$dN/dt = k_2SN - k_0N, \tag{9}$$

where

$$M = S + N, \tag{10}$$

such that the total population's biomass is

$$dM/dt = k_1CM - k_0M, \tag{11}$$

where C, S, N, and M are the total population values of c, s, n, and m in Eqs. (4)–(6). They are thus the extensive population properties.

Since cell division is asynchronous, and because of assumption (iv), the number of cells in the population will be proportional to N; if N is measured in average cell equivalents, then cell number equals N. We shall also measure C and M in equivalent units, avoiding the need for conversion factors.

Clearly the representation of the extensive properties of the population in this manner is an (good) approximation based on the law of large numbers. But it is important to note that, even if we had *perfect* synchrony (an impossibility), we could never be more than 40% in error (see model of intensive properties) when estimating cell number by measuring the quantity of N. By contrast, much interesting population behavior takes place over several orders of magnitude.

C. Properties of the Model

The steady state and transient behavior of the extensive population has been studied by analog computer (see Williams, 1967, for program), and confirmed by digital computer (M. J. Bazin, personal communication). All of the twelve universal features of microbial populations, and most of the experimental results described above, are successfully mimicked by the model.

D. Precision of Steady State

Questions concerning precision of steady state do not really apply to this model. Since the model is asymptotically stable, any wobble about a steady state would have been noise in the analog computer. Perhaps the few percent variability observed in the experimental cultures is noise in the biological computer.

E. Steady State Dependence on Turnover Rate

For steady state chemostat populations, Eqs. (7)–(11) yield

$$\bar{C} = \frac{k_0}{k_1}, \tag{12}$$

$$\bar{S} = \frac{k_0}{k_2}, \tag{13}$$

$$\bar{M} = C_0 - \frac{k_0}{k_1}, \tag{14}$$

$$\bar{N} = C_0 - \frac{k_0(k_1 + k_2)}{k_1 k_2}, \tag{15}$$

$$\frac{\bar{M}}{\bar{N}} = 1 + \frac{k_0 k_1}{k_1 k_2 C - k_0(k_1 + k_2)}, \tag{16}$$

$$\frac{\bar{S}}{\bar{M}} = \frac{k_0 k_1}{k_2(k_1 C_0 - k_0)}, \tag{17}$$

and

$$\frac{\bar{S}}{\bar{N}} = \frac{k_0 k_1}{k_1 k_2 C_0 - k_0(k_1 + k_2)}. \tag{18}$$

Most of these steady state relations are shown graphically (Fig. 23) as

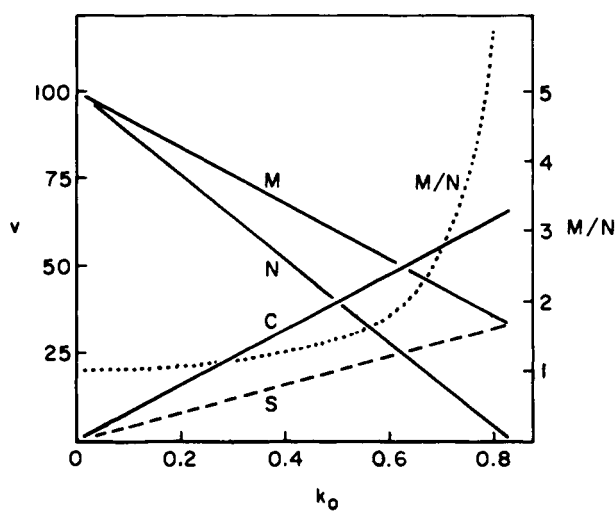

FIG. 23. Steady state turnover rate versus numbers, biomass, synthetic material, and average cell size for the model population. Compare with Figs. 2 and 3; compare chlorophyll (ϕ) with S. (See text.)

functions of turnover rate (equal to steady state growth rate k_0). Average cell size ($\overline{M/N}$) is a positively accelerating, increasing function of growth rate. Biomass ($\overline{M}$) and number ($\overline{N}$) decline with k_0 ; number declines more rapidly than biomass. The amount of synthetic portion (S) in the population increases, despite the decline of biomass and numbers. The higher the growth rate, the greater the fraction of biomass devoted to synthetic functions.

Compare Fig. 23 with Figs. 2 and 3. The experimental results are in good agreement with the theoretical. Let us interpret total chlorophyll (ϕ) as part of the synthetic portion (S); note that both show a linear increase with growth rate. Though not shown graphically, $\overline{S/M}$ and $\overline{S/N}$ are both positively accelerating, increasing functions of k_0 [Eqs. (17) and (18)], comparing favorably with ϕ/M and ϕ/N in Fig. 3.

The only discrepancy between theoretical and experimental is in the curvature of the M and N lines. The discrepancy results from there being in the model no hyperbolic saturation relation (Monod, 1942; Hinshelwood, 1946; Novick and Szilard, 1950; Williams, 1965; Caperon, 1967, 1968) for nutrient uptake. I have fitted my own data with the hyperbolic relation (Williams, 1965), but I have consciously avoided it here, in order to visualize most clearly the S–N relationships proposed. In a later paper I shall discuss the combined S–N model and hyperbolic relation.

With the exception noted, agreement is good for the *Chlorella* populations. Agreement is just as good with bacterial populations (Herbert, 1959; Maaløe and Kjeldgaard, 1966), where it has been shown that increased cell size is due to increased numbers of ribosomes, certainly a major part of the cells' synthetic machinery (S).

F. Temperature Effects

The model also predicts cell and population changes as a function of temperature. As is reasonable for chemical and biological rate constants, we assume the uptake and division rates are functions of temperature, each with a temperature optimum. Let $k_1 = f(T)$ and $k_2 = g(T)$ with optima at T_1 and T_2, respectively. These are shown schematically in Fig. 24. Then, for the chemostat steady states,

$$\bar{M}(T) = C_0 - \frac{k_0}{f(T)}, \tag{19}$$

$$\bar{N}(T) = C_0 - \frac{k_0}{f(T)} - \frac{k_0}{g(T)}, \tag{20}$$

and

$$\frac{\overline{M}}{N}(T) = 1 + \frac{k_0}{g(T)[C_0 - k_0/f(T)] - k_0}. \tag{21}$$

These relations predict a dependence of cell size on temperature which varies in intensity with turnover rate. Rapidly growing cells will change size much more radically than slowly growing cells, as illustrated in Fig. 25.

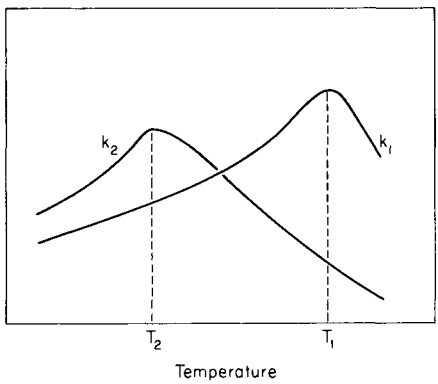

FIG. 24

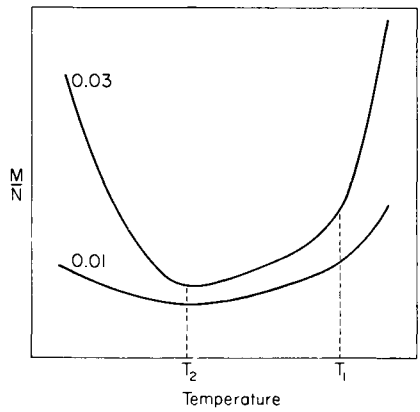

FIG. 25

FIG. 24. Assumption of temperature dependence of biological rate constants in model population, each with different optima T_1 and T_2.

FIG. 25. Average cell size versus temperature at two different turnover rates (k_0), under assumption in Fig. 24. Compare with Figs. 4 and 5. Size minimum occurs at optimum for cell division (T_2).

For numbers and biomass, the temperature dependence is identical to that shown in Fig. 5, where I have schematically represented Blaug's results (1970) on *Chlorella*. Clearly my data in Fig. 4 can be segments of such curves. The model predicts that the *biomass maximum* occurs at the temperature optimum for uptake (T_1), while the *cell size minimum* occurs at the temperature optimum for division (T_2).

Since batch culture is always transient, simple predictions are not as easy. But from Eq. (10), plus Eqs. (25)–(27) in the next section,

$$\frac{d \ln M}{d \ln N} = \frac{f(T)}{g(T)} \cdot \frac{C_0 + M_0 - M}{M - N} \tag{22}$$

Let $R = f(T)/g(T)$. If $dR/dT > 0$, cells will be larger at higher temperatures. Thus $dR/dT = 0$ implies cell size independent of temperature, while $dR/dT < 0$ implies smaller cells at higher temperatures. All the examples I have found are of the last type, cells smaller at higher temperatures (Jollos, 1913; Scherbaum and Loefer, 1964; Morimura, 1959). Maaløe and Kjeldgaard (1966) claim temperature independence for *Salmonella* cell size, but close examination of the data shows a slight decrease at higher temperatures. Aside from *Chlorella*, *Tetrahymena* has been investigated most extensively (Zeuthen, 1964), showing a curve very similar to those in Fig. 25, with a cell size minimum at the division optimum.

Then $dR/dT < 0$ is a formal statement of the generalization (Zeuthen, 1964) that cell division processes are more temperature sensitive than uptake processes.

G. Batch Culture

By setting $k_0 = 0$ in Eqs. (7)–(11), we simulate the unrenewed or batch culture, a closed system

$$dC/dt = -k_1CM, \tag{23}$$

$$dS/dt = k_1CM - k_2SN, \tag{24}$$

$$dN/dt = k_2SN, \tag{25}$$

and

$$dM/dt = k_1CM. \tag{26}$$

Consider for the moment only biomass and nutrient, and let M_0 and C_0 be their initial values, respectively. Since this is a closed system,

$$C = M_0 + C_0 - M \tag{27}$$

at any later time, due to conservation of mass. Substituting into Eqs. (23) and (26),

$$dM/dt = -dC/dt = k_1M(C_0 + M_0) - k_1M^2. \tag{28}$$

Integrating,*

$$M = \frac{C_0 + M_0}{1 + (C_0/M_0)\exp[-k_1t(C_0 + M_0)]}, \tag{29}$$

and

$$C = \frac{C_0 + M_0}{1 + (M_0/C_0)\exp[k_1t(C_0 + M_0)]}. \tag{30}$$

* This expression was printed incorrectly in my original paper, and has been quoted in its incorrect form (Thrall *et al.*, 1967).

Equation (28) is formally identical to the logistic equation,

$$dN/dt = rN - (r/K)N^2, \tag{31}$$

where r is the so-called "intrinsic rate of increase," and K is the stationary value, or "carrying capacity of the environment." Here r corresponds to $k_1(C_0 + M_0)$, while K corresponds to $(C_0 + M_0)$. Thus, in this model the intrinsic rate of increase is neither a constant nor intrinsic; it is a function of nutrient concentration and initial population size. The "carrying capacity" is also a function of initial population size. I reemphasize a point made by Smith (1952): that the logistic equation is conceptually restricted to closed system populations. Note that the formal similarity to the logistic holds only for biomass.

Figure 26 shows the dynamic behavior of the model population in

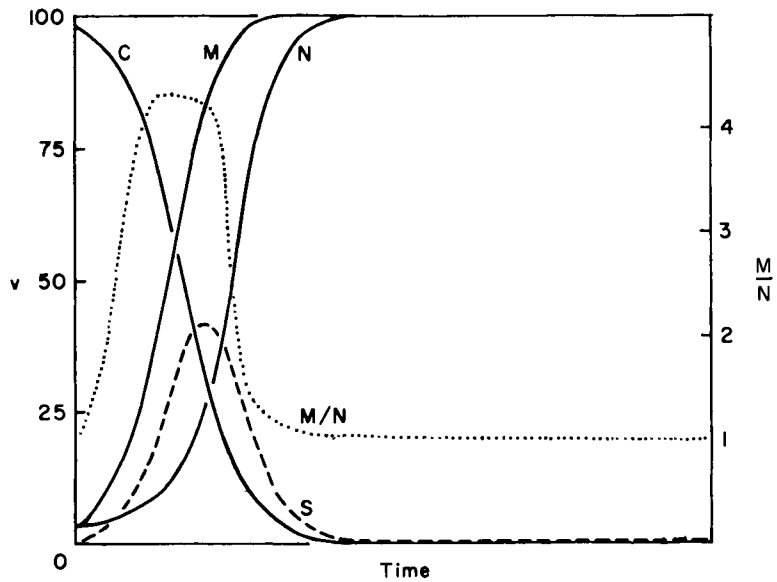

FIG. 26. Batch culture growth cycle for model population, showing lag in numbers but not biomass, exponential and stationary phases. Note cyclic cell size changes. Compare with Figs. 6 and 7; compare chlorophyll (ϕ) with S.

batch culture, when inoculated with stationary cells. These are non-growing cells which are the smallest possible cells still intact and viable (set Eqs. (23)–(26) equal to zero with $M, N > 0$; then $C = S = 0$ and $M = N$). The growth cycle clearly shows:

(i) a lag phase with biomass increase, but little increase in numbers;

(ii) an approximately exponential phase with biomass and numbers increasing;

(iii) cells largest during exponential phase;

(iv) since cell size changes as the result of changes in S, the cells' "chemical composition" changes through the cycle;

(v) biomass becomes stationary before number;

(vi) a stationary phase as defined above.

Comparison with the experimental results in Figs. 6 and 7 shows strong similarities. Again compare chlorophyll (ϕ) with S, where the exponential decline in ϕ is simulated by the asymptotic approach of S to 0. These features are typical of virtually all kinds of cells in batch culture (Hershey and Bronfenbrenner, 1938; Maaløe and Kjeldgaard, 1966; Scherbaum, 1956; Harris, 1964).

Again we lose exact detail in the shape of the curve because there is no hyperbolic nutrient uptake term present (see discussion in Section III.E).

Inoculation of a culture with already rapidly growing cells (M/N large) reduces or eliminates the lag phase. This is illustrated in Fig. 27, where

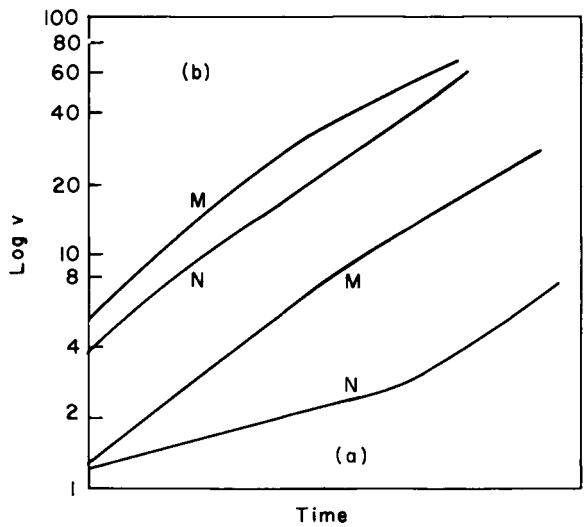

FIG. 27. Semilog plot of initial growth of model populations started with (a) stationary cells ($M_0/N_0 = 1$), and (b) rapidly growing cells ($M_0/N_0 = 4$). Curves spaced arbitrarily on ordinate.

the initial phases of population growth are shown for a stationary and a rapidly growing inoculum. Although the lag in the stationary inoculum is not perfect ($dN/dt = 0$), neither is it experimentally in Fig. 6.

It is a common observation that cells can continue to divide once or twice after having been removed from all nutrient. This means essentially that division can occur from utilization of nutrient absorbed at an earlier time. Similar experiments have shown that starved cells can rapidly absorb nutrient for use in division at a later time (Ketchum, 1939). Figure 28 shows a simulation of nutrient removal from a growing

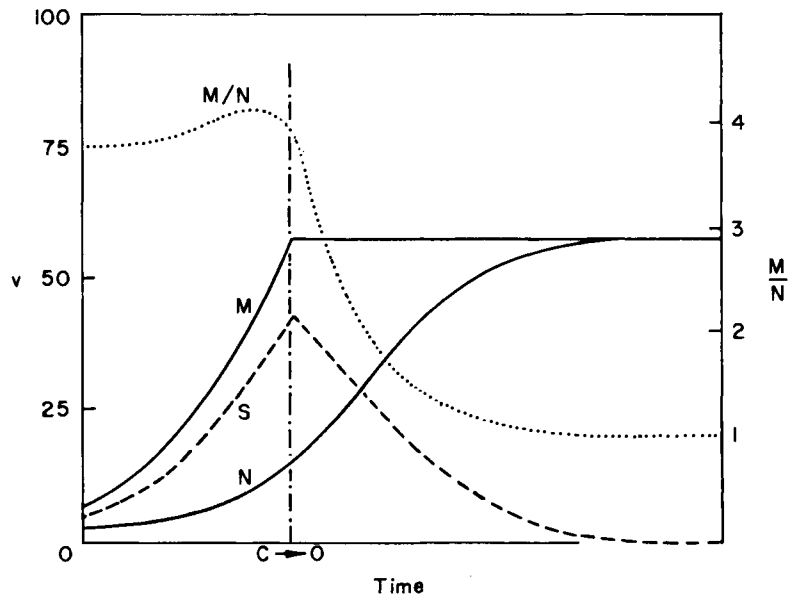

FIG. 28. Population's nutrient removed at vertical broken line; note continued increase in cell number.

population. In the absence of nutrient no further biomass increase occurs, but cells continue to divide, yielding a final fourfold increase in numbers. This may be thought of as an abrupt version of what happens when organisms exhaust their nutrient (cf. Fig. 26): biomass no longer increases but cell division continues, until internal synthetic pools are exhausted.

H. CHEMOSTAT TRANSIENTS

The behavior of a new inoculum in the chemostat is simulated in Fig. 29, starting from a stationary inoculum. Note the small but definite initial decrease in cell number (this is confirmed by Bazin's more precise digital simulation). Recall the discussion in Section II.F.2 concerning

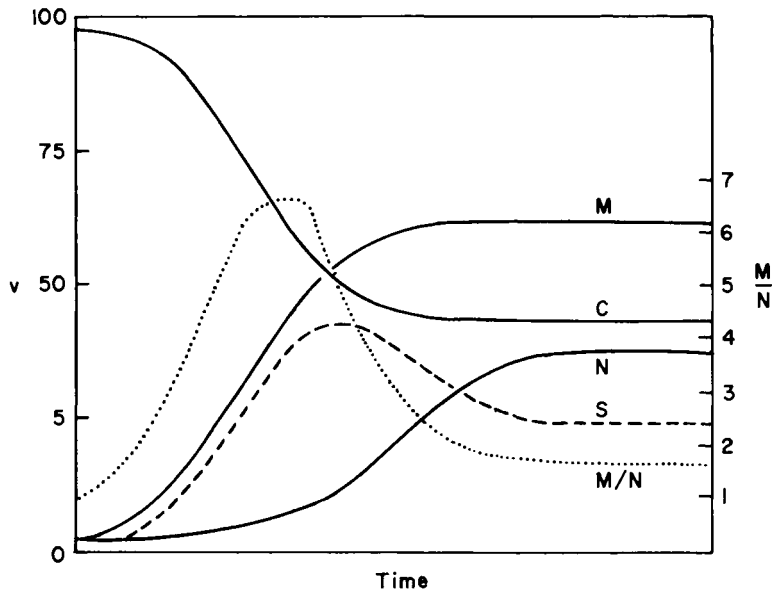

FIG. 29. Approach to chemostat steady state of new inoculum of a model population. Compare with Fig. 10.

the difficulties of starting chemostat cultures with flow on. Minor instabilities in the analog computer did in fact cause a few similar computer runs to go to extinction during the initial phases.

Cell size becomes very large as the population increases toward its steady state, then declines into its appropriate steady state value. Again biomass reaches its steady state much sooner than cell number. Essentially, the features shown here are similar to those shown for batch culture, except that the population terminates in an open system steady state. This simulation corresponds most closely to the experimental results shown in Fig. 10, where similar features will be found.

Step function changes are illustrated in Fig. 30, where flow rate is reduced to 25% of its original steady state value. Again we see a lag in the response of population numbers: cell division continues at essentially the previous rate until the new steady state cell size and composition are reached. Again biomass responds more readily and reaches a steady state sooner than number. Although this is a more extreme shift than that shown in Fig. 12, the similarities are clear, except for the oscillatory behavior of the experimental population numbers.

An example of a square wave cessation of flow rate is shown in Fig. 31.

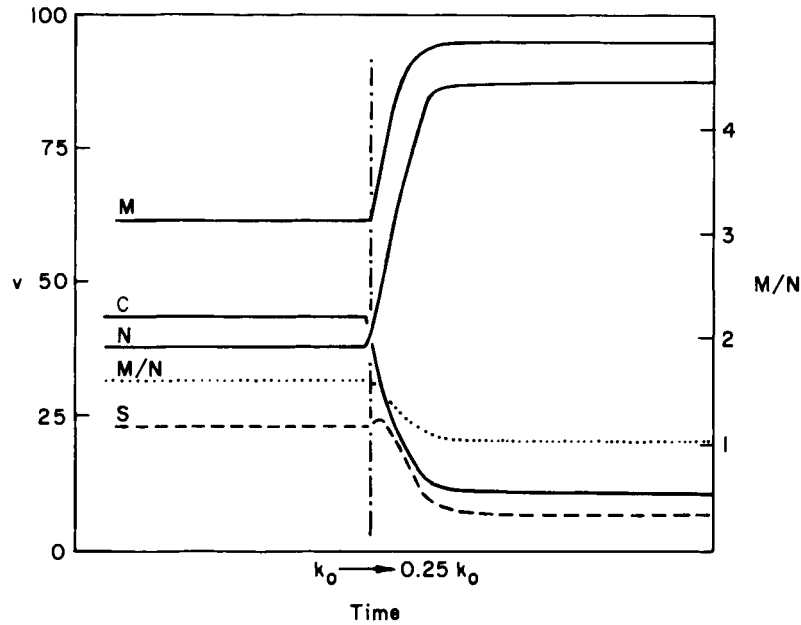

FIG. 30. Step function decrease to 25% turnover rate for model population in chemostat. Corresponds to "shift down" experiment in batch culture. Note relatively larger change in cell number than in biomass, causing decrease in cell size. Compare with Fig. 12.

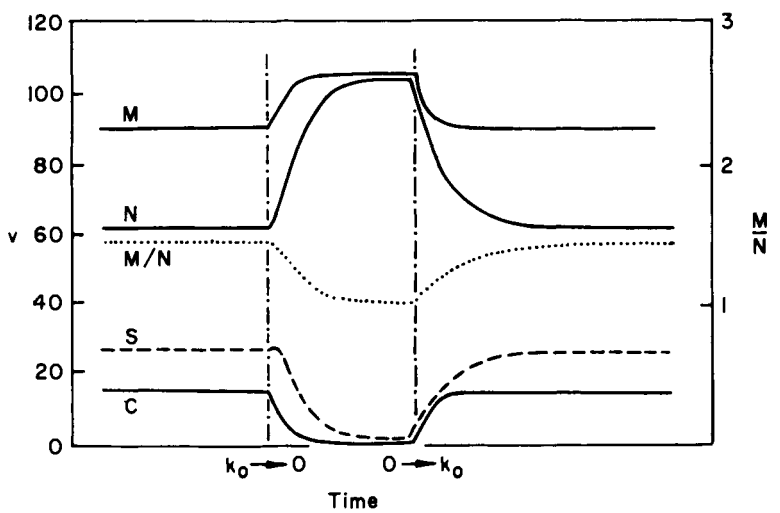

FIG. 31. Square wave cessation of flow rate for a model population in chemostat. Compare with Fig. 13; note absence of oscillation in model population.

Although the overall behavior is similar to that shown in Fig. 13, clearly there is a large discrepancy in oscillatory behavior.

These transient experiments are the chemostat equivalents of the bacterial batch culture "shift" and "double shift" experiments done by Maaløe and Kjeldgaard (1966). Translated to a batch culture condition, the above transients correspond well to their results.

I. Environmentally Entrained Synchrony

The extensive model was by no means designed to be concerned with questions concerning synchronous growth and division, since synchrony involves considerations of age structure not mentioned in the model.

It is of interest, therefore, that under certain conditions the model does predict synchronous behavior somewhat resembling that observed experimentally.

To simulate the photoperiod-induced synchrony described above, we mimic the dark period by setting $k_1 = 0$ for about 40% of a generation time. The population is otherwise identical to that shown in Fig. 29. (Although nitrates and phosphates have been shown to be taken up in the dark (Ketchum, 1939), overall growth effectively ceases in inorganic medium, as shown by the above experiments (and, e.g., Cook, 1961); hence we are justified to a first approximation in simulating darkness by $k_1 = 0$.)

The results are shown in Fig. 32. (I am most grateful to M. J. Bazin

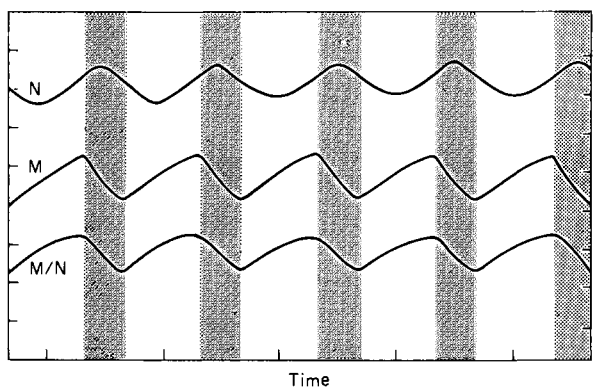

Fig. 32. Simulation of photoperiod-induced growth and division synchrony in a model population. Compare with Fig. 20.

for these digital computer results.) The biomass and cell size behavior are reasonable approximations of those observed experimentally, but

cell number behavior is inferior: although the phasing is approximately correct (number maxima in dark period), the sharpness and amplitude of oscillation are poor compared to those observed experimentally (Fig. 20; Cook, 1961; Morimura, 1959). Since it has been shown that light inhibits the process of cell division (Sorokin, 1960; Tamiya, 1964), we could realistically improve the synchrony by depressing the value of k_2 during the light period. This latter approach seems for now to be forced and artificial, however.

Pulsing of nutrient gives similar results, resembling chemostat experiments by Goodwin (1969) and Hansche (1969), pulsing phosphate to bacteria, and glucose to yeast, respectively. Figure 32 is very similar to Goodwin's results.

Although the degree of realism achieved in simulating synchrony is not good, it seems enticing that some of the basic dynamics of synchronous populations can be mimicked without introducing an age structure.

J. Generation Time Correlations

Without developing a stochastic model to pursue cell generation time correlations, we simply note in passing that the model predicts such correlations.

Since the initial values of the synthetic portions of neonatal cells ($s_{0,1}$, $s_{0,2}$,..., $s_{0,D}$) are by definition each $(1/D)$ times the value of s in the ripe mother cell, we see that a large mother cell will endow each of its daughters with a large s-portion, while a small mother cell will endow each of its daughters with a small s-portion.

The initial growth rates of the n-portion are functions of the initial s-portion, $dn_0/dt = k_2 s_0 n_0$. Other things equal, larger s_0 will give the n-portion a head start on its D-fold maturation growth. Hence n-portions with larger s_0 will be D times larger in a shorter time, i.e., will have shorter generation times. Thus there will be a positive sister–sister correlation in generation times.

Positive sister–sister generation time correlations have been observed several times (e.g., Powell, 1958; Kubitschek, 1966); generation time correlation with initial size is partly confirming, partly not (Kubitschek, 1966).

There is no relation specified between mother and daughter cell generation times, since we have not specified the time course by which the ripe mother cell accumulated a large or small s-portion. Experimentally, there is usually no mother–daughter correlation.

K. Discussion and Critique

I have attempted to show that a number of seemingly unconnected but universal features of microbial population dynamics can be predicted, and hence "explained," by one new, simple but obvious, postulate concerning the nutritive (s) and reproductive (n) functions of a cell. I have tried to maximize simplicity throughout to gain breadth. Qualitatively, most of the features of the model are insensitive to the exact way in which the s–n interaction kinetics are specified. The kinetics, as well as the environmental postulate (chemostat), are the simplest I can think of to explore the consequences of the model. There seem to be a large number of testable consequences, such that experiments can be done to provide future modification or rejection of the model. It has the desirable property of anacalyptic theories: vulnerability. It is therefore more important to explore what the model *cannot* do.

First, the model in its present form cannot account for any of the oscillatory behavior I have observed in the chemostat (except under photoperiod entrainment). The model *does* produce transient overshooting, but it is non-oscillatory. Finn and Wilson (1959) and Droop (1966) have also reported some oscillatory behavior in the chemostat, particularly following large, sudden, environmental changes. Since oscillation in numbers in the chemostat implies a division synchrony, it is likely that an age structure will have to be introduced in order to simulate realistically the observed oscillations in cell number. I make some attempts in this direction in the next section.

Second, as I have mentioned, the model does not take account of saturation conditions leading to a maximum growth rate. I shall discuss this in a later paper, where I shall show that the usual Michaelis–Menten type rectangular hyperbola is inappropriate except for batch culture.

Third, I cannot account for the observed very low nutrient concentrations with the model, although its explanation by intracellular pools is consistent with the model's fundamental assumption. It is not clear how universal my very low nutrient concentrations, or Caperon's (1969) nitrate constancy at different growth rates, may be.

Fourth, the model cannot account for some of the anomalous results obtained at very high or very low flow rates (e.g. Williams, 1965; Jannasch, 1967; Herbert, 1959).

Fifth, the model cannot account for the observed CO_2 effects or effects such as autoinhibition by exometabolites, simply because there have been no extra variables introduced to cover such effects.

Other shortcomings, of more cell-biological than ecological relevance, are discussed in the original paper.

Finally, I have not fitted the model statistically to the data; I feel it is premature, and a good fit might be misleading. To quote A. J. Lotka:

> It must be remembered that the mathematical method is concerned, not only, and indeed not primarily, with the calculation of numbers, but also, and more particularly, with the establishment of relations between magnitudes (Lotka, 1925).

IV. The Model for Intensive Properties

I shall first explore some aspects of the age distributions within microbial populations, and then explore the implications of age distribution with respect to age-dependent cell properties, such as size, chemical composition, etc.

Although Lotka investigated age distributions of populations in general in 1911 (see 1925), much of the recent activity has been in microbiological research, some highly abstract (e.g., Fredrickson *et al.*, 1967; Trucco, 1965), and some devoted to experimental findings (Collins and Richmond, 1962; Kubitschek, 1969; Scherbaum and Rasch, 1957; Harvey *et al.*, 1967). Lotka showed that the age distribution of a population is stable in the face of perturbations, *if* mortality and fecundity are time independent. He thus tended to dismiss age structure as having no profound effect on population growth.

Perhaps we are more accustomed today to think of rapidly changing environments: daily changes in light, temperature, etc., for microorganisms, as well as medical and nutritional advances in longevity, pollution, etc., for human populations. At any rate a population's age structure seems increasingly important for understanding its dynamics; I want to emphasize that age structure cannot be dismissed in the study of microbial populations. I hope the microbial populations may serve as a model for higher organisms. Many of the results that I present here are not new, but I want to present derivations which I have tried to develop for their intuitive appeal in the classroom, as well as to provide a framework for the new aspects to be presented. For now I restrict myself to the steady state (equal to constant specific growth rate), for that is currently where the best data occur for testing. The most rigorous formulation, suitable for transient analysis, is in the work by Fredrickson, *et al.* (1967); to my knowledge, it has not been applied to experimental populations.

A. Age Density Function: Notation

I shall use the following notation (most of which will disappear in the final formulation):

(i) t is clock time;
(ii) s is cell age (in clock time units, $\Delta s = \Delta t$; but $s = 0$ for a neonatal cell); $0 \leqslant s \leqslant \tau$;
(iii) τ is cell *generation* time (*not* doubling time);
(iv) D is number of daughter cells produced per cell per generation;
(v) μ is population specific growth rate ($\mu = \ln D/\tau = d \ln N(t)/dt$);
(vi) $N(t)$ is total number of cells at time t;
(vii) $N(t, s/ds)$ is *number* of cells in the age interval s to $s + ds$ at time t;
(viii) $n(s/ds)$ is *fraction* of cells in age interval s to $s + ds$;
(ix) $\partial(s)$ is death rate per cell at age s (or emigration or predation rate);
(x) $\sigma(s)$ is fraction of neonatal cells surviving until age s;
(xi) $n(s)$ is age density function, to be derived.

B. Batch Culture

We make only one assumption: that we have an *exponentially growing population of ideal cells*. By "ideal" cells I mean cells which divide into D daughters at exactly age $s = \tau$.

Then,

$$N(t) = N(0)\, e^{\mu t}; \qquad dN(t)/dt = \mu N(t), \tag{32}$$

where μ is a constant, and $\mu = \ln D/\tau$.

Since cells divide into D daughters at age τ,

$$N(t, 0/ds) = (1 - \partial(\tau)\, ds)\, DN(t - ds, \tau - ds/ds); \tag{33}$$

there are D times as many neonatal cells (age interval 0 to ds) at time t, as there were ripe cells (age interval $\tau - ds$ to τ) at time $t - ds$, minus the fraction $\partial(\tau)\, ds$ not surviving.

But since the mother cell "ceases to exist" at division, the net increase to the population in that time interval ds has been D daughters minus the one lost mother cell

$$N(t) - N(t - ds) = (1 - \partial(s)\, ds)(D - 1)\, N(t - ds, \tau - ds/ds), \tag{34}$$

The total population at t has increased by $(D - 1)$ times the number of ripe cells at $t - ds$, minus the fraction $\partial(s)\, ds$ not surviving.

Combining Eqs. (33) and (34),

$$N(t) - N(t - ds) = [(D - 1)/D]\, N(t, 0/ds). \tag{35}$$

But by definition,

$$N(t) - N(t - ds) = (dN(t)/ds)\, ds,$$

and

$$[N(t) - N(t - ds)]/N(t) = 1 - e^{-\mu ds} = \mu\, ds; \tag{36}$$

The *fractional* increase of the population in the time interval ds is simply the specific growth rate, and is time independent. Thus, combining Eqs. (35) and (36) with definition (viii),

$$n(0/ds) = N(t, 0/ds)/N(t) = [D/(D - 1)]\, \mu\, ds; \tag{37}$$

the fraction of neonatal cells in the population is a constant, independent of time, and is $[D/(D - 1)]$ times the specific growth rate. This defines our essential boundary condition.

To derive the distribution curve, we return to the *number* of cells, and note that

$$N(t + s, s/ds) = \sigma(s)\, N(t, 0/ds). \tag{38}$$

The population of cells at time $t + s$ with age s to $s + ds$ is exactly the surviving portion of the population of neonatal cells at time t.

Since we have shown that $n(0/ds)$ is time independent,

$$[N(t + s, s/ds)]/N(t) = \sigma(s)\, n(0/ds) \tag{39}$$

is also time independent. Since $e^{\mu s}$ is also time independent for any given s,

$$\frac{N(t + s, s/ds)}{N(t)\, e^{\mu s}} = \frac{N(t + s, s/ds)}{N(t + s)} = \sigma(s)\, n(0/ds)\, e^{-\mu s} \tag{40}$$

is also time independent. That is, the fraction of cells in any age class s to ds is a constant.

Thus we may write

$$n(s/ds) = \sigma(s)\, n(0/ds)\, e^{-\mu s}. \tag{41}$$

Returning to Eq. (37),

$$n(s/ds) = \sigma(s)[D/(D - 1)]\, \mu e^{-\mu s}\, ds, \tag{42}$$

for which the corresponding density function is

$$n(s) = \sigma(s)[D/(D-1)]\,\mu e^{-\mu s}. \tag{43}$$

Under conditions of exponential growth, mortality is usually negligible, or at least unmeasurable by viable counts. Thus, unless demanded by the experimental condition, we let $\sigma(s) = 1$, and *the final age density function is*

$$n(s) = [D/(D-1)]\,\mu e^{-\mu s}, \qquad 0 \leqslant s \leqslant \tau. \tag{44}$$

C. Chemostat Culture

In a steady state chemostat culture, the population numbers do not increase exponentially but remain constant. Thus $\mu = 0$ in Eq. (32).

But mortality is not negligible in the chemostat, in the form of emigration (washout). If the turnover rate of the chemostat is k_0, then $\partial(s) = k_0$, and is age independent. The fraction of cells surviving the washout "mortality" at age s is

$$\sigma(s) = \frac{N(t+s, s/ds)}{N(t, 0/ds)} = \frac{-1}{N(t, 0/ds)} \int_0^s N(t+s, s/ds)\,\partial(s)\,ds, \tag{45}$$

and substituting k_0 for $\partial(s)$,

$$\sigma(s) = \exp(-k_0 s), \tag{46}$$

assuming no other sources of mortality. Since we have a steady state, let $N(t) = N$ be time independent. Again we have

$$N(t, 0/ds) = (1 - k_0\,ds)\,DN(t - ds, \tau - ds/ds), \tag{33'}$$

by substituting k_0 for $\partial(s)$ in Eq. (33).

Since cells are washed out at rate k_0, the number of cells born in the age interval ds to just replace those lost will be, in order to maintain the steady state,

$$k_0 N\,ds = (1 - k_0\,ds)(D-1)\,N(t - ds, \tau - ds/ds), \tag{47}$$

similar to Eq. (34). Combining Eqs. (33') and (47), we have

$$n(0/ds) = [D/(D-1)]\,k_0\,ds. \tag{48}$$

Substituting Eq. (46) into Eq. (38),

$$N(t+s, s/ds) = \exp(-k_0 s)\,N(t, 0/ds). \tag{49}$$

Dividing by N, along with definition (viii),

$$N(t + s, s/ds)/N = n(0/ds) \exp(-k_0 s), \tag{50}$$

which because of time independence becomes

$$n(s/ds) = n(0/ds) \exp(-k_0 s), \tag{51}$$

and with Eq. (48) yields,

$$n(s/ds) = [D/(D - 1)]\, k_0 \exp(-k_0 s)\, ds, \tag{52}$$

whose density function is

$$n(s) = [D/(D - 1)]\, k_0 \exp(-k_0 s), \qquad 0 \leqslant s \leqslant \tau, \tag{53}$$

exactly corresponding to the batch culture density function in Eq. (44), but with k_0 , the washout rate, replacing μ, the batch culture growth rate.

D. Variable Generation Times

Powell (1958) has shown that if there is a distribution of generation times within the population, where the probability that a cell will have a generation time τ is governed by some function $f(\tau)$, then the age density function will be

$$n(s) = 2\mu e^{-\mu s} \int_0^\infty f(\tau)\, d\tau. \tag{54}$$

To complicate things, this unknown distribution $f(\tau)$ will be truncated in a chemostat.

Since we rarely have information concerning the distribution of generation times, and since the measurement of individual cell generation times microscopically is of doubtful significance to an entire population, I prefer the following to handle the variability in generation times.

Consider a chemostat in a steady state. *Any distribution of generation times must be independent of time.* Otherwise, a fluctuation of the generation time distribution would produce a fluctuation in growth rate, thus violating the steady state assumption.

This means that, for every interval of generation time τ to $\tau + d\tau$, there exists a stable subpopulation with that generation time. Let that subpopulation be a fraction $p(\tau)$ of the total population. Each subpopulation will have an age distribution governed by Eq. (52). Remembering that the birth rate of cells must equal the washout rate,

$$k_0 = \ln D/\tau,$$

and

$$n_\tau(s/ds) = [(D \ln D)/(D - 1)\tau] \exp(-s \ln D/\tau), \tag{55}$$

giving us explicit dependence on τ.

Let us introduce the variable representing *relative age* a. We define $a = s/\tau$, such that $0 \leqslant a \leqslant 1$. That is, relative age is measured as a fraction of a generation time, and a cell divides at relative age $a = 1$. Since $da = ds/\tau$, we can transform Eq. (55) into the *relative age distribution*

$$n_\tau(a/da) = [(D \ln D)/(D - 1)]\, e^{-a \ln D}\, da. \tag{56}$$

Equation (56) is an age distribution which is independent of generation time; it is identical for all populations, regardless of growth rate, and hence regardless of generation time.

Now returning to the chemostat population, the overall relative age distribution will be

$$n(a/da) = \int_0^\infty p(\tau)\, n_\tau(a/da)\, d\tau. \tag{57}$$

Since $n_\tau(a/da)$ is independent of τ, and since $\int_0^\infty p(\tau)\, d\tau = 1$, $n(a/da) = n_\tau(a/da)$, and thus

$$n(a/da) = [(D \ln D)/(D - 1)]\, e^{-a \ln D}\, da, \qquad 0 \leqslant a \leqslant 1. \tag{58}$$

Thus if we consider only relative ages, we do not have to consider the distribution of generation times, for it will be eliminated in a steady state population. This will be very useful in calculating the size distributions in the next sections.

E. Ideal Size Distributions

Consider a population of cells, each of which has an interphase growth law governed by some function of relative age $f(a)$. Then, for an individual cell,

$$m = f(a), \qquad m_0 \leqslant m \leqslant Dm_0, \tag{59}$$

where m_0 is the neonatal cell size and Dm_0 is the ripe cell size for cells dividing into D daughters.

If the growth function is monotonically increasing throughout the cell cycle, we may readily define the inverse function f^{-1},

$$a = f^{-1}(m). \tag{60}$$

(If f is not monotone, we may piece together monotone segments, giving us a set of inverse functions over different age ranges; this does not alter the argument.)

Given an age distribution $n(a/da)$ as in Eq. (58), we want to derive the distribution of sizes in a population whose cells grow according to Eq. (59). Let $h(m/dm)$ be the fraction of cells in the size interval m to $m + dm$. Using the tautology $da = (da/dm)\, dm$, we transform the coordinates of the age distribution to those of size

$$h(m/dm) = n(f^{-1}(m))\,(da/dm)\, dm, \tag{61}$$

or

$$h(m/dm) = \frac{1}{dm/da} \cdot \frac{D \ln D}{D - 1} \cdot \exp(-f^{-1}(m) \ln D)\, dm, \tag{62}$$

whose corresponding density function is

$$h(m) = \frac{1}{dm/da} \cdot \frac{D \ln D}{D - 1} \cdot \exp(-f^{-1}(m) \ln D). \tag{63}$$

Thus we see that the density function governing cell size distribution within a population is exactly the *age density function divided by the individual cell's growth rate* (dm/da).

Associated with the steady state, there is the notion of *balanced growth* (Maaløe and Kjeldgaard, 1966) which occurs if all components of the population increase at the same specific growth rate. That is, numbers, biomass, protein, DNA, RNA, etc., all stay in constant proportions. There are only two conditions under which balanced growth can obtain:

(i) a D-fold increase over the cell cycle, and
(ii) a start from zero in the neonatal cell, and a return to zero by the time the cell divides.

Thus, the density function in Eq. (63) applies to every constituent of the population, whether it be a particular chemical, an organelle, or the overall cell size. [For case (ii), we will have to piece together at least two monotone segments of $m = f(a)$.]

As examples of ideal size density functions, we consider exponential, linear, surface uptake, and half-sinusoid growth models.

Example 1

For exponential growth, the exponent must exactly equal the rate of increase of the population in order to have steady state balanced growth.

Thus

$$m = m_0 e^{a \ln D}, \qquad dm/da = m \ln D, \tag{64}$$

and

$$a = f^{-1}(m) = \ln(m/m_0)/\ln D. \tag{65}$$

Substituting into Eq. (63),

$$h_e(m) = [D/m(D-1)] \exp(-\ln(m/m_0)),$$

or

$$h_e(m) = Dm_0/(D-1)\, m^2. \tag{66}$$

Example 2

For linear growth,

$$m = m_0(1 + (D-1)a), \qquad dm/da = m_0(D-1),$$

and

$$a = f^{-1}(m) = (m - m_0)/m_0(D-1). \tag{67}$$

Substituting into Eq. (63), we have*

$$h_l(m) = \frac{D^{D/(D-1)} \ln D}{m_0(D-1)^2} \exp\left[-\frac{m \ln D}{m_0(D-1)}\right]. \tag{68}$$

Example 3

For surface limited uptake by a sphere (or other shape which remains geometrically similar throughout its cell cycle), growth rate will be proportional to surface area, which is in turn proportional to the $\frac{2}{3}$ power of mass,

$$m = m_0[(D^{1/3} - 1)\, a + 1]^3,$$

$$dm/da = 3(D^{1/3} - 1)\, m_0^{1/3} m^{2/3},$$

and

$$a = f^{-1}(m) = \frac{m^{1/3} - m_0^{1/3}}{m_0^{1/3}(D^{1/3} - 1)} \tag{69}$$

* An approximation was used in my original derivation (1965) for linear growth. The exact growth expression producing the approximate density function is $m = m_0 \exp[(D \ln D)(1 - e^{-a \ln D})/(D-1)]$, which deviates nowhere from linear by more than 0.3% over a cell doubling.

The corresponding size density function is

$$h_s(m) = \frac{D^{2-D^{1/3}} \ln D}{3(D-1)(D^{1/3}-1)\, m_0^{1/3} m^{2/3}} \exp\left[-\frac{\ln D}{D^{1/3}-1}\left(\frac{m}{m_0}\right)^{1/3}\right], \quad (70)$$

which is a curve with intermediate slope between the linear and exponential distributions.

Example 4

The last example is somewhat different, concerning a substance that is synthesized *de novo* in the neonatal cell, then decays to zero before the cell divides. The pulsed synthesis of a labile enzyme might behave this way. We approximate this behavior by the top half of a sine curve. Let

$$m = \sin \pi a, \qquad 0 \leqslant a \leqslant 1,$$
$$dm/da = \pi \cos \pi a,$$
$$a = (1/\pi) \sin^{-1}(m),$$

and

$$da = \pm dm/\pi(1-m^2)^{1/2}. \quad (71)$$

Note that the expression for a is not single-valued, as shown by the $\pm$ sign for da. We piece together the two monotonic segments of this function to yield,

$$h_\pi(m) = \frac{D \ln D}{\pi(D-1)(1-m^2)^{1/2}} \times \left\{\exp\left[-\frac{\ln D}{\pi}\sin^{-1}(m)\right] + \exp\left[\frac{\ln D}{\pi}\sin^{-1}(m) - \ln D\right]\right\}. \quad (72)$$

These growth curves are shown in Fig. 33 for $D = 2$ cells. The corresponding size density functions are shown in Fig. 34. The sinusoidal growth function is clearly very different from the others. Note (Fig. 33) that the other three, linear, exponential, and surface uptake have nearly identical growth curves over a cell doubling; the maximum difference is 6% between exponential and linear over the growth cycle. Clearly it would take very good data to resolve these differences. But in Fig. 34, we note that there has been a process of amplification, such that there is now approximately a 45% difference between the size density functions for linear and exponential growth.

Thus the indirect method of observing good steady state size distributions can provide us with more resolving power to test cell growth theories than

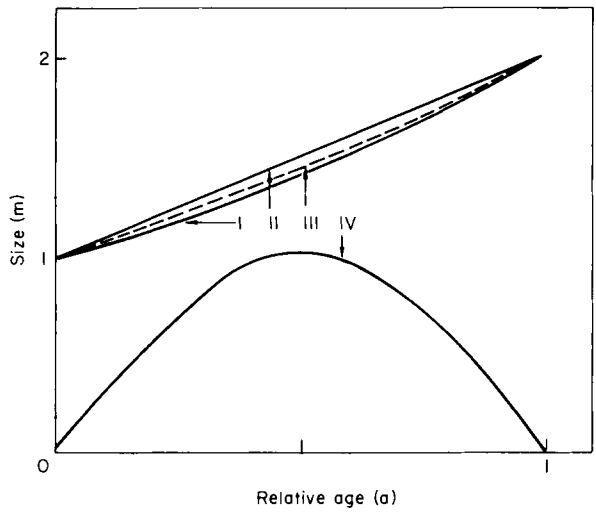

FIG. 33. Growth curve examples used in deriving examples of cell size distributions. I: exponential growth; II: linear growth; III: surface-limited uptake; IV: pulsed synthesis and decay of cell constituent. Note closeness of curves I–III.

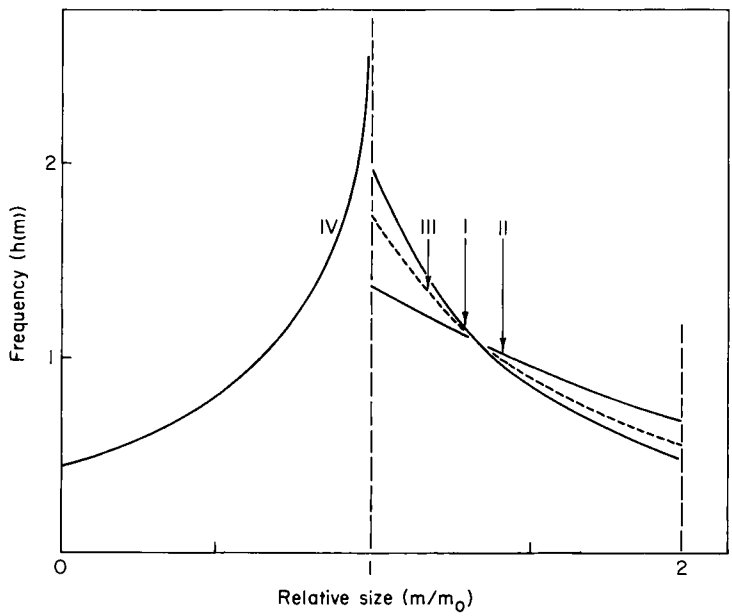

FIG. 34. Ideal size distributions based on growth models shown in Fig. 33. Note greater separation and resolution of curves I–III, compared with those in Fig. 33.

can direct observation of the cells as they grow. Conversely, knowledge of details of individual growth can give us very precise predictions of population distributions.

F. Size Distributions with Variability

In order to apply the above size distributions, we must account for the variabilities in size for cells of a given relative age. We do this in the following way:

Given $h(m)$, the ideal size density function, we assume that cells with an expected size m_E will be distributed over other values m according to a probability distribution function $p(m_E, m)$ such that

$$h(m_E) \int_{-\infty}^{\infty} p(m_E, m)\, dm = h(m_E), \tag{73}$$

where admissible values of m_E are $1 \leqslant m_E \leqslant D$.

Then the new density function with variability, $h^*(m)$, is given by

$$h^*(m) = \int_1^D h(m_E)\, p(m_E, m)\, dm_E . \tag{74}$$

Note that m_E, the expected value, is the variable of integration; we are integrating over the contributions to a particular size m by cells smeared out from all possible expected values m_E.

G. Fitting Data

In order to fit the data to be shown below, we have assumed that $p(m_E, m)$ is a normal density function with constant coefficient of variation. We have assumed normality for want of a better hypothesis; we have chosen a constant coefficient of variation because the experimental size distribution data in Fig. 21 from a *synchronous* population shows peaks with widths which are almost exactly proportional to the modal size. Although confounded by the presence of two subpopulations dividing into two and four daughter cells, the shapes of the distributions are not inconsistent with approximate normality, although they may be somewhat positively skewed.

Under this assumption, the size density function with variability in Eq. (74) becomes

$$h^*(m) = \int_1^D \frac{h(m_E)}{cm_E(2\pi)^{1/2}} \exp\left[-\frac{1}{2}\left(\frac{m - m_E}{cm_E}\right)^2\right] dm_E , \tag{75}$$

where c is the coefficient of variation. While some of these density functions may be evaluated analytically, it is more prudent to let a reliable computer do the job. As one example, Fig. 35 shows predicted

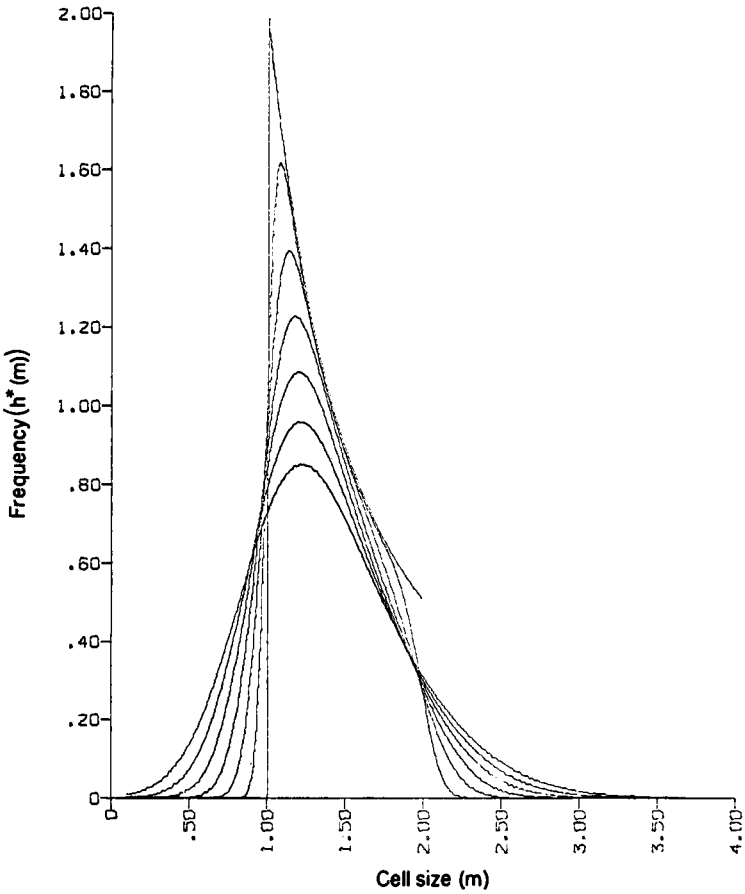

FIG. 35. Theoretical size distributions of exponentially growing cells with seven different coefficients of variation: 0, 0.05, 0.10, 0.15, 0.20, 0.25, and 0.30, top to bottom.

size distributions for exponentially growing cells with six different coefficients of variation, plus the ideal distribution.

The data are fitted visually, after normalizing the theoretical and experimental distributions for equal areas and equal means. Different growth models and coefficients of variation may then be tried.

Results are shown for the steady state *Chlorella* populations, the experimental results of which were given in Figs. 18 and 19. Recall

that there were subpopulations of cells dividing into two and four daughter cells. Consequently Fig. 36 has been fitted with a 25%

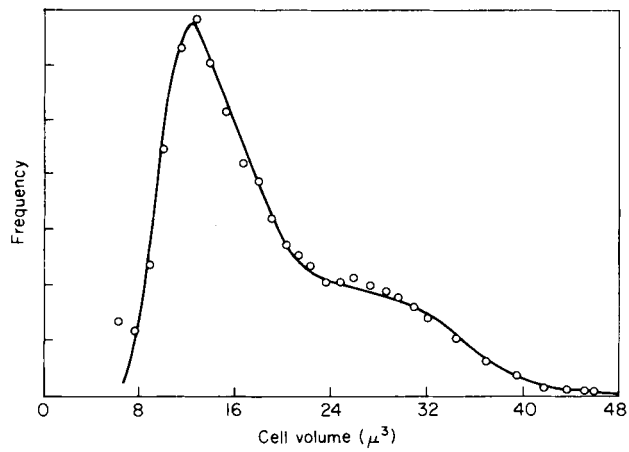

FIG. 36. Example of a fit of a theoretical to experimental size distribution for *Chlorella*, under assumption of linear growth (Fig. 33, curve II), coefficient of variation 0.10, with 75% of population dividing into four, and 25% into two, daughter cells. Line is theoretical; points experimental.

subpopulation with $D = 2$ daughter cells, plus a 75% subpopulation with $D = 4$ daughter cells. It was impossible to come anywhere near the observed distribution with a hypothesis of exponential growth (Williams, 1965). The model used in Fig. 36 is linear growth* and a coefficient of variation $c = 0.10$. Overall, theoretical and observed results agree excellently.

Further, the similarity of the eight distributions shown in Fig. 19, each from populations with different growth rates and different mean sizes, allows the conclusions that:

(i) the cell growth function does not change appreciably under very different conditions, and

(ii) there is thus a well-defined relative size (m/m_0) for every cell of relative age a, regardless of absolute sizes or growth rates.

Thus, pending further data, we conclude that for all experimental conditions of nutrient, growth rate, CO_2, and temperature, *Chlorella* grows linearly between divisions.

To show a somewhat simpler example, I present data from the blue–

* Actually the fit shown is the approximation mentioned earlier (p. 254).

green alga, *Anacystis nidulans*, grown in the chemostat by Dr. Bazin. *Anacystis* divides into two daughter cells only. Figure 37 shows how even the ideal size distributions may be used for approximate testing. Clearly the exponential growth model is superior to the linear one. Figure 38 shows the same experimental distribution compared to linear and exponential growth models with a coefficient of variation $c = 0.2$. Again the best fit is clearly provided by the exponential growth model.

H. Discussion

Thus, *Chlorella* populations comprise $D = 2$ and $D = 4$ cells, which grow linearly with a coefficient of variation $c = 0.10$. *Anacystis* populations comprise only $D = 2$ cells, which grow exponentially with a coefficient of variation $c = 0.20$. These results seem less ambiguous than we could have gotten by direct measurement of individual cells.

There is dissent on this last point, however. Koch (1966) and Kubitschek (1969), each using derivations different from the one presented above, and different from each other, feel that the general approach of fitting size distributions is a highly ambiguous one. Their derivations, both of which depend on differences between integrals of neonatal and ripe cell size distributions, do not seem to provide the resolution required to distinguish adequately theoretical distributions based on linear versus exponential growth. While we seem to get a clear distinction, our method is different [cf. Eqs. (74) and (75)]. Resolution of these differences must await a better understanding of the causes underlying variability in organisms.

Ecologically, the relevance of such cell growth studies may lie along the following lines:

First, a knowledge of how an individual organism grows is a necessary step in formulating the growth dynamics of a population; indeed, that is the central thesis of the theoretical development I have undertaken with both models.

Second, the form of cell growth will have obvious implications for the dynamics of nutrient in the environment. We may take *Chlorella* and *Anacystis* as examples. First, for *Chlorella*, linear growth implies a constant rate of removal of nutrients from the environment over the whole cell cycle. This means that the *nutrient drain imposed upon the environment will be a function of numbers of organisms present*, regardless of their ages (or sizes).

On the other hand, the exponential growth of *Anacystis* implies a doubling of the uptake rate over the cell cycle, such that the nutrient

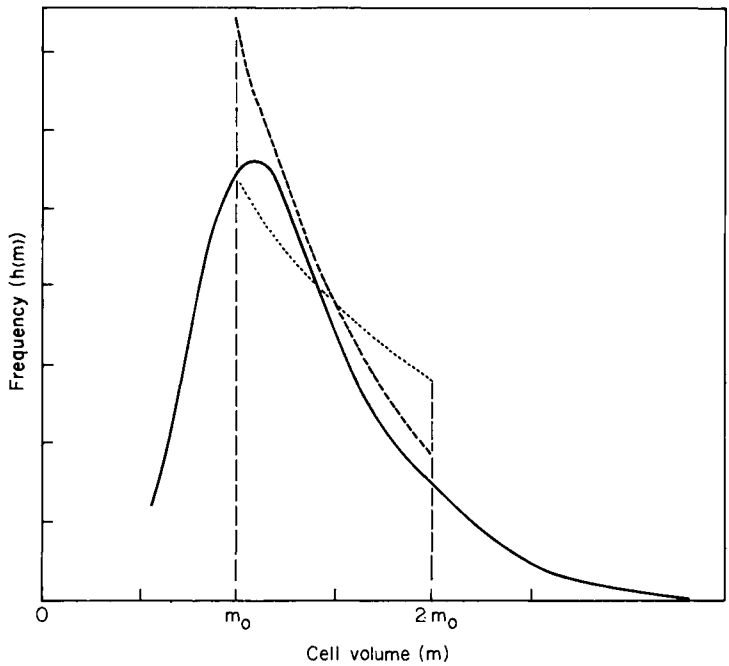

FIG. 37. Example of rough hypothesis testing with ideal size distributions. Data (solid line) is from *Anacystis* chemostat population of Bazin. Dashed line represents exponential; dotted line represents linear growth models. Cells divide into two only.

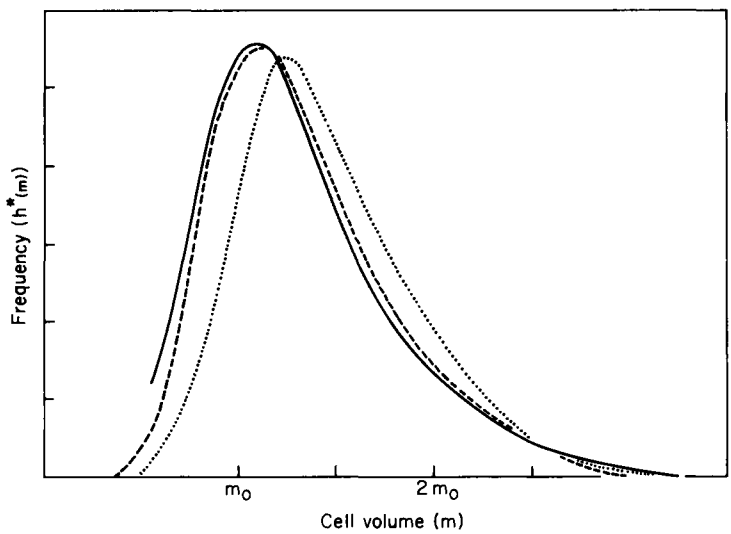

FIG. 38. Bazin's *Anacystis* data (solid line) shown with linear (dotted line) and exponential (dashed) growth models, with a coefficient of variation 0.20.

drain on the environment may differ by a factor of two, depending on ages (or sizes). *Nutrient drain will be a function of biomass present*, not numbers.

In terms of intraspecific competition in the face of nutrient deficiency, all ages of *Chlorella* cells are equally good competitors with each other. On the other hand, older, and hence larger *Anacystis* will have a competitive advantage over younger cells. Everything else being equal, we expect that the dynamics of these two populations will be different, especially in transient phases.

I. On the Plankton Paradox

Finally, and perhaps most important ecologically, is the insight that these studies can provide into the question of interspecific competition. I refer specifically above to what Hutchinson (1961) has so aptly called "The Paradox of the Plankton." The question is simply:

How do we reconcile the competitive exclusion principle with the obvious long-term coexistence of very large numbers of species of photoautotrophs in a homogeneously dispersed environment, when each of these photoautotrophic species has almost exactly the same needs in terms of inorganic carbon, nitrogen, phosphorous, and other elements?

Hutchinson has suggested (i) the existence of symbiosis or commensalism, such as might occur if a vitamin requirer utilized vitamin excreted by a synthesizer, (ii) selective predation on the plankton can establish stable, multispecies steady states, (iii) the plankton does not exist, being simply the washout from stable chemostatic communities in the heterogeneously diverse littoral benthos, and (iv) competition is never brought to equilibrium because of rapidly and randomly changing conditions.

I suggest here another mechanism for stable multispecies associations in phytoplankton, which seems to me more universally applicable, and independent of such details as vitamins and selective predators. The mechanism relies on known temporal phasing of cyclic events in the cell cycle.

I begin with a simple illustrative example. Assume:

(i) two autotrophic species with the same growth requirements (nitrate, phosphate, carbon, etc.)

(ii) each starts the day with a unit biomass M_0.

(iii) each is just capable of doubling M_0 over the course of the daylight hours. Thus each will consume exactly the same quantity of nutrient over the period of daylight.

As seems to be universally true of photoautotrophs (see above), cell division is phased to the photoperiod. For this example we assume simply that:

(iv) both species have divided during the night, beginning the daylight hours as neonatal cells.

Finally we assume:

(v) one species (L) grows linearly over its cell cycle, while the other species (E) grows exponentially.

Since growth is just uptake of nutrient from the environment, we define the *nutrient demand* on the environment as

$$dM/dt = -dC/dt; \tag{76}$$

evidently the total nutrient demand of the species E and L together is

$$-dC_{E+L}/dt = dM_L/dt + dM_E/dt. \tag{77}$$

Since each species is just capable of a doubling over the daylight period of length T,

$$dM_L/dt = M_0/T,$$

and

$$dM_E/dt = (\ln 2/T)M_E = (\ln 2/T)M_0 \exp[t \ln 2/T]. \tag{78}$$

[We have seen above that there will be at most a 6% difference in these curves over a doubling (Fig. 33).]

The result is a precise phasing of the nutrient demand on the environment over the course of the day length T. In the early morning, at $t \approx 0$ and $M_L = M_E = M_0$ the ratios of the nutrient demands are

$$dM_L/dM_E = 1/\ln 2 \approx 1.44; \tag{79}$$

Near midday, at $t \approx 0.53T$, the ratio will be

$$dM_L/dM_E = 1. \tag{80}$$

In the evening the ratio will be reversed; at $t \approx T$,

$$dM_L/dM_E = 1/2 \ln 2 \approx 0.72. \tag{81}$$

Thus, we see that in the morning the linearly growing species (L) has a 44% competitive advantage over the exponentially growing species, while in the evening the exponentially growing species (E) has a 39% competitive advantage.

The regular cyclic changes of nutrient demands, and hence competitive advantages, over the course of one day, would seem to ensure a stable two-species system.

We now ask: What would be the optimal strategy for an invader (F) with similar nutrient requirements, given the impossibility of displacing either E or L? The strategy is clearly for the invader F to maximize his nutrient demand when the existing total nutrient demand is minimal. Since the total nutrient demand of E and L is

$$-\frac{dC_{E+L}}{dt} = \frac{dM_L}{dt} + \frac{dM_E}{dt} = \frac{M_0}{T} + \frac{\ln 2}{T} \exp\left(\frac{t \ln 2}{T}\right), \tag{82}$$

it is clear that $-dC_{E+L}/dt$ is a minimum at $t = 0$.

Thus the invader F will maximize his ability to survive by growing most rapidly in the early morning, when the combined nutrient demand of the existing species is at a minimum.

With this simple example I hope I have demonstrated adequately the principle involved, the substance of which is: *that the one inescapable periodic regularity in the environment, photoperiod, plus the demonstrated phasing of cell cycles to this photoperiod, will allow subtle differences in cell growth behavior to establish stable, multispecies equilibria by means of regular, cyclic changes in competitive advantage.*

Applying this principle over an evolutionary time course, we predict that there will develop:

(i) differences in phasing to the photoperiod. [This has occurred (Hastings and Sweeney, 1964).]

(ii) more and more exotic differences in details of the cell cycle for these otherwise "simple" cellular organisms. (Ask any algologist.)

(iii) greater diversity in cell cycle details for organisms in the homogeneously diverse planktonic environment than in a heterogeneous environment such as soil. (I do not know if this is true.)

V. General Summary

I have tried to develop a rationale for the study of basic problems in population dynamics via the use of microbial populations. I describe both experimental and theoretical aspects of the study.

Experiments are reported on the chemostat culture of *Chlorella* and *Selenastrum*. The state of a population cannot be characterized by numbers or biomass alone. Differences in behavior of several population measures, both in steady state and transient experiments, are emphasized.

The looseness of coupling of the growth and replicative processes is evidenced repeatedly in the results.

A cell model is developed, based on a separation of the growth (uptake) and replicative properties of a cell. The population consequences of this cell model are deduced. Most of the behavior of the experimental populations can be predicted from the model. This behavior is not restricted to green algae, but seems universally true of all cell populations from bacterial to mammalian cell cultures.

Models are developed for the distribution of properties within populations: age structure, size distributions, etc. The models are fitted to experimental size distribution data. The consequences of the conclusions drawn are explored. A possible solution to the "paradox of the plankton" is discussed.

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4

Of Sowbugs and Systems: The Ecological Bioenergetics of a Terrestrial Isopod

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I. Introduction

During the past fifteen years there has been an explosive increase of interest in measuring, understanding, and predicting energy flow through ecological systems. This interest derives from the hope that knowledge of energy flow will help us comprehend biological structure and function at the levels of organism, population, and community. We have come to recognize that all living organisms are energy transducers, and that a great many seemingly unlike biological processes can be described and compared in terms of energetic yield and cost. Moreover, important questions about the evolution of efficient use by organisms of their potential energy supply have been raised by the fact that the biosphere as a whole appears to be energy limited (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967). Yet, in spite of considerable effort

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to describe the caloric stores and flows associated with diverse biological processes, our generalizations have been relatively few in number and slow to accumulate. Certainly in large part the slow rate of advancement is due to the enormous complexity of the systems with which we are dealing. But perhaps some of the difficulty also stems from our approach.

A frequent problem is that we expect too much of energy considerations: One fairly common view is that much if not all of biology will someday be describable in thermodynamic terms. Attempts to reduce ecology to thermodynamics have not been notably successful thus far, but the usual reason given for their lack of success is the current inadequacy of theory in nonequilibrium, steady state thermodynamics. Aside from the fact that it is somewhat questionable whether biological steady states are commonplace or even exist, it cannot be expected that energy considerations alone will ultimately explain biological structure and function. Morowitz (1968) concludes that energy flowing through a system will tend to "organize" that system, but that the course of development and the nature of this organization cannot be predicted. Thus, for example, it is difficult to conclude much from thermodynamics about the rates of entropy production by ecological systems, except perhaps that the rates are not minimal because of the complex feedback characteristics of such systems (Slobodkin, 1962). Yet conclusions about entropy production in ecological systems are continuing to appear in the literature. Note the comment by Margalef (1968, p. 29): "It is probably justified to say that any system formed by reproducing and interacting organisms must go on to develop a kind of assemblage in which the production of entropy per unit of preserved and transmitted information is at a minimum." It is not clear from Margalef's preceding or following remarks why this statement is "probably justified."

The laws of thermodynamics merely define a set of rather broad "boundary conditions" within which all natural systems must operate; they are necessary but not sufficient conditions for determining the actual operation of natural systems. This is a restatement of Polanyi's argument (1968). In a natural world which can be viewed hierarchically, laws governing events at one level must be consistent with all laws at lower levels of organization. The lower-level laws establish bounds on the possible for higher levels; but it is the higher-level laws which restrict the possible to the "actual," a narrower set of possibilities. Thus, it is unrealistic to expect the laws of thermodynamics ever to be sufficient to explain the organization and function of biological systems. At the same time, no correct law about biological systems may violate thermodynamic principles.

A second problem with our approach to ecological bioenergetics is

that, for the most part, we have seriously underestimated the importance of a basic characteristic of life: control. This concept is almost entirely missing from the flow diagrams developed by the Odums (1959, 1960, 1963, 1968) and widely used by other ecologists to describe energy flow through organisms, populations, and communities. The historical importance of these diagrams is clear: they have been instrumental in focusing the attention of ecologists on whole-ecosystem energy relationships. Moreover, they continue to serve the useful purpose of conveniently summarizing gross energy partitioning within different types of ecosystems.

The value of such flow diagrams for research and predictive purposes, however, seems quite limited. As Slobodkin (1962) put it, they violate common sense. The dominant impression they give is of a series of conveyor belts rushing along until they meet a set of strategically placed knife edges, which then split each belt into a series of narrower belts of varying widths. Odum (1960) reinforces this impression when he intentionally eliminates the idea of control from his thinking. According to Slobodkin (1962) he states, "The validity of this application may be recognized when one breaks away from the habit of thinking that a fish, or bear, etc., takes food and thinks instead that accumulated food by its concentration practically forces food through the consumers." If this view is correct, then a consumer is nothing more than a passive, open-loop, energy-partitioning device that is dealt an input of energy to divide among a series of physiological processes.

But this is *not* what an animal or plant is doing. An organism is an active agent which takes in, or attempts to take in, potential energy to meet some internally defined "need." To us, animals are generally more obvious than plants in their efforts to control energy intake and expenditure. Yet plants, while unable to turn the sun on and off, have a high degree of control over the rate at which they fix radiant energy photosynthetically, exerted on a short-term basis through a variety of biochemical mechanisms and phototropic responses, and on a long-term basis through vegetative growth plasticity.

In my view the prevalent treatment of organisms as passive agents has hindered further development in the field of ecological bioenergetics by producing few significant questions about what living systems are really doing with energy. Such a treatment ignores perhaps the most fundamental characteristic of life: the capacity of living organisms to regulate, within the bounds established by the laws of thermodynamics, the rates at which they accumulate and dissipate energy. No other naturally occurring set of physicochemical systems has this remarkable property.

Once this fact is seriously taken into account the approach to energy flow in ecology is, as it were, turned inside out. One is no longer on the outside of an organism, energy input in hand, looking in to see how it will be partitioned physiologically. Instead, one is inside the organism, aware of its energy requirements, and looking outside at the varying potential energy supply. Now one can ask more than simply how an organism partitions a given input of energy. The dominant question is now how the organism, faced with a varying energy supply and a fluctuating physical environment, regulates energy intake and expenditure in an attempt to maintain *energetic* and physiological homeostasis. It should be emphasized that this change in approach to ecological bioenergetics does not mean that we lose interest in how organisms partition energy. Indeed, it is the newly reexamined *dynamic* characteristics of energy partitioning, as organisms adapt physiologically and behaviorally to a changing environment, which are so interesting.

It should not be inferred from this discussion that energy regulation is the only important business of organisms. Certainly reproduction is equally important. Moreover, it is not all clear that energy regulation is even a small part of the business of populations and communities, as distinct from the business of individuals. Nevertheless, the energy-regulating abilities of individual organisms have a profound effect on, and response to, the temporal and spatial patterns and nature of energy flow through populations and communities. Consequently, energy regulation cannot be safely ignored in any study of ecological bioenergetics, particularly in studies of organisms or populations.

I shall be concerned here with how energy control is accomplished dynamically in individual animals, and more particularly in the terrestrial isopod, *Armadillidium vulgare* Latr. Before developing this topic, however, I will briefly discuss systems analysis and a philosophy on modeling.

II. Systems Analysis and Model Building

To understand and have the power to predict quantitatively the energy dynamics of an animal's response to its environment and to its own nutritional condition, we need the conceptual framework and mathematical tools of the systems analysis approach. *Systems analysis* means many different things among ecologists. For some it simply means any organized systematic research in ecology. In this discussion, however, the term refers to the branch of applied mathematics and engineering sciences of the same name. I shall only touch briefly on its logical foundations and on my prejudices concerning methodology, since this

is not the place for a lengthy discussion of systems analysis. For this, the reader is referred to the introductory chapters of this book, especially Chapter 2, and to texts such as Milsum (1966), Schwarz and Freidland (1965), and Elgerd (1967).

Fundamental to systems analysis is the assumption that natural processes are organized in a hierarchy of complexity, a notion familiar to biologists in the ordered sequence: cell, organ, individual, population, and community. Each process or system in the hierarchy is assumed to be the combined result of the actions and interactions of a set of simpler processes. No system is isolated, of course; every system interacts with others, both on its own level of organization, and on higher and lower levels as well. Thus, to an extent, system boundaries are arbitrary and a matter of convenience. The interaction with other systems constitutes the input and output of a particular system, as matter, energy, or information.

The internal dynamics of a system are characterized mathematically by the relationship between output and input; to understand the dynamic behavior of a system, then, we must thoroughly analyze its input–output relationships. Once these are known, it remains to determine the dynamics of the intervening system component ("system identification"). This type of problem is more difficult than the "forward-analysis" problem typically encountered in engineering, in which the output must be calculated from the input and system dynamics, which are given.

As biologists, we commonly tend to think of input–output relationships in terms of statistical correlation, and build regression models to explain the organization of biological systems. We generally recognize the problems associated with causal inference from regression models, as well as the fact that physical and biological systems do not work on the basis of relationship by correlation. It is less generally recognized, however, that such systems operate on the basis of the relationships between *quantities* ("storages" or "levels") and *transfers* ("flows") of matter and energy. In part we have relied upon regression models because we have not known enough about most biological systems to build storage-and-flows models, but also in part because we are used to thinking in terms of *relationship* and not in terms of *process*.

The methodology of systems analysis embodies a close feedback between theory and experiment, as Holling (1966a, b) has emphasized. This feedback distinguishes it from the almost unguided empiricism and also from the nearly "pure" deductive reasoning evident in some of the ecological literature. The study of a biological system usually begins with the construction of a block (flow) diagram, a graphic model in which the storages and flows associated with known or suspected

components of the system and their interactions are identified. Initially, the object is to develop a qualitative or semiquantitative overview of the system, often merely in terms of educated first guesses. This graphic model provides the logical framework upon which to build experiments designed to select one of several alternate model formulations. As results from experiments become available, modifications can be made in the flow diagram, and also in the design of future experiments. Gradually a quantitative model is developed to replace the qualitative one, as transfer functions ("operational" output–input ratios) for each system component are empirically determined.

At an intermediate point in the analysis, it becomes possible to begin computer simulation of the model, using transfer functions already identified plus guesses about those which remain to be determined. In this way the performance of the model can be compared with that of the real system, often hastening the discovery of the remaining transfer functions in the system. Computer simulation can occasionally offer a type of internal check on the accuracy and consistency of empirical results: if a significant error exists, the model will probably not behave like the real system. It must be established, however, that the fault lies in measurement and not in the model, a task that is frequently difficult. Thus, at each step in the development of the model, its performance can be tested against the real system, until the model simulates reality with acceptable accuracy.

The purpose of modeling, then, is twofold. First, a model is an essential tool in on-going research: It is a conceptual structure of hopefully testable guesses about how some natural system is organized. As such it should help to determine relevant experiments to perform or data to collect, or both, thereby increasing the efficiency of the research effort. Second, a model can be put to predictive use once it exhibits a satisfactory performance. "What if" questions can be asked about the consequences of different input conditions upon the behavior of the system of interest. In addition, the model's parameters, corresponding to the system's attributes, can be systematically changed to find out more about the reasons for a particular biological system's organization, as well as to test its generality when applied to systems other than those intensively studied. It is usually far more economical to conduct "experiments" on the model than on the real system, especially in ecology.

It is sometimes easy and always risky to forget that a model is not the real system. Models hold only certain properties in common with reality. As Levins (1968) has pointed out, there is no such thing as an "all-purpose model," which is simultaneously precise, realistic, and

general. This is particularly obvious in constructing models of hierarchical systems: In moving from one level of organization to the next, information is invariably lost. This results from the practical necessity of approximating or lumping the dynamics of systems at one level before they can be incorporated into systems models on the next higher level of organization. There are few general rules about how to do this, although the lumping procedure that is optimal has a minimal effect upon the performance of the higher-level model while remaining consistent with lower-level laws. There is always the danger of making unwarranted assumptions that generate more fiction than fact about the supposed performance of the modeled system. Unfortunately, it is frequently not clear to what extent assumptions are unwarranted until for some reason it is "too late"; thus, the anticipated cost of a model's inaccuracy may determine in part what approximations to make or which lower-level detail to save. It would be disastrous, for example, to have a model of a proposed chemical plant which simulated the plant closely under normal conditions, but which failed to predict a destructive explosion under some rare but eventual circumstances. Fortunately for ecologists, the tight control characteristic of biological systems below the organismal level makes assumptions about the mean performance of physiological processes reasonably safe.

III. Models of Energy Regulation and Growth in Animals

There is a vast literature on the physiological and ethological control mechanisms directly or indirectly involved in energy intake and expenditure in mammals, particularly in man and the domestic animals (Brody, 1945; Hamilton, 1965; Hardy, 1961, 1965; Kalmus and Wilkins, 1966; Kinne and Locker, 1966; Kleiber, 1961; Mayer and Thomas, 1967; Tepperman, 1962; Tepperman and Brobeck, 1960). There is also a rapidly growing body of information about energy regulation in other groups of animals, especially fish (Gerking, 1967), birds, and insects. Until quite recently this literature has had little effect upon the field of ecology because of its diffuse and fragmented nature and because of its rather strict physiological orientation. Although numerous models of physiological systems "in isolation" have appeared, only a few of these have been constructed with an eye to the possible ecological and adaptive significance of the physiological processes for the organism as a whole. Moreover, in general they contain far more detail than is necessary or advisable in a model of the ecological bioenergetics of entire organisms. Physiological and ethological processes that have been modeled include thermoregulation (Benzinger, *et al.*, 1961; Crosby, *et al.*, 1961; Hardy,

1961, 1965), respiration and circulation (Grodins, 1963; Priban and Fincham, 1965), feeding and prey capture (DeRuiter, 1963; Holling, 1965, 1966a, b; Mittelstaedt, 1957, 1962), drinking and water balance (McFarland, 1965; Stevenson, 1965), embryological growth and development (Weiss and Kavanau, 1957; Kavanau, 1960, 1961), endocrinological systems (e.g., DiStefano and Stear, 1968; Brown-Grant, 1966), and others. In the last few years there have been a few attempts at synthesis. One notable attempt has been made by DeRuiter (1963), who constructed flow diagrams depicting qualitatively the overall nutritional control system of a mammal, bringing together data both of a physiological and an ethological nature relating to nutrition and the control of feeding.

In spite of this rather extensive modeling in physiology and ethology, there has been relatively little effort to develop models of whole-animal growth and energy regulation suitable for use in ecology, models which are realistic and general, but which forfeit some physiological and precision because of the essential lumping of lower-level systems' dynamics. Several attempts have been made to fit simple descriptive equations to observed or smoothed growth curves of animals, but usually no effort was made to assess the biological significance of the equations. Furthermore, most of these equations attempt to describe only idealized growth under optimal conditions without providing for environmentally imposed physical or biotic perturbations of growth processes.

Three of the most commonly used models of growth are the logistic, Gompertz, and von Bertalanffy equations, all of which have a basically sigmoid form with an asymptotic adult body weight (Ricklefs, 1967). Brereton (1955) attempted to fit the logistic curve to his data on growth of the terrestrial isopod, *Porcellio scaber*. Wieser (1965), working from growth data on *P. scaber* collected by Matsakis (1955), showed that von Bertalanffy's equation gave a better fit. I have found, however, that this model is inadequate to describe the growth of *Armadillidium vulgare*.

Bertalanffy's equation is derived from the model proposed by Pütter in 1920 (Ursin, 1967), who appears to have been the first to recognize that the instantaneous growth rate of an animal can be expressed as the difference between the instantaneous rates of anabolism and catabolism. Pütter assumed that the rate of assimilation of food is surface-dependent, whereas the rate of dissipation of energy throughout the body is dependent on body weight. He assumed further that the area of the food-absorbing surface changed as the $\frac{2}{3}$ power of body weight, giving

$$dw/dt = aw^{2/3} - bw, \tag{1}$$

where w is weight and a and b are constants, with $a > bw^{1/3}$ at time zero. The final or asymptotic weight is approached as bw approaches $aw^{2/3}$.

Since this model was proposed, knowledge of metabolic processes has advanced greatly, although there still are significant gaps to be filled before a general theory of growth can be constructed. We can now be certain, however, that Pütter's equation is based on incorrect assumptions. First, there is abundant evidence to show that the rate at which animals expend energy is only rarely proportional to body weight; rather it is proportional to some fractional power of body weight, reflecting the fact that respiratory processes are also surface dependent. This power varies from species to species (Zeuthen, 1953; von Bertalanffy, 1951) as a result of different surface–volume relationships and other factors (Prosser and Brown, 1961). Second, the area of the absorbing surface of the gut is highly variable between species, and even between individuals; and it is rarely proportional to the $\frac{2}{3}$ power of body weight because of allometric growth of the intestine and food habits. Attempts have been made, therefore, to generalize Pütter's formulation by specifying only that the exponents are species-specific constants between zero and one (Zeuthen, 1953; von Bertalanffy, 1951). Parameter values for this equation have been estimated for a diverse set of organisms, notably fish (Ursin, 1967; Paloheimo and Dickie, 1965, 1966a, b; Ricklefs, 1967; Taylor, 1958, 1962). The species-specific constancy of these parameters, however, has been seriously questioned. Environmental factors, particularly temperature, and nutritional condition have been found to influence the slope of the log–log relationship between oxygen consumption and weight in a number of animals (Armitage, 1962; Clark, 1955; Norris *et al.*, 1963; Vernberg, 1959).

The most serious weakness of Pütter's equation is its overly simplistic representation of the growth process. His model implies that growth is entirely passive, because the rates of anabolism and catabolism are viewed merely as passive functions of the current weight of the animal, unable to make any compensation for perturbations. As with energy regulation, treating growth as a passive process completely ignores the adaptive and regulatory features of physiological processes. Unlike nonliving physicochemical systems which exhibit growth (Oparin, 1953), living organisms control their growth homeostatically. Such regulation implies that organisms have built-in mechanisms for evaluating their growth performance, and for modifying energy intake and expenditure to compensate for performance "errors" resulting from environmental or physiological disturbances. Compensatory modifications of this sort are the result of stabilizing negative feedback, an almost universal feature of energy-regulating control systems.

The generic structure of such systems will be familiar to most readers. The actual performance or output of the system is compared with some criterion of "ideal" performance, known as the "reference input." If the actual and ideal performance of the system differ, an "error" signal is used to compute the appropriate "control effort" to force the output of the system closer to the desired level, thereby reducing the performance error. Output rarely equals the reference input exactly, however, primarily because the system must continually counteract disturbance effects of exogenous factors over which the system has no direct control, but which act upon the controlled process.

The importance of negative feedback in the regulation of growth has been recognized for some time (Glinos, 1958; Mayer and Thomas, 1967; Weiss and Kavanau, 1957), but there have been few attempts to develop control systems models of growth processes. Ursin (1967), working from Pütter's equation, introduced feedback into a model of fish growth by making catabolism a function of the rate of food absorption, although such feedback, by itself, produces no control. He also attempted to describe the effects of temperature on rates of anabolism and catabolism. Perhaps the most notable dynamic model of growth was proposed by Weiss and Kavanau (1957) and developed mathematically by Kavanau (1960, 1961). This model, however, is unsuited for studies of ecological bioenergetics. It was intended as a model of the embryological growth and development of various tissues and organs within the body, containing more detail about the hormonal and cellular aspects of growth regulation than practical in an ecologically oriented model. Moreover, it is not a caloric model, and no provision is made for environmental disturbances of growth because time is the only independent variable.

IV. Generalized Bioenergetics Model

Models of biological control systems are complicated because they usually have variable, rather than constant, reference inputs. That is, they are servomechanisms which have the task of tracking variable signals. In addition, biological control systems contain nonlinear elements, nested feedback loops, positive as well as negative feedback, and parameters which change with time. Finally, the parameters themselves may be under the partial or complete control of the system, in which case the system is said to be adaptive.

The most difficult problems in analyzing a biological control system, however, are probably not in coping with its mathematical complexity.

One major difficulty lies in isolating the system of interest sufficiently to permit its study. What one would like is to open feedback loops and manipulate some of the system's internal variables that are otherwise inaccessible, as if they were extrinsic in origin and independent of the system. Unfortunately, opening loops in biological systems often destroys the systems themselves. Instead, the biologist frequently is left only with environmental disturbances that can be controlled.

A second major difficulty lies in determining just what feedback loops do, in fact, exist in biological systems. This is the problem of determining the performance criteria of the system. Technical problems of measurement may be considerable, but these aside, the task is made harder by the fact that the controlling variable or variables may bear little resemblance to the controlled variables. For example, the firing rate of temperature-insensitive neurons in the hypothalamus may establish the "set-point" for mammalian thermoregulation (Hardy, 1965). Neuron firing rates are obviously rather different variables from body temperatures. Mammals do not have an actual set-point temperature, somehow physically stored, with which actual body temperature is compared. Moreover, conceptual difficulties may arise out of the difference between the abstract mathematical representation of feedback and the actual physical process for which it stands. Real biological control mechanisms are almost bewildering in their variety, some involving actual reference inputs, others not. Well-known examples of control systems without reference inputs can be found in the mammalian neuroendocrine system (Gorbman and Bern, 1962). Commonly they are composed of a system of coupled elements, the first being excitatory of the second, and the second being inhibitory of the first. In such a system the concept of reference input has only an abstract and arbitrary meaning. Nevertheless, in dealing with lumped models of such systems, it is useful to retain this concept. Even if particular reference inputs of the model have no exact physical counterpart, they can be made to mimic the behavior of the controlling element in the real system as accurately as desired. I shall make use of such reference inputs in the bioenergetics model developed below.

Many subsystems contribute to the overall ecological and evolutionary success of an organism. The performance criteria of these different subsystems will be different and will depend on the selective forces acting upon the species. That is, performance criteria are adaptive. In considering the evolutionary success of an individual or species, performance criteria are related to the production of the maximal number of surviving offspring. However, with regard to how organisms regulate the rate at which they accumulate and dissipate energy,

reproductive success is not an issue. An immature animal must grow to maturity if it is to reproduce successfully, and during this period of growth it must control its daily maintenance. Even after it reaches maturity, reproduction is frequently intermittent. Thus animals have performance criteria relating to growth and energy balance; and in addition they have reproductive criteria while they are reproducing. These criteria need not be mutually exclusive if both energy regulation and reproduction are under a higher level of control within the organism. For present purposes, we shall assume that there is only one reference input for growth and energy regulation, and one for reproduction, although we recognize that this design is physiologically too simple.

My work to date on the isopod, *Armadillidium vulgare*, has dealt primarily with the regulation of energy balance and growth. Details of reproduction and its performance criteria are currently being investigated by L. Lawlor (personal communication). As a descriptive term for the growth and energy balance criterion, I have chosen "*desired*" *growth rate*; *desired* is put in quotation marks to indicate avoidance of teleological implications. I view desired growth rate as some measure of the optimal growth rate of an animal, but because of the difficulty of assessing whether a given growth rate is, in fact, optimal, I have avoided use of that word. I am using the word *growth* to mean an increment in the caloric content of the body, rather than to mean an increment in the proteinaceous components of the body, as is customary in physiology. My object is to make the meaning of the term more consistent with the ecological notion of productivity.

The concept of desired growth rate is incorporated into the bioenergetics model whose generalized information flow diagram is illustrated in Fig. 1. Each block in the diagram represents a subcomponent of the system which computes an output storage or flow variable from its input variables. The circles are comparators, which produce a new variable from the sum or difference of other variables. Solid lines with arrows denote variables in units of calories or calories per time, and dotted lines with arrows indicate environmental disturbance variables, i.e., physical factors whose units depend on the factor considered.

At the upper comparator the growth performance of the individual is evaluated by subtracting current growth rate (net energy accumulation rate) from the desired growth rate. The difference constitutes a measure of how well the animal has been growing; if, according to this measure, growth has been poor, then corrective action is taken to force the actual growth rate closer to the desired growth rate. The block at the lower left computes current gross rate of energy accumulation (calories assimilated per unit time) as a function of the availability of energy

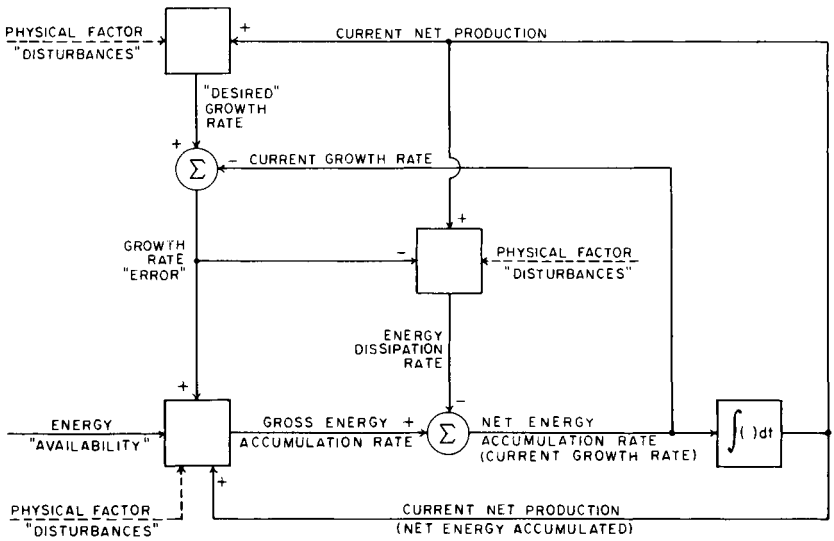

FIG. 1. Generalized block diagram of bioenergetics model. (See text for explanation.)

resources, i.e., food. For a given food availability, an input to this block of positive growth error would result in a greater rate of energy accumulation.

The comparator at the lower center subtracts the rate of energy dissipation (respiration rate) from the gross rate of energy accumulation. The difference constitutes the net energy accumulation rate, or current growth rate. Note that a positive growth error acts negatively upon energy dissipation; this feature results from the fact that starving animals show a reduced respiration rate. By summing (integrating) the net rate of energy accumulation over the life of the animal, the current net production (current total caloric content) of the animal is obtained. This net production signal feeds back positively to the blocks which determine the rates of energy accumulation and dissipation. Thus, as the individual increases in body size, it eats and respires more. Net production also acts positively on the desired growth rate of immature individuals of any species, such as *Armadillidium*, which has an accelerating growth rate.

Finally, all of the transfer functions are subject to disturbance by physical factors (dotted lines with arrows) including desired growth rate (which we assume to be a physiological process). The system must continually counteract these disturbances as well as the effects of varying levels of food availability. There are two additional ways that an organism can counteract the effects of such disturbances besides using

its "regular" feedback control mechanisms. The animal can adapt physiologically, and it can seek out preferred conditions in a heterogeneous environment. Under physiological adaptation we shall include physiological responses both to short-term cyclic inputs that are predictable, such as the daily light regime, and to long-term acyclic, or otherwise less predictable inputs, such as seasonal temperature and moisture patterns. Mathematically, physiological adaptation is equivalent to modifications of parameter values in the model's transfer functions; to the extent that these modifications are controlled by the system itself, we are dealing with a so-called adaptive system, as defined earlier. Physiological acclimation to temperature is already included in the model. As yet, however, I have not included behavioral attributes. *Armadillidium* is known to exhibit preferenda in gradients of certain physical factors, particularly temperature and humidity (Barlow and Kuenen, 1957a,b; Miller, 1938). Behavioral modification of disturbance inputs will be incorporated into future versions of the model, after more is known about the choice of conditions available to *Armadillidium* in the field, relative to its preferenda.

The success of the individual bioenergetics model outlined above depends to a large extent upon the adequacy of the concept of desired growth rate as an approximation of the actual physiological subsystems controlling growth and energy balance in an animal, and also upon our ability to deal with the concept operationally. One of the first questions to arise is whether the feedback controller should be modeled as a rate-sensitive element. In models such as Pütter's, the implicit "control" is exerted by the difference between the current size of an animal and its final body size. However, if we were to use the final body size as the reference input for growth control, we would find it difficult to account for the phenomenon of stunting, as well as for the response of animals to starvation, appropriately scaled for their current body size. Also, in many animals, particularly invertebrates and including *Armadillidium*, there is no obvious asymptotic adult body size; growth continues throughout life.

In choosing rate sensitivity for the growth controller, we should recognize that the actual physiological controllers of growth and energy balance are, in reality, responding to stores and levels. Stores such as the quantity of glucose in the blood, or the concentration of hormones are involved; and variables such as neuron firing rates are sensed as levels of discharged acetylcholine. As we recall from calculus, however, every store may be treated as a rate, and every rate a store, simply depending upon the magnitude of the time scale on which we observe a particular process, *relative* to the scale on which we observe other

processes. For our purposes, milliseconds, even tens of minutes, is a very short time; consequently, the dynamics of stores on this time scale can be ignored or time-averaged, when necessary, to produce a rate.

For the ecologist interested primarily in the implications of energy-regulating capacities of animals for population and community level phenomena, it need not matter that desired growth rate has no actual physical correlate in the animals, provided that the lumped model has similar properties to that of the real system. There is certainly a neurohormonal system whose function the comparator and desired growth rate could mimic operationally. In mammals, for example, there is a complex central regulatory system centered in the hypothalamus, which closely matches energy intake with energy expenditure, as energy demands and the nutritional value of the food vary (Mayer and Thomas, 1967). The feedback control is achieved through a glucostatic mechanism, and feeding is initiated or inhibited by the hypothalamic centers, depending on information received from chemoreceptors detecting the glucose concentration in the blood. Long-term energy regulation may involve a separate lipostatic control mechanism. Growth regulation appears to result from the interaction of these energy-regulating systems and hormonal systems.

Less is known about the energy-regulating and hormonal control systems of invertebrates. Information is most complete for arthropods, but it concerns primarily the hormonal control of growth and molting (Knowles and Carlisle, 1956; Waterman, 1960, 473 ff.; Wigglesworth, 1965, 175 ff.). The work of Dethier *et al.* (1956) on the sheep blowfly provides some of the most relevant information on energy regulation in an invertebrate. They found that feeding was initiated by oral chemoreceptors and was terminated by unidentified receptors in the foregut. Termination was independent of blood sugar level and of crop and mid-gut contents.

We intend that the desired growth rate signal and the feedback comparison of actual growth rate in the model should approximate the combined action of physiological processes such as those known for mammals and insects. Although energy regulation and growth control represent separate physiological systems, they can be lumped into one process in the model of individual bioenergetics. To illustrate, consider an animal which reaches a constant adult body size; when this size is reached, desired growth rate becomes zero, and the animal simply balances energy intake against respiratory demand. On the other hand, a growing animal must acquire energy in excess of the amount dissipated in respiration; hence desired growth rate is positive. Thus, in the model a single comparator of desired and actual growth rates simulates

the action of at least two control systems in the body. For ecological purposes, this analog should be adequate.

We turn now to operational considerations of desired growth rate. Clearly growth rates can be measured; but can we, in fact, measure a *desired* growth rate? The answer is probably no, at least in the usual sense of the word *measure*, simply because the desired performance of an unknown system may or may not be its actual performance, which is all that we can observe. Nevertheless, there are at least two basic indirect methods for assessing what the desired performance of a biological system might be. The first might apply be called "the optimal environment method." In this approach one tries to provide the best possible set of conditions to the system for its operation, based upon what is already known about the system's dynamics. This is the most straightforward approach, and it assumes that the actual and desired performances will most nearly coincide if the system does not have to correct errors caused by disturbance inputs. The weakness of the method, of course, is that the environment provided for the system may not be truly optimal. The second approach can be called "the perturbation method," in which no attempt is made to provide optimal conditions. On the contrary, the object is to determine how the system reacts to precisely controlled disturbance inputs. From the dynamics of recovery from controlled disturbances, the nature of the system's controller can often be ascertained. This method is frequently more difficult, but is also theoretically more sound than the optimal environment approach. It should be noted that analyzing a system's response to a controlled disturbance input is different from the common engineering problem of analyzing the system's response to a transient change in a reference input. In the bioenergetics model, the reference "input," desired growth rate, is an internally generated performance criterion, not subject to manipulation because it is under the control of the system itself. This characteristic is common to many biological control systems: Frequently the differential equations that describe the system form a set of *implicit functions*; that is, the separation of "independent" and dependent physiological variables is impossible.

Both methods have been used to establish desired growth rates for *Armadillidium vulgare*. The details of this work will be published elsewhere (Hubbell and Paris, in preparation), but a brief resumé of the results of the optimal environment method is presented below:

Under a wide variety of constant conditions of temperature, moisture, and food availability, *Armadillidium vulgare* exhibits two characteristic growth phases: an exponential phase as a juvenile, and a linear phase, gradually assumed as an adult. Superimposed upon this basic growth

pattern are the effects of molting and, in females, of reproduction. Molting causes the growth curve to take on the "staircase" appearance typical of arthropod growth, whereas the brooding of young by females is accompanied by a temporary cessation of growth. Figure 2 illustrates this growth pattern for a typical individual grown at 24.5 C at 100% relative humidity with unlimited food. Note the relatively constant percentage increase in weight with each molt during the exponential

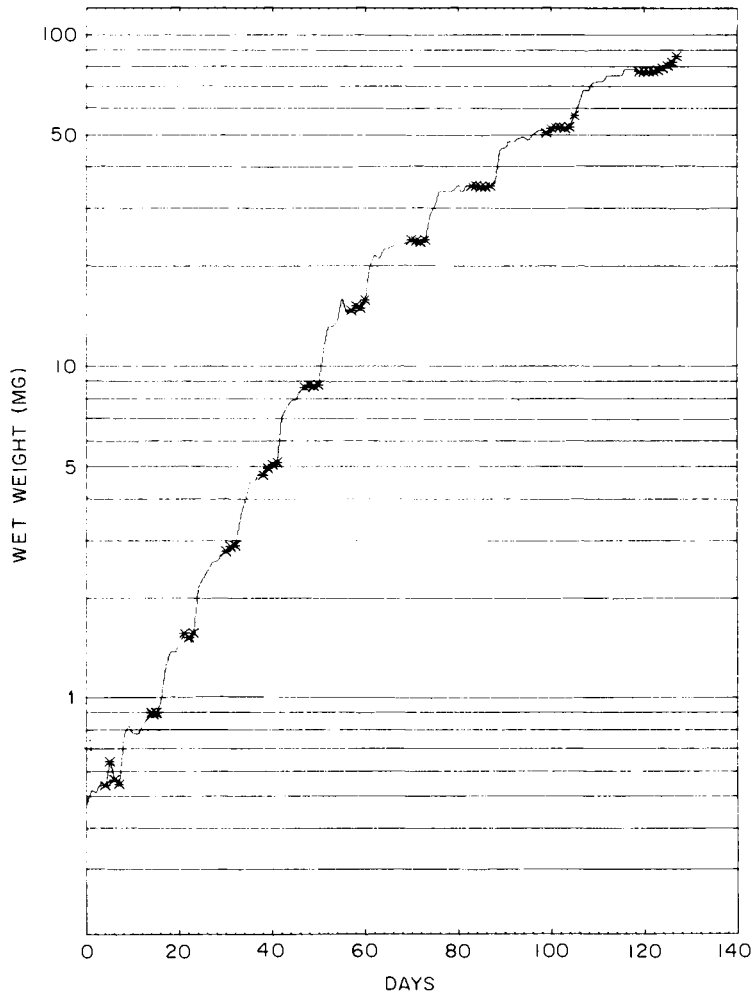

FIG. 2. Growth pattern in an individual of *Armadillidium vulgare* at 24.5 C and 100% relative humidity with unlimited food. Asterisks denote premolt condition.

growth phase. There is also a relatively constant percentage weight gain with each adult molt; however, the intermolt stage lasts for successively longer periods, resulting in the arithmetic growth pattern. For simplicity, the modifying effects of molting and reproduction upon the rates of energy accumulation and dissipation will not be included in the mathematical treatment of the bioenergetics model to follow. The details of these effects will also be published elsewhere (Hubbell, in preparation).

The coefficient of exponential growth is exponentially related to temperature in the range between 5 and 31.5 C (Fig. 3), as described by the equation

$$\log \hat{K} = -2.4761 + 0.03657\ (C). \tag{2}$$

Here K has a time base of one day, and is the coefficient in the growth equation,

$$P = P_0 e^{(K/0.43429)\cdot t}, \tag{3}$$

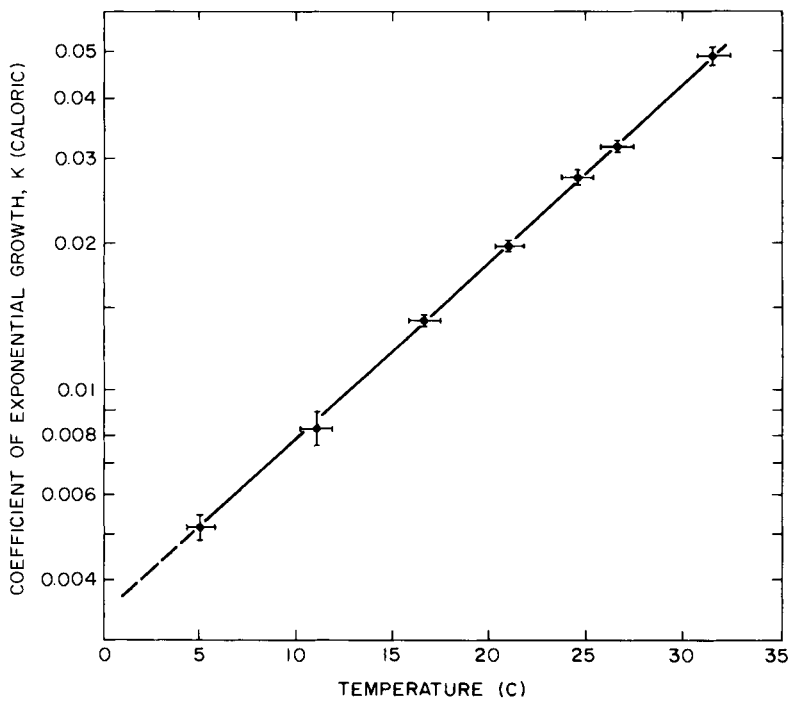

FIG. 3. Relationship between the coefficient of exponential growth and constant temperature with a time base of one day, expressed Eq. (2).

where P is weight (expressed in the model in calories), P_0 is weight at birth, t is age in days, and 1/0.43429 is the factor converting K from a power of 10 to a power of e. Equation (3) is adequate only until the isopods reach sexual maturity. The linearity of adult growth is illustrated in Fig. 4, which is a plot of the average growth of a cohort of animals.

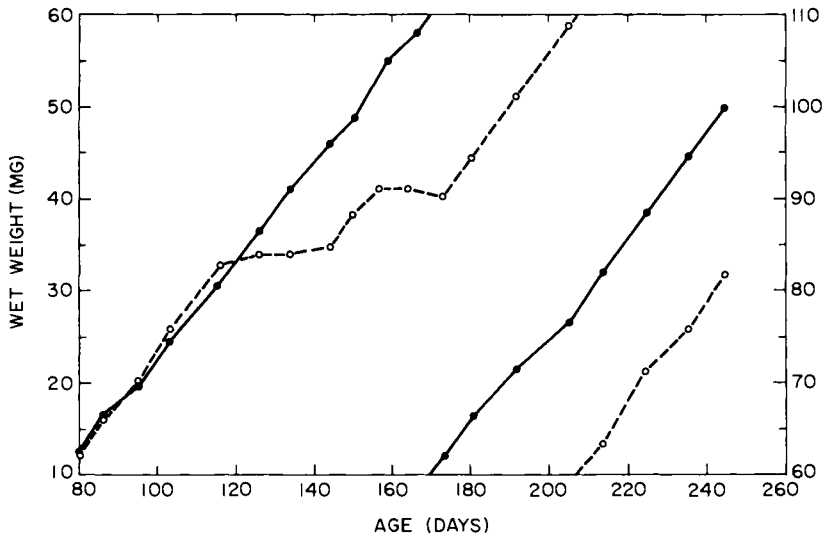

FIG. 4. Growth rate curve of adult isopods at 21.6 C. Scale of weight on left applies to left-most portion of curves, and scale on right to right-most portions. ●: males, ○: females.

The influence of molting is obscured because of a lack of precise molt synchrony between individuals. Females grow at the same rate as males except when they are carrying eggs, during which time their weight remains constant. Note that two broods were produced in rapid succession. During the arithmetic growth phase, weight or caloric content can be expressed as

$$P = P_{\mathrm{sm}} + c(t - t_{\mathrm{sm}}), \tag{4}$$

for $P > P_{sm}$ and $t > t_{sm}$, where P_{sm} and t_{sm} are the weight and age at sexual maturity, and c is a temperature-dependent constant.

Desired growth rate is obtained by taking the derivatives of Eqs. (3) and (4). In the exponential phase of growth, desired growth rate is proportional to the current weight or total caloric content (net production) of the individual. If DG is desired growth rate, then

$$DG = KDG(P_0)e^{(KDG)t} = KDG(P), \tag{5}$$

where $KDG = K/0.43429$. In the arithmetic phase of growth, desired growth rate becomes independent of the size of the animal; hence

$$DG = c. \tag{6}$$

Age appears to have no effect on growth rate in *Armadillidium*. Immature animals grow at a rate which is characteristic of their weight, given a specific temperature. After reaching sexual maturity, and after a period of switching from exponential to linear growth, the isopods grow at a temperature-dependent, constant rate, whatever their age or weight. Size- or weight-dependent growth rates have been described in a variety of other animals (Larkin *et al.*, 1956; Rasmussen, 1967).

Desired growth rates are apparently independent of soil moistures above a soil water content of 12% by weight, except for exceedingly wet conditions; below 12%, however, growth rates are lowered as the isopods attempt to conserve water by restricting their intake of dry food. The effects of varying temperature and food availability will be considered in a later section.

V. An Improbable Linear Bioenergetics Model

It is an often stated truism that nature is inherently nonlinear. Biological systems particularly are full of threshold phenomena and saturating nonlinearities (Holling, 1966a, b), synergisms (multiplicative effects), hysteresis, and the like. In spite of these complications, it is often possible to construct linear models of biological processes which are reasonable approximations of the dynamics of the real system. It should be noted that the linearity of a systems model does not mean that it produces only straight lines. Unlike a regression model, the time-domain solution of a system of linear differential equations consists of a sum of exponential curves, not straight lines. *Linearity* as used here means additivity; thus, if $y_1 = f(x_1)$ and $y_2 = f(x_2)$, then $(y_1 + y_2) = f(x_1 + x_2)$. Note that the equation $y = a + bx$ is nonlinear by this definition because $(y_1 + y_2)$ does not equal $f(x_1 + x_2)$.

The reason we go to the trouble of building linear models when we are really interested in nonlinear systems is that we then acquire the power to evaluate the dynamic performance of the system analytically, not just numerically. In fact, we can analytically solve for the response of a linear system to *any* conceivable input function, however complicated. Even exceedingly complex linear systems can be simplified enormously using the techniques of so-called "operational" mathematics.

It should be emphasized that the linear models developed below

are only exercises to acquaint us with some of the most basic properties of energy-regulating biological control systems; they are by no means intended as definitive models of such systems. Biological systems which control energy have a number of essential nonlinearities which ultimately cannot be ignored. At the end of this chapter in Section VII, we shall consider progress that has been made toward developing a realistic and hopefully somewhat general nonlinear model of growth and energy regulation in animals.

Hence, once we thoroughly understand the linear approximation, we can begin to introduce more realistic nonlinear elements into the model one by one, to determine how they modify the behavior of the linear system. There is, of course, no guarantee that the nonlinear system will behave anything like the linear system. Generally, however, the performance of the two systems will not differ so greatly as to make the linear exercise worthless, especially when the linear system was designed to approximate the behavior of the real system. Often, nonlinear systems exhibit greater control accuracy, although they may be less stable in the face of large perturbations than their linear counterparts.

In constructing a model of a hypothetical "linear" isopod, I shall have two primary concerns: first, the adequacy of each system component as an approximation of the actual physiological process; and second, the capacity of the assembled model to regulate energy accumulation and dissipation, as it is supposed to do. The first model we shall consider is very simplistic and inadequate as a physiological model, but it will serve to illustrate ideas about control and the differences in performance of open- and closed-loop systems.

For simplicity, we shall be making use of Laplace transforms in the following discussion, rather than differential equations, although a completely parallel treatment of the material is possible using differential equations. For those not familiar with this transform technique, the Laplace transform of a function of time, $F(t)$, is given by

$$F(s) = \mathscr{L}[F(t)] = \int_0^\infty F(t)\, e^{-st}\, dt. \tag{7}$$

Clearly, one effect of this transformation is to eliminate time as the independent variable, substituting for it a new variable s in the "complex frequency" domain. Convergence of this integral is assured for only certain s and $F(t)$, but the class of permissible $F(t)$ is broad. Moreover, the transformation is linear; and when it is applied to a linear system, it has the remarkable property of reducing the operations of differentiation and integration essentially to simple algebraic multiplication and

division by the complex variable s. Using this technique, we shall obtain overall transfer functions for two linear bioenergetics models of increasing complexity. In particular, we are interested in the transfer function characterizing the dynamic relationship between actual growth rate (the "output") and desired growth rate (the "input"). Obtaining this transfer function for a study of how accurately the model will track a given desired growth rate signal requires that we open the feedback loop of net production (body caloric content) P upon desired growth rate DG (henceforth called the "desired growth rate loop"). This simplification will not alter the model's growth control abilities, and it eliminates the implicit nature of the model's functions. In addition to opening this feedback loop, we shall also be opening the loop in which actual growth rate is compared with desired growth rate, to compare the control abilities of the open- and closed-loop systems.

Consider the linear model illustrated in Fig. 5a, which is one of the simplest that can be derived from the generalized bioenergetics model of Fig. 1. To compute the output variable from each block, the expression in the block is multiplied by the input variable. As mentioned above, the desired growth rate loop has been broken, and is indicated by the dotted line. In this model, the assimilation rate, $\dot{A}(s)$, is assumed to be composed of a body size component $RP(s)$, an error-correcting signal $AE(s)$, and a disturbance input $DA(s)$. As is required of a linear system, all of these signals are additive, not multiplicative, and they are related to other variables as simple proportions. In the nonlinear model, of course, some or all of these signals may be multiplicative and/or nonlinear functions of other variables. For example, the body size component of assimilation rate will become an exponential function of body size, rather than a linear one. Also it will become apparent that all environmental disturbance inputs, including food availability, enter the model nonlinearly. Respiration rate $\dot{R}(s)$ likewise has three components here: a body-size component $RP(s)$, a growth rate error compensator, $RE(s)$, and a disturbance input $DR(s)$. The difference $(\dot{A}(s) - \dot{R}(s))$ is the actual growth rate of the isopod $AG(s)$; integrating this signal by multiplying it with $1/s$ gives the current net production of the animal $P(s)$. The control of growth is assumed here to be of the "integral" variety; that is, the controller variables, $AE(s)$ and $RE(s)$, respond to $E(s)$, the integral of $GE(s)$, rather than to the instantaneous growth rate error itself. This is equivalent to the biological statement that the animal has a "memory" of prior nutritional history, a fact that is amply documented in the literature (cf. Brody, 1945). Here we unrealistically assume, however, that the animal has an indefinite memory of its past nutritional states. In the second linear model we shall eliminate this unreal feature.

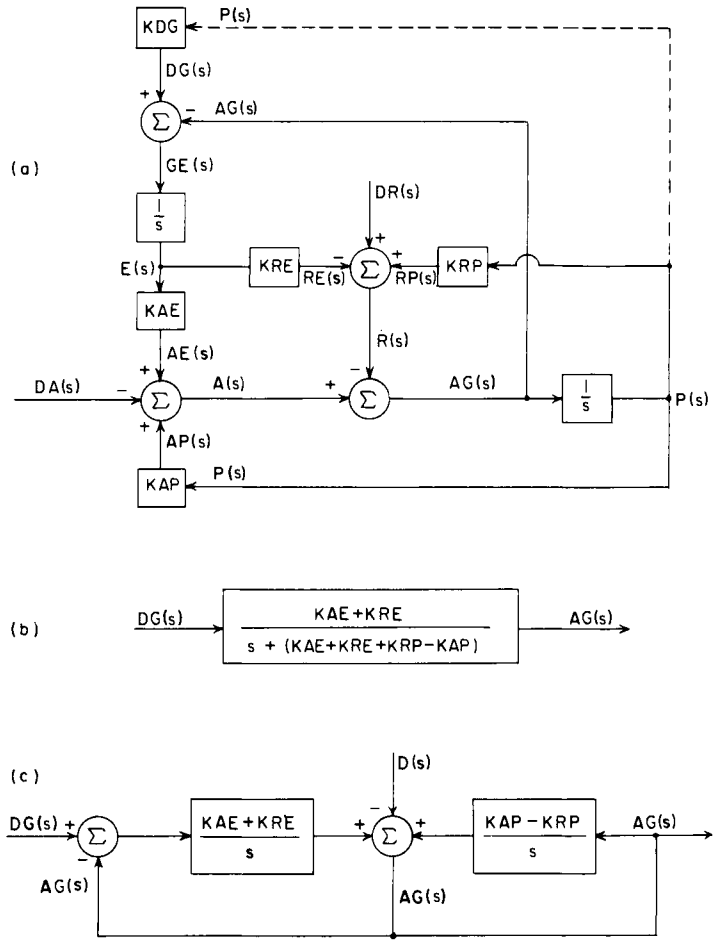

FIG. 5. (a) Block diagram for simple linear model. (b) "Open-loop" transfer function for model in (a). (c) Rewritten block diagram emphasizing the difference in the locus of disturbance inputs and of the reference input.

To find the transfer function $H(s) = AG(s)/DG(s)$, we "solve" the system for $AG(s)$ as a function of $DG(s)$, assuming for the moment that there are no disturbance inputs. Formally this is the same as eliminating intermediate variables from a set of simultaneous differential equations.

$$AG(s) = (\dot{A}(s) - \dot{R}(s)) \tag{8}$$

$$= (KAP/s)(AG(s)) + (KAE/s)(DG(s) - AG(s)) + (KRE/s)(DG(s) - AG(s)) - (KRP/s)(AG(s)). \tag{9}$$

Separating the variables in Eq. (9) and cross-multiplying, we obtain

$$H(s) = \frac{AG(s)}{DG(s)} = \frac{KAE + KRE}{s + (KAE + KRE + KRP - KAP)}. \tag{10}$$

This is the transfer function relating $AG(s)$ to $DG(s)$ shown in Fig. 5b, and it is equivalent to the block diagram in Fig. 5c. The effect of our algebraic manipulation has been to "collapse" the three feedback loops in the model, to give a much more straightforward, "open-loop" function. When $DG(s)$ is multiplied by $H(s)$, we obtain $AG(s)$. Suppose, for example, that we are interested in the dynamic response of $AG(s)$ to one of the following three commonly used "transient" test inputs: impulse (the Dirac delta function), step, or ramp (Fig. 6). Because we

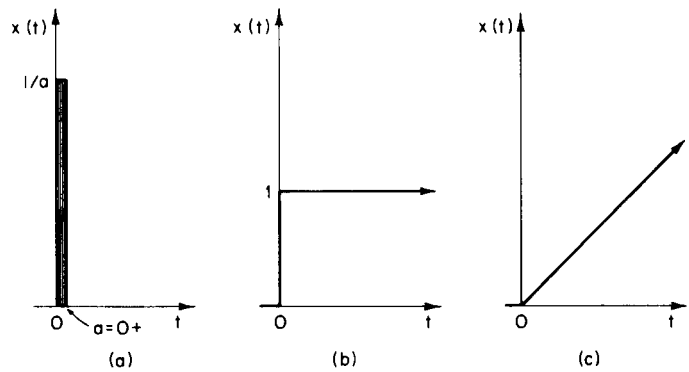

FIG. 6. Three commonly used transient "test" inputs: (a) impulse, $x(s) = 1$. (b) step, $x(s) = 1/s$. (c) ramp, $x(s) = 1/s^2$.

are operating in the complex frequency domain, we need the Laplace transform of their time functions, which are respectively: 1, $1/s$, and $1/s^2$. Multiplying any one of these by $H(s)$ gives the Laplace transform of the response of $AG(s)$ to that input.

The generalized transfer function of an arbitrary linear system is a so-called *rational algebraic fraction*, consisting of numerator and denominator polynomials in s

$$F(s) = \frac{A(s)}{B(s)} = \frac{a_0 + a_1 s^1 + \cdots + a_m s^m}{b_0 + b_1 s^1 + \cdots + b_n s^n}, \tag{11}$$

where $m \leqslant n$ for a physically realizable system. The roots of the numerator, called *zeros*, are concerned with the gain (the ratio of output and input amplitudes) and the phase of the response relative to the input,

but not with the basic character of the response. The latter is determined by the roots of the denominator polynomial, known as the system *poles* or *eigenvalues* (Chapter 2). The number of eigenvalues determines the *order* of the system. In general, eigenvalues are complex numbers, and their position on the complex plane is critical for the control capabilities of the system and its stability. All of the system's eigenvalues must have negative real parts; otherwise the system's response in the time domain will diverge exponentially to infinity. If the set of eigenvalues contains one or more complex-conjugate pairs, the system will be oscillatory; on the other hand, no oscillations will appear if the eigenvalues are real.

Equation (10) indicates that our simple bioenergetics model is a first-order control system with its eigenvalue located at

$$s = KAP - KAE - KRE - KRP. \tag{12}$$

The sum of KAE, KRE, and KRP must be greater than KAP for the system to be stable. The system is incapable of oscillatory behavior because it has only one pole, and imaginary poles occur only in pairs.

Once we have a transfer function for the system we are analyzing, we usually want to determine the corresponding function in the time domain. The inverse transformation of going from the complex frequency domain to the time domain is commonly made by the method of *partial fractions*. Any rational algebraic fraction such as Eq. (11) can be expressed as a sum of the form

$$\frac{A(s)/b_n}{(s+r_1)(s+r_2)\cdots(s+r_n)} = \frac{C_1}{s+r_1} + \frac{C_2}{s+r_2} + \cdots + \frac{C_n}{s+r_n}, \tag{13}$$

where the constants C_i are equal to

$$C_i = [(s+r_i)\,A(s)/B(s)], \qquad \text{where} \quad s = -r_i\,. \tag{14}$$

The ith member of this sum is then equivalent to

$$C_i/(s+r_i) = C_i \exp(-r_i t) \tag{15}$$

in the time domain. As an example, we solve for the time-domain response of Eq. (10) exposed to a unit step input of $DG(s)$. Letting $K_1 = KAE + KRE$ and $K_2 = KAE + KRE + KRP - KAP$, we have

$$\frac{1}{s}\,\frac{K_1}{s+K_2} = \frac{K_1/K_2}{s+0} + \frac{-(K_1/K_2)}{s+K_2} = \frac{K_1}{K_2}\{1 - \exp(-K_2 t)\}. \tag{16}$$

Thus, the response of actual growth rate $AG(t)$ to a hypothetical step from 0 to 1 in $DG(t)$ is an exponentially decelerating rise to a plateau value of K_1/K_2 (Fig. 7), with a time constant of $1/K_2$.

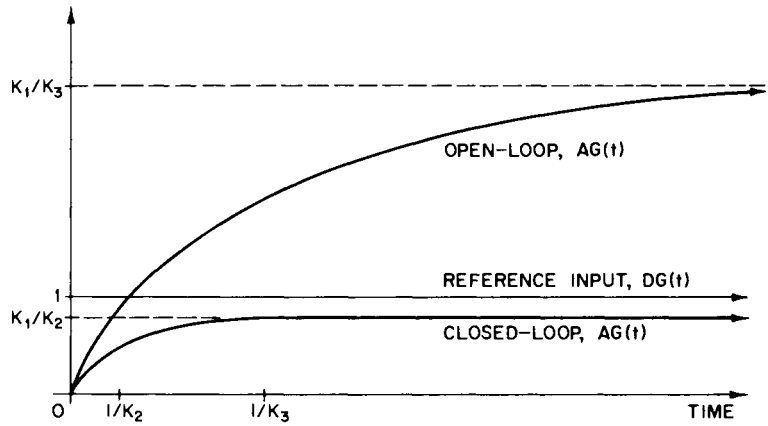

FIG. 7. Comparison of step responses of open- and closed-loop simple linear bioenergetics model.

By use of the step response, we can compare the ability of the open- and closed-loop versions of the model to track a desired growth rate input signal. If we eliminate the feedback comparison of $AG(s)$ with $DG(s)$, the open-loop transfer function becomes

$$H(s) = \frac{KAE + KRE}{s + (KRP - KAP)}. \tag{17}$$

Letting $K_3 = KRP - KAP$, the time-domain step response of Eq. (17) is

$$F(t) = (K_1/K_3)\{1 - \exp(-K_3 t)\}. \tag{18}$$

Thus the open-loop system exhibits the same first-order type of response to the reference input shown by the closed-loop system, but responds more slowly than the closed-loop system and reaches a higher steady-state level, resulting from the fact that $K_2 > K_3$. The more rapid response of the closed-loop system indicates an important and desirable effect of negative feedback upon the system's dynamics. The "loop gain" (the amount by which the signal is multiplied by feedback on itself) of the system is very important in setting this response time. Thus, the more we amplify the error-correcting signal by increasing KAE

and KRE, the more negative the eigenvalue becomes, and the smaller the time constant becomes.

One undesirable but partially correctable feature of negative feedback is that the steady-state level finally achieved, K_1/K_2, is below the desired level, unity (if we input a unit step). This is a better situation, however, than in the open-loop model, whose steady-state value K_1/K_3 need be nowhere near the desired level (Fig. 7). When the loop gain of the system is known, the problem of undershooting the desired level in the closed-loop system may be overcome by premultiplying the reference input by a constant so that the desired level is achieved. In our case, we can simply scale $DG(s)$ by K_2/K_1. Note also that increasing the loop gain by increasing the amplification of growth rate error relative to the difference ($KRP - KAP$) will likewise tend to bring the steady-state performance of the system closer to the desired performance, as K_1 approaches K_2. Yet another way that control could be improved would be to make the model respond not only to the integral of growth error, but to $GE(s)$ as well. In none of these cases, however, is it possible to achieve a steady-state error of zero for finite loop gain.

Not only does the open-loop model respond slowly to changes in reference inputs, and assume steady states frequently nowhere near the desired states, but also the open-loop model is incapable of compensating for disturbances. Thus, if we are interested in an animal's ability to correct growth errors due to environmental disturbances, including variations in food availability, the closed-loop model is clearly far superior to the open-loop one. To explore how these two versions of the model respond to a disturbance input, the block diagram shown in Fig. 5a has been modified as illustrated in Fig. 5c, combining for convenience the disturbances of assimilation rate and respiration rate into one input $D(s)$. In this form the diagram emphasizes the difference between the locus of disturbance inputs, which act directly upon the controlled process, and the locus of the reference input, which does not.

In the model, with the desired and actual growth rate loops closed, the transfer relations between $AG(s)$ and $DG(s)$ with $D(s)$ included are

$$AG(s) = \frac{K_1}{s + K_2} \cdot DG(s) - \frac{s}{s + K_2} \cdot D(s). \tag{19}$$

For the model in which the actual growth rate loop is open, the transfer relations are the same with K_3 substituted for K_2. Since we are primarily interested here in the responses of $AG(s)$ to disturbances, we shall set $DG(s)$ equal to zero and consider only the second term of Eq. (19).

Note that $s/(s + K_2)$ is a transfer function of the same order in the numerator and denominator, so that the time-domain equivalent of this equation will not remain finite with the input of an impulse transient. Nevertheless, we can explore the frequency response of this system. If we let $D(t)$ be a sinusoidal input, $A \sin \omega t$, of amplitude A and angular frequency ω, the Laplace transform $D(s)$ is given by

$$D(s) = \mathscr{L}[A \sin \omega t] = \frac{A}{2j}\left[\frac{1}{s - j\omega} - \frac{1}{s + j\omega}\right] = \frac{A\omega}{s^2 + \omega^2} \tag{20}$$

from Euler's equation, where $j = \sqrt{-1}$. Substituting Eq. (20) for $D(s)$ in Eq. (19), setting $DG(s)$ equal to zero, and applying the method of partial fractions to Eq. (19), we obtain the time-domain solution for $AG(t)$

$$AG(t) = \frac{-A\omega K_2}{K_2^2 + \omega^2} \exp(-K_2 t) + \frac{A\omega}{(K_2^2 + \omega^2)^{1/2}} \sin\left(\omega t + \frac{\pi}{2} - \alpha\right), \tag{21}$$

where $\alpha = \sin^{-1}(\omega/(K_2^2 + \omega^2)^{1/2})$.

In time, the first term of Eq. (21) goes to zero. Thus, the amplitude of the steady-state oscillation of $AG(t)$ is given by

$$|AG(t)| = A\omega/(K_2^2 + \omega^2)^{1/2}. \tag{22}$$

Earlier we noted that K_2 of the closed-loop system was greater than the corresponding constant in the open-loop system K_3. Substitution of K_3 for K_2 in Eq. (22) significantly increases the amplitude of the oscillations in $AG(t)$. For example, if we let $\omega = A = 1$, $K_3 = 0.5$, and $K_2 = 8$, the oscillations in the model with the actual growth rate loop open are 7.22 times greater than in the corresponding closed-loop model. Clearly, then, the closed-loop model exhibits far lower sensitivity to disturbances than does the open-loop model.

Before turning to the second linear bioenergetics model, we note the effect of closing the desired growth rate feedback loop, which we earlier broke to eliminate the implicit character of the model's functions. We may close this loop and still compute a transfer function for the model if we treat the disturbance input as the "reference input" of the model. While this is biologically meaningless, this approach will enable us to discover what happens to the order and stability of the system when this loop is closed. The transfer function $AG(s)/D(s)$ is given by

$$\frac{AG(s)}{D(s)} = \frac{s^2}{s^2 + s(KAE + KRE + KRP - KAP) - KDG(KAE + KRE)} = \frac{s^2}{s^2 + K_2 s - K_4}, \tag{23}$$

where $K_4 = KDG(KAE + KRE)$. This equation has two eigenvalues, rather than one. The eigenvalues are located at

$$r_1 = (-K_2 - (K_2^2 + 4K_4)^{1/2})/2 \quad \text{and} \quad r_2 = (-K_2 + (K_2^2 + 4K_4)^{1/2})/2. \quad (24)$$

Thus, one effect of closing the desired growth rate loop is to increase the order of the system to two, by putting the two integrators in the model in series, or "in cascade," instead of in parallel. Earlier we noted that the system without the desired growth rate loop could be either stable or unstable, depending upon the value of K_2. The intact model, however, is exponentially unstable regardless of whether K_2 is positive or negative: since K_4 is greater than zero, the second eigenvalue is always positive. It should be noted that this instability is *desirable*, because we want our "linear" isopod to grow exponentially with time as a juvenile. When the isopod reaches sexual maturity, we simply break this feedback loop, and thereafter the isopod will grow arithmetically.

VI. Another Improbable Linear Bioenergetics Model

Obviously the bioenergetics model we have just considered is physiologically too simple, notwithstanding its linearity. Yet, for many ecological studies of higher level systems, a *nonlinear* version of this simple model—such as might be obtained by adding feedback control to a modification of Pütter's equation—may be an adequate model of individual growth performance, especially if the time scale is measured in terms of months, years, or other long periods relative to the time constants of physiological processes. If, on the other hand, one is interested in ecological events for which days or even hours are important, certainly greater physiological detail must be introduced into the model. The price paid for more detail is, of course, a certain risk of losing generality. Nevertheless, apart from its linearity, the model developed below will hopefully have general aspects, although it is specifically meant for an isopod. I have, in fact, drawn upon work done on other organisms wherever the information necessary was not yet available for *Armadillidium vulgare*.

We consider first the process of energy accumulation. In the simple model, no account was taken of the dynamics of the digestive system of an animal. The model responded instantly to an increase in food availability, whereas in reality the time necessary to digest consumed food may cause a significant time lag in the response of the system to

changes in food supply. Moreover, the direct impact an animal makes upon its food supply could not be assessed, because there was no measure of ingestion; only assimilation was modeled.

Although considerable efforts have been devoted to the measurement of ingestion and assimilation rates of terrestrial isopods (Bakker, 1956; Dunger, 1958a, b, 1960; Gere, 1956, 1962, 1963; Hartenstein, 1964; Hubbell *et al.*, 1965; Paris and Sikora, 1967; Wieser, 1965, 1966), no attempt has been made to model the dynamic behavior of the digestive system of isopods as a whole. The model developed here is based in part upon the work of Ivlev (1961) and Holling (1966a), and upon studies on *Armadillidium* (Hubbell and Paris, in preparation).

Holling has found that in a variety of invertebrates the amount of food ingested after starvation rises at an exponentially decreasing rate until the gut capacity is reached; by using radioactively labeled food we have confirmed that this is also true for *Armadillidium*. This result suggests that ingestion rate is proportional to the unfilled volume of the gut. If SA is the current contents of the gut, SC is the gut capacity, and dC/dt is ingestion rate, then

$$dC/dt = KC \cdot (SC - SA) = KC \cdot SE, \tag{25}$$

where KC is the proportionality factor and SE is the remaining unfilled capacity of the gut. In the nonlinear model, KC is a function of food availability and physical factor disturbances and SC, which is the reference input for this control system, is a function of the body size of the animal P. According to this model, then, the desired condition of the digestive system is for the gut to be full at all times.

Assimilation rate dA/dt and defecation rate dD/dt are assumed here to be proportional to the amount of food actually in the gut SA.

$$dA/dt = KA \cdot SA, \tag{26}$$

and

$$dD/dt = KD \cdot SA. \tag{27}$$

We have direct evidence of this proportionality for defecation rate, from pulse feeding experiments involving radioactive and nonradioactive food presented sequentially to the isopods (Hubbell and Paris, in preparation). The exponential rate at which isopods lose radionuclide has two main components: a fast gut component, and a slower body component attributable to assimilated radionuclide (Hubbell *et al.*, 1965). There is some curvilinearity to the gut component on a semilogarithmic plot, indicating the existence of several isotopic compartments in the gut. Nevertheless, the gut component of the radionuclide loss rate curve

can be approximated reasonably well by a single-compartment model for our purposes; and if greater accuracy is ever required, we can always model the gut as a series of first-order systems in cascade, instead of a single first-order system.

The proportionality assumption for assimilation rate is based upon the fact that the metabolic cost related to assimilation, including the specific dynamic action (*SDA*) component of respiration rate and associated metabolic costs of digestion, falls exponentially with time in a starving isopod, with the same time constant as that for the disappearance of food from the gut (Fig. 8). This indicates that *SDA* is

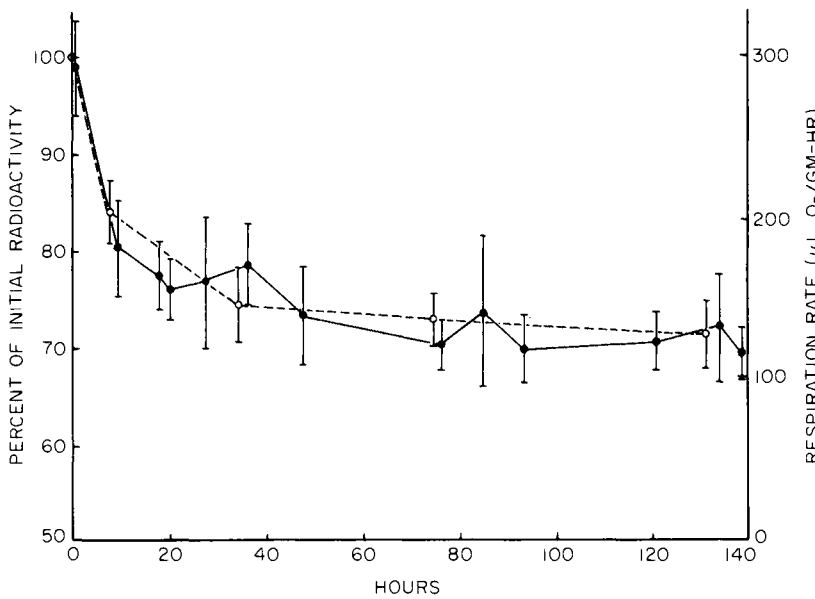

FIG. 8. Superimposed curves of the decrease in respiration rate (●—●) and the loss of radionuclide from the gut (○- - -○), in a starving isopod at a temperature of 30 C.

roughly proportional to *SA*. Since *SDA* is generally regarded as the metabolic cost of digesting and assimilating food (cf. Kleiber, 1961) and is approximately proportional to assimilation, we can assume here that there is a similar approximately proportional relationship between dA/dt and *SA*. The processes of assimilation and defecation result in calories being removed from the current cut contents. Thus, *SA*, the amount of food in the gut, is computed as ingested calories minus assimilated and defecated calories:

$$SA = C - A - D. \tag{28}$$

To compensate for growth performance errors, control must be exerted over this system. In the simple model this was accomplished in a direct fashion, by adding to assimilation rate the amplified and integrated growth rate error. Clearly, however, an animal cannot do this in such a direct manner. What happens, in fact, is that an animal increases its tendency to feed, regardless of whether or not food is available. When animals are starved, they not only eat more rapidly, but also eat more totally to satiation than their unstarved counterparts. Figure 9 illustrates this phenomenon in *Armadillidium*, which depicts the

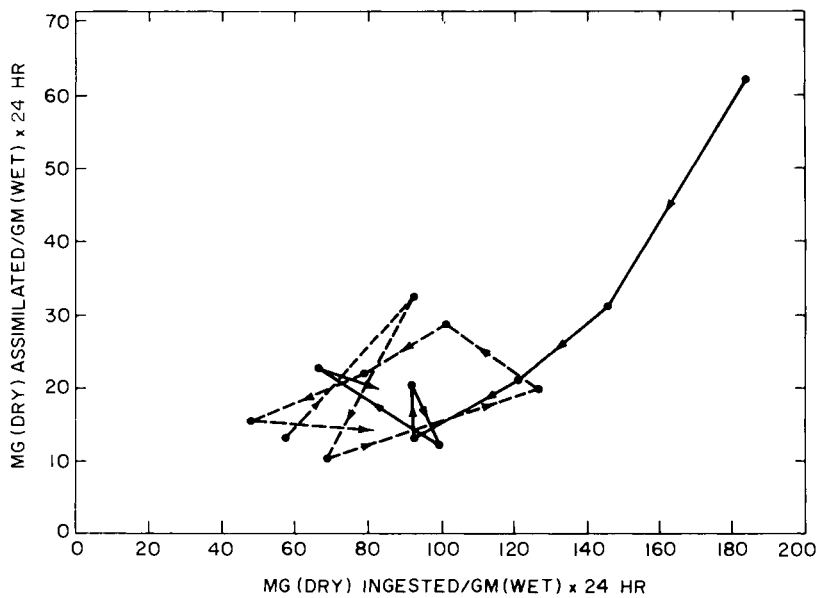

FIG. 9. Average weight-specific ingestion and assimilation rates of 25 isopods for an eight-day period. Numbers indicate day of measurement. Solid-line group was starved for five days before the first measurement. Dotted-line group was not starved.

changes that occurred in average daily ingestion and assimilation rates for 8 days, in one group of 25 animals that had been starved for 5 days, and in another group that had not been starved. These results suggest that gut capacity can be treated as a variable which is a function of the growth error compensator as well as a function of body size. This is in contrast to the approach used by Holling (1965, 1966a), in which gut capacity imposes a fixed physical limitation on the amount of food that an animal can eat. I shall consider it here, not as the physical

capacity of the gut, but as the optimal amount of food that an animal should ingest for its size and nutritional condition. Hence,

$$SC(s) = E(s) + KSC \cdot P(s), \tag{29}$$

where KSC is a constant.

The assembled linear version of the digestive system component of the bioenergetics model is illustrated with a block diagram shown in Fig. 10a. To compute a transfer function for it, we solve for $SA(s)$

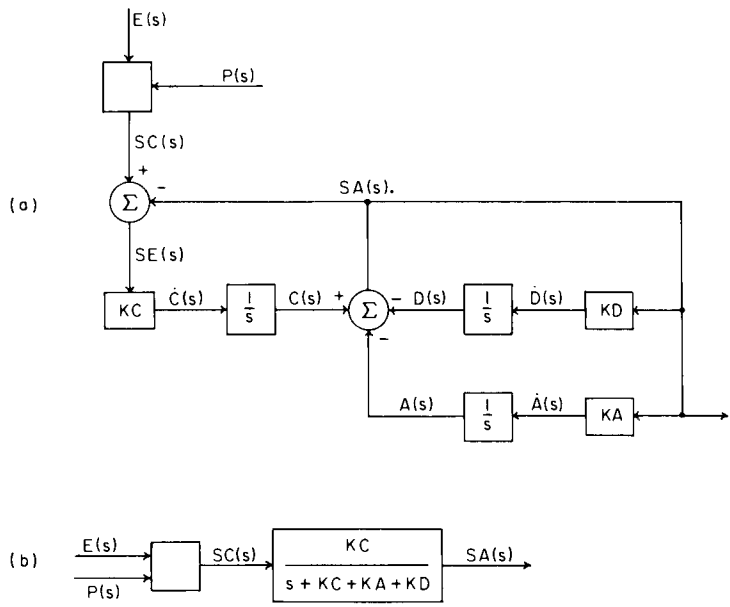

FIG. 10. (a) Linear version of the digestive system component of the bioenergetics model. (b) Open-loop transfer function of model in part (a).

in terms of $SC(s)$, noting that $SA(s)$ is the controlled variable and $SC(s)$ the reference input. Then, dividing both sides of the equation by $SC(s)$, we obtain

$$H_1(s) = \frac{SA(s)}{SC(s)} = \frac{KC}{s + (KC + KA + KD)} = \frac{KC}{s + K_1}, \tag{30}$$

where $K_1 = KC + KA + KD$. Evidently the gut is a first-order system (Fig. 10b) with a time constant of $1/K_1$. With a unit step input in $SC(t)$, $SA(t)$ rises at an exponentially decreasing rate to a plateau value of KC/K_1; clearly, the smaller KA and KD are relative to KC, the closer $SA(t)$ gets to $SC(t)$ in the steady state.

We turn now to the process of energy dissipation. In the simple linear model, respiration rate was assumed to be directly and negatively affected by the growth rate error compensator *RE*. This representation may be closer to the truth in homeotherms than it is in invertebrate poikilotherms. For *Armadillidium* in particular, the fall in respiration rate that accompanies starvation appears to be a passive rather than an active process (Hubbell, in preparation). The decrease is exponential, and as a first-order approximation appears to have two major additive components (Fig. 8). The fast component has been attributed to specific dynamic action and other costs of digestion, and the second, slow component, to a gradual reduction in the amount of respiring tissue (*P*). (The curve in Fig. 8 does not result from a decrease in muscular activity because *Armadillidium*, like some insects, spends little time searching for food in the absence of olfactory stimuli, even when starving.) The ability, passive or otherwise, of *A. vulgare* to reduce its respiration rate when starving is of special adaptive value in California grassland, where dry atmospheric conditions may prevent the isopods from surfacing to feed for periods of up to two weeks during the summer and fall drought (Paris, 1963). Laboratory experiments have shown that *A. vulgare* can survive up to 45 days without food.

Little is known about the effect of muscular activity on respiration rate in *Armadillidium* because many variables which determine the activity state of the isopod have not yet been examined quantitatively. Physical factors known to influence activity include temperature, vapor pressure deficit, soil moisture, light intensity, and wind speed. Physiological variables include the nutritional condition of the isopod (when olfactory stimuli are present—the usual state of affairs in soil in the field), feeding, and reproductive condition. I have made simultaneous recordings of respiration rate and activity (Hubbell, in progress), and although this work is not nearly complete, some general conclusions can be drawn. From an energetics standpoint, *A. vulgare* has essentially two important activity states. Individuals either sit motionless, often hours at a time, making only an occasional preening movement, or else they walk slowly at a temperature-dependent rate (White, 1968; Hubbell, unpublished results). A third temporally important activity, eating, has a rate of energy expenditure close to the resting state, and can be treated as resting. A maximal metabolic scope of about two was obtained for metabolic rates (averaged over hourly periods) between times of low and unusually high activity. The isopod is nocturnal, with a peak in activity usually just before midnight (Paris, 1963; Hubbell, unpublished results). Finally, when isopods are starved in the presence of a food stimulus they cannot reach, total daily activity increases up to about

five days, and then begins to decrease as the animals weaken. The functional form of this relationship, however, has not yet been well defined. Until more information is available about activity, we shall model its effect upon respiration rate as a simple additive term proportional to integrated growth rate error E. This signal will be continuously "on" in the linear model because of the linearity assumption; in the nonlinear model, on the other hand, it will only be "on" for positive values of E and when physical factors are appropriate for activity. In other words, we are assuming that the isopod will exhibit locomotory activity in proportion to its current nutritional state, modified by the current state of the "weather."

The linear model of energy-dissipating processes in a poikilotherm emerging from this discussion is as follows: If $\dot{R}(s)$ is respiration rate,

$$\dot{R}(s) = KRA \cdot SA(s) + KRE \cdot E(s) + KRP \cdot P(s), \tag{31}$$

where KRA, KRE, and KRP are proportionality factors, and $SA(s)$, $E(s)$, and $P(s)$ are as before. The first term is the contribution of specific dynamic action, while the second and third terms are the activity and body size components, respectively. In the nonlinear model the body size component becomes an exponential function of P. Omitted from this discussion are the important nonlinear effects of molting and reproduction on respiration rate; however, discussion of these effects, as mentioned earlier, will appear elsewhere.

Before considering the assembled model, we examine briefly the concept of the "nutritional state" of an animal. Obviously, since we are dealing only with calories, our use of the term is less inclusive than that usually meant by nutritional physiologists. Thus, our model of nutrition will not explain changes in an animal's growth performance due to protein or micronutrient deficiencies. Nevertheless, the effects of such deficiencies can eventually be included in our model if desired, and without drawing our attention away from the problem of energy regulation in animals. This can be accomplished by interpreting noncaloric limitations on growth performance as the result of measurable "degenerative" changes (i.e., changes away from optimal values) in the parameters of the bioenergetics control system.

Recognizing, however, that currently we can attempt only to explain the effects of caloric deficiencies on growth, we still face a major problem with the concept of nutritional state as modeled thus far. In the simple linear system the variable E (defined as the caloric nutritional condition of an animal) is simply the growth rate error signal integrated over the life of the individual. According to this definition, an animal has a

complete memory of its nutritional history over its entire lifetime. If this were true, no animal could be permanently stunted by starvation. From the point of view of the model, if an animal grew at a suboptimal rate indefinitely, it could conceivably build up an enormous integrated growth rate error which, when added to the body size component, would produce an impossibly large gut capacity. It would also produce an activity component of respiration rate that was unrealistically large. Clearly, animals do not have an indefinite memory of prior nutritional history; in reality, they "forget" past food deprivation, and in general, the farther back in time the deprivation is, the more it is forgotten.

We have evidence of this "memory loss" in growth rate experiments which we have conducted on *Armadillidium* (Hubbell and Paris, in preparation). Cohorts of newborn isopods were maintained either on a continuous food regime or on different pulse feeding regimes (in which they were fed one day for every one, two, four, six, or eight days starved). At the end of about 50 days, all cohorts were put onto a continuous food regime to test for "memory" of long-term nutritional history. During the 50 days of exposure to pulsed food availability, the isopods grew at greater exponential rates than would be expected simply from the percentage time exposed to food (see Fig. 11). This result indicates that on a short-term basis, isopods "remember" their nutritional history and attempt to compensate for it. When the isopods were shifted to continuous food, the initial weight-specific growth rates in all but the ninth-day cohort were greater than the average weight-specific rates in the continuously fed cohort, but only for the first four or five days. However, the initial growth rates of the cohorts fed every fifth, seventh, and ninth days were no greater than those of the cohorts fed every other day or every third day. This suggests that after about three to five days of starvation, further starvation cannot significantly increase the isopod's compensatory efforts. Of course, if the animal is starved a very long time, system degeneration takes place, reducing even its limited abilities to compensate, as in the case of our ninth-day cohort.

In modeling the limited ability of animals to respond to their nutritional history, I have assumed that animals forget at an exponentially decreasing rate. Accordingly, they will remember immediately past nutritional events more accurately than events long ago. In the model this can be accomplished simply by decreasing the integrated growth rate error E at a rate which is proportional to the size of E. Thus, instead of KGE/s for the transfer function of $E(s)/GE(s)$, we have

$$E(s)/GE(s) = KGE/(s + KE), \tag{32}$$

where KGE is the amplification factor of growth rate error and KE is

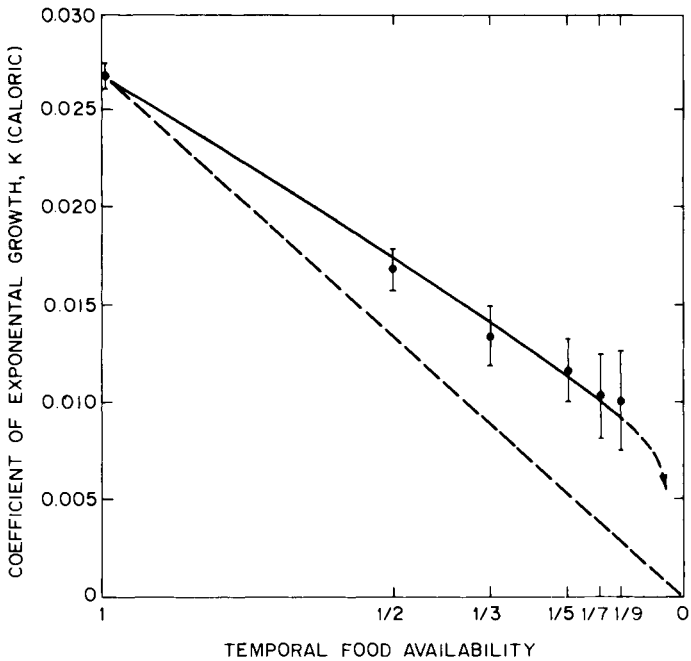

FIG. 11. Relationship between the coefficient of exponential growth at 24.5 C and the fractional amount of time (in days) exposed to food. The dotted line indicates the growth rate coefficients to be expected if the isopods grew at a rate simply proportional to the fraction of time exposed to food. The vertical bars indicate 95 percent confidence limits about the mean growth rate coefficient. (Time unit is one day.)

the gain term in the negative feedback in the forgetting process. When Eq. (32) is exposed to a unit impulse in $GE(t)$, $E(t)$ falls from an initial value of KGE/KE at an exponential rate, with a time constant of $1/KE$.

The assembled linear bioenergetics model is illustrated in Fig. 12. The diagram includes two nonlinear multipliers, shown as circles containing a multiplication sign, which should be disregarded for the moment. As in the case of the simple linear model, we wish to determine the transfer function $AG(s)/DG(s)$; accordingly, we again open the desired growth rate feedback loop. Simplification of a block diagram of this complexity is most conveniently carried out in steps. The first step has already been taken with the determination of the digestive system transfer function $SA(s)/SC(s)$; substituting Eq. (30) for the gut component in Fig. 12 gives the somewhat simplified diagram of Fig. 13a. Note that the output from $H_1(s)$, the amount of food in the gut, is an input at two points in the remainder of the model: the specific dynamic

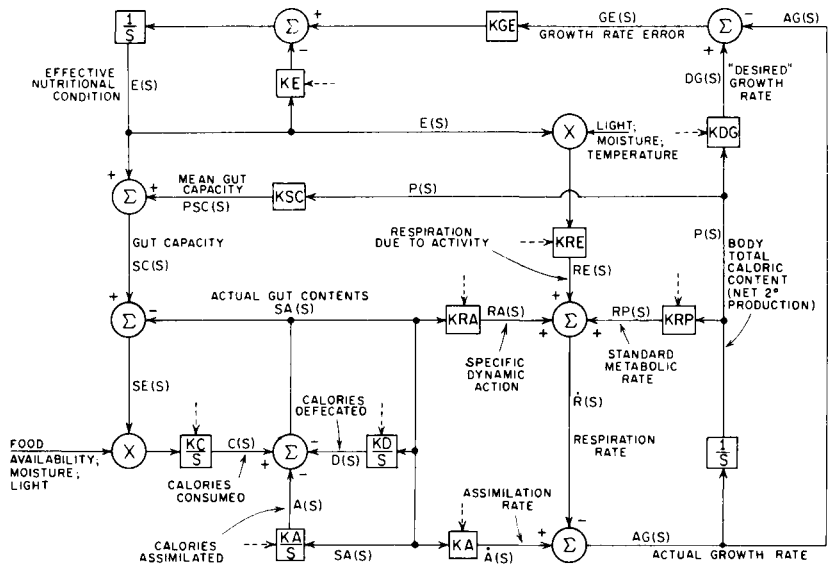

FIG. 12. Second linear version of bioenergetics model.

action component of respiration rate as well as the assimilation rate of the "linear" isopod.

The next simplification we can make is to find the transfer function $AG(s)/E(s)$.

$$AG(s) = A(s) - \dot{R}(s) \tag{33}$$

$$= (KA - KRA) \cdot H_1(s) \cdot SC(s) - (KRP/s) \cdot AG(s) - KRE \cdot E(s). \tag{34}$$

Since $SC(s) = E(s) + (KSC/s) \cdot AG(s)$, we have

$$H_2(s) = \frac{AG(s)}{E(s)} = \frac{s[H_1(s) \cdot (KA - KRA) - KRE]}{s + KRP - H_1(s) \cdot (KA - KRA) \cdot KSC}, \tag{35}$$

as shown in Fig. 13b.

The final simplification removes the two remaining feedback loops in the model. From Eq. (32)

$$AG(s) = \frac{H_2(s) \cdot KGE}{s + KE} \cdot GE(s), \tag{36}$$

which gives the open-loop transfer function in Fig. 13c

$$\frac{AG(s)}{DG(s)} = \frac{KGE}{s + KE + KGE \cdot H_2(s)}. \tag{37}$$

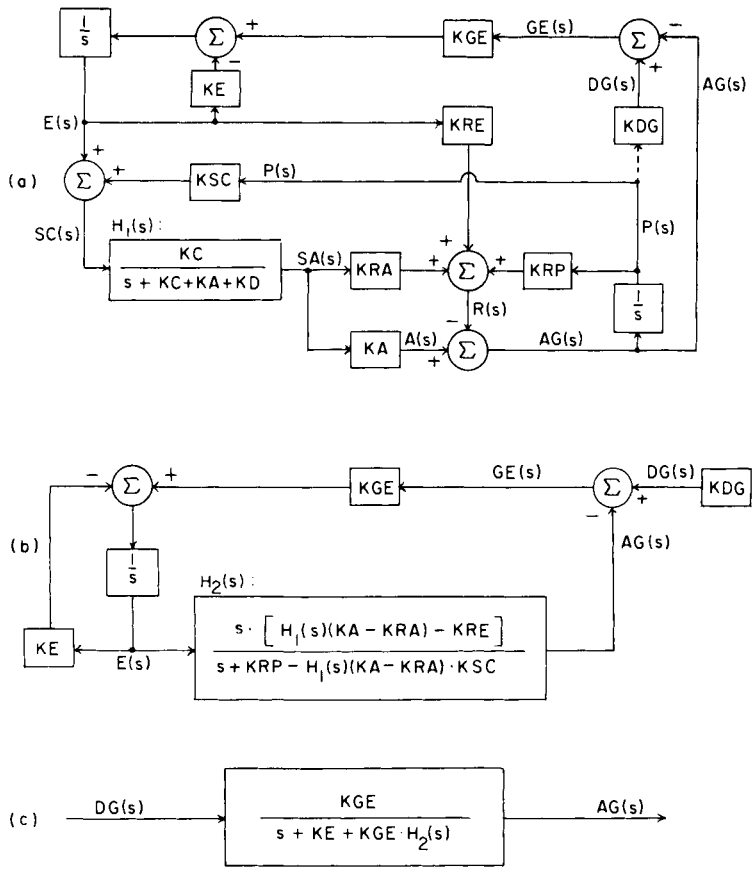

FIG. 13. (a–c) Sequential steps in the simplification of the second linear bioenergetics model (see text).

To obtain $AG(s)/DG(s)$ as a rational algebraic fraction of the form of Eq. (11), we substitute $H_1(s)$ into Eq. (35) and $H_2(s)$ into Eq. (37) and obtain

$$\frac{AG(s)}{DG(s)} = \frac{as^2 + bs}{s^3 + cs^2 + ds + e}, \tag{38}$$

where $a = -KRE \cdot KGE$, $b = KGE \cdot [KC \cdot (KA - KRA) - KRE \cdot (KC + KA + KD)]$, $c = KC + KA + KD + KE + KRP - KRE \cdot KGE$, $d = (KE + KRP - KRE \cdot KGE) \cdot (KC + KA + KD) + KC \cdot (KGE - KSC) \cdot (KA - KRA) + KRP \cdot KE$, and $e = KE \cdot [KRP \cdot (KC + KA + KD) - KC \cdot KSC \cdot (KA - KRA)]$.

This linear bioenergetics model is a third-order system, so it can have either three real eigenvalues or one real and two complex eigenvalues; in the latter case it is oscillatory. Unlike the simple linear model, closing the loop of $P(s)$ onto $DG(s)$ does not increase the order of this system, but it does change the position of the system's eigenvalues as well as its phase and gain. Thus, if we again assume the existence of a direct and additive disturbance $D(s)$ on growth rate in order to compute a closed-loop transfer function for the model, we have

$$AG(s) = \dot{A}(s) - \dot{R}(s) + D(s), \tag{39}$$

which can be rewritten

$$\frac{AG(s)}{D(s)} = \frac{s^3 + fs^2 + gs}{s^3 + cs^2 + hs + j}, \tag{40}$$

where $f = KC + KA + KD + KE$, $g = KE(KC + KA + KD)$, $h = d - KDGa$, and $j = e - KDGb$.

The caloric *state* of our "linear" isopod at any instant in time can be completely characterized by just three *state variables*. In our case these are net production (P), the amount of food in the gut (SA), and the nutritional condition of the animal (E). All other variables in the model are intermediate variables that are eliminated in the algebra of computing a transfer function for the model. The order of a system (in our case three) determines the *minimum* number of state variables necessary to completely determine the system's behavior. These state variables form a *state vector* which, when specified at some arbitrary time t_0, together with the inputs that arrive during the interval between t_0 and some later time t_1, uniquely determines the values of the vector at time t_1, as well as at any time between t_0 and t_1. Thus, once the initial values of P, SA, and E are known, along with the values of the inputs through time, the caloric state of the isopod can be predicted analytically at any later time.

As in the case of the simple linear model, we are interested in the stability of the system as a function of the parameter values in Eqs. (38) and (40). Because there are 10 parameters in the model, a very thorough parameter space study of all its parameters would be an exceedingly great task. In such complex cases, however, one is usually not interested in "global" characteristics because of the many constraints upon values that the parameters can take in the real system. For our bioenergetics model of whole animals, broad constraints are imposed by the laws of thermodynamics, and narrow constraints by the laws of lumped, lower-level, physiological systems. One function of the empirical half of

systems analysis is to determine what these constraints are, as well as their variability in natural systems.

For purposes of illustration, I shall describe here the response of the model's eigenvalues to changes in just one parameter *KGE*. This parameter determines the loop amplification of growth rate error. A more extensive study of parameter constraints and spaces will be published elsewhere (Hubbell, in preparation). I have chosen *KGE* for illustration for two reasons. First, recall from the simple linear model that the control abilities of a system are strongly affected by the loop gain of the system. Second, unlike most of the other parameters in the model, the value of *KGE* can be estimated only indirectly by empirical means; consequently, a parameter space study is essential as a corroborative check. A 3-dimensional graph showing the movement of the system's three eigenvalues as the value of *KGE* is increased from zero to about thirty is shown in Fig. 14; I used what I consider to be a reasonable set of parameters for an isopod living at a constant 20 C temperature. It should be noted that these linear system parameters are based upon, but modified from, parameters measured on a *nonlinear*

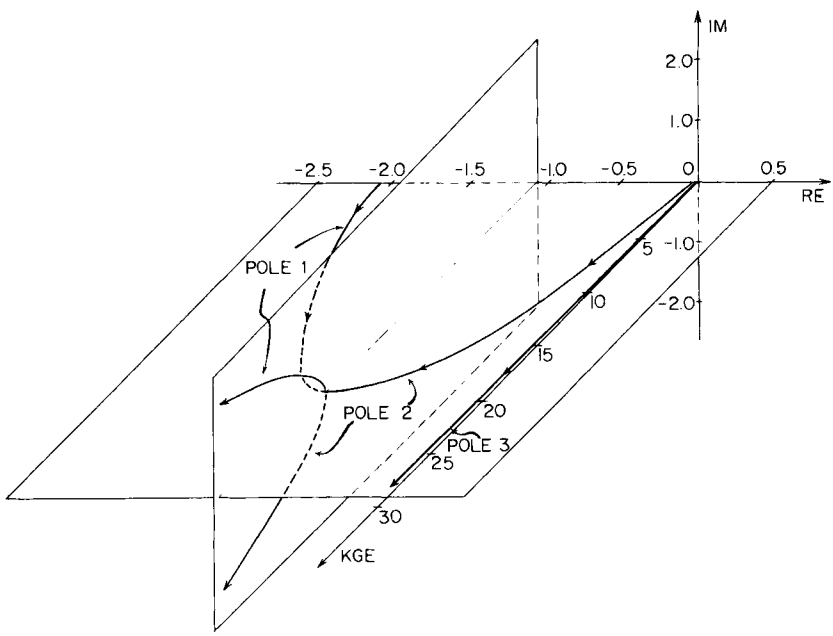

FIG. 14. Parameter space study of *KGE*, the growth rate error amplification factor, showing the response of the system's eigenvalues (see text).

system—the isopod; therefore, they should be regarded as relatively crude approximations to the real parameters of the nonlinear system. Moreover, the optimization of the parameter estimates has not yet been undertaken, so that some changes can be expected in future publications (Hubbell, in progress). Tentative values for the parameters other than KGE are

$KC = 2.0$/hr	(ingestion rate factor)
$KA = 0.05$/hr	(assimilation rate factor)
$KD = 0.085$/hr	(defecation rate factor)
$KRA = 0.02$/hr	(specific dynamic action factor)
$KRP = 0.002$/hr	(body size factor in respiration)
$KRE = 0.003$/hr	(activity factor in respiration)
$KE = 0.0021$/hr	(nutritional condition loss rate factor)
$KSC = 0.068$	(body size factor in gut capacity)
$KDG = 0.00173$/hr	(desired growth rate factor at 20 C).

The poles of the unforced system with the desired growth rate loop open are illustrated in Fig. 14. By *unforced*, we mean that the system has been exposed to a unit impulse input of desired growth rate. Since the Laplace transform of a unit impulse is one (Fig. 6), the response of actual growth rate to a hypothetical impulse in desired growth rate is identically Eq. (38). Pole 1 in the figure is associated with the state variable describing the amount of food in the gut (in calories), pole 2 with the nutritional condition of the animal, and pole 3 with the isopod's caloric content (net production). In the system with the desired growth rate loop open, we want the actual growth rate $AG(t)$ to be asymptotically stable (Chapter 2) in response to the impulse transient in $DG(t)$. The figure indicates that the system is stable for all positive values of KGE, because the real parts of all three eigenvalues are negative.

Note that as the amplification of growth rate error increases above a value of about 20, poles 1 and 2 take on imaginary parts, and the system becomes unrealistically oscillatory (although the oscillations are damped). Oscillations are particularly unrealistic for the gut, because they may cause negative values of caloric gut contents SA. Hence, KGE must have a value somewhere between 1 and 20. This range is narrowed considerably more by the fact that the value of KGE chosen must result in time constants for the disappearance of food from the gut, and for the memory of prior nutritional history, that are the same as the empirically determined time constants for these processes. Accordingly, the amplification factor of GE must be relatively low, somewhere between 1

and 4.5, because only in this region do poles 1 and 2 give realistic values for these time constants.

By comparison with the simple linear model, this model is less successful at tracking a desired growth rate signal, both because of the lag introduced by the time to fill the gut and, more importantly, because our "linear" isopod now gradually forgets its nutritional history. Hence, if the model is exposed to a unit step input in $DG(t)$, $AG(t)$ rises rapidly toward the desired level of one at first, but quickly slows down, reaching a maximum below one. Then it slowly decays back to zero at an exponentially decreasing rate. In other words, the isopod cannot remember indefinitely the step transient in desired growth rate, resulting from its limited memory of growth rate error. Note that if the nutritional condition loss rate factor (KE) is zero, then the system will once more successfully track a desired growth rate signal indefinitely. Also note that if KE is zero, the parameter e of Eq. (38) becomes zero, which reduces the order of the system to two.

In spite of the reduced ability to track a desired growth rate signal, however, the intact model will still grow exponentially. As in the simple linear model, closing the desired growth rate loop has the desirable effect of introducing exponential instability. While in the open-loop model, parameters c, d, and e of Eq. (38) are all positive, in the closed-loop model parameters h and j of Eq. (40) are positive and negative, respectively, so that one eigenvalue (pole 3) becomes a positive real number. It should be emphasized, however, that the isopod will not grow at a rate equal to $KDG \cdot P$: because the nutritional state is gradually forgotten, actual growth rate will lag increasingly behind $DG(t)$. Therefore, the model will grow at the exponential rates measured on *Armadillidium* by the optimal environment method (Section IV) only if we increase the magnitude of the desired growth rate signal by increasing the value of KDG listed above.

Figure 14 makes it possible to evaluate the relative importance of the behavior of the three state variables in the dynamics of energy and growth rate control. Each pole of a linear system is the negative inverse of the time constant of one of the additive exponential terms in the time-domain solution. Hence, the more negative a pole is, the smaller its time constant, and the "faster" is that component in the time-domain solution. An exponential component whose time constant is large relative to the other time constants in the system, given equal scaling of all exponential terms by constants, will tend to dominate the dynamics of the system's response to inputs. In the bioenergetics model, the time constants of the body caloric content and the nutritional condition of the isopod are large relative to that of the gut contents, and have larger

scale factors as well. Thus, the dynamics of nutritional state and net production will tend to dominate the tracking behavior of actual growth rate on desired growth rate, whether *DG* is generated endogenously in a natural manner, or exogenously in an artificial manner.

Figure 14 also indicates the existence of emergent properties of the bioenergetics model, properties which are determined as much by the interaction of the system's components as by the behavior of these components "in isolation." Note that the parameter *KGE* partly determines the location of all three poles of the system. Thus, *KGE* amplifies growth rate error, but in so doing it influences the rate at which the gut fills and empties, the rate at which the isopod forgets its nutritional state, and to a lesser extent, the rate at which the isopod grows. Similarly, the other parameters of the system influence the behavior of the system as a whole, not simply the behavior of the subcomponent to which they belong.

VII. Toward a More Realistic Nonlinear Bioenergetics Model

Although the linear model developed in the previous section has a fair amount of physiological detail, at least for ecological purposes, its linearity severely limits its ultimate heuristic and predictive value. Given a reasonable value for the state vector at some moment in time, and a set of parameters reasonable for current body size, the linear model can probably predict quite accurately the major aspects of the bioenergetics of an isopod for a relatively short period of time—a few days or perhaps a week or two—*provided* that the isopod's environment is *completely constant.* By suitable parameter manipulation, the linear model might even be made to predict *one* variable, such as body caloric content, accurately over the period of exponential growth. This "prediction" would be more coincidental than otherwise, however, because variables other than *P* would have unrealistic values. Again a constant environment is required. Perfectly constant environments are rare; also they tend to be rather uninteresting.

Environmental variables influence the bioenergetics of animals nonlinearly, usually with a multiplicative effect. Consider the two multipliers which we previously ignored in Fig. 12, one of which interrupts the ingestion rate signal, and the other of which interrupts the signal computing the activity component of respiration rate. Food availability is one environmental factor which influences multiplicatively the rate at which an isopod eats. If we scale food availability (*F*) from zero to one, and multiply it by *SE*, we can simulate the effect of varying food availability on ingestion rate and on the animal's ability to control energy and growth rate. Thus, when food is unlimited, *F* equals one,

and the animal completely determines the rate at which it consumes food, according to internally defined needs. On the other hand, when no food is available, F equals zero, and the animal eats nothing in spite of its "inclination" to feed at the rate $KC \cdot SE$.

Similarly, physical factors alter in a multiplicative fashion an animal's tendency to search actively for food. The daily light regime probably entrains the isopod's circadian activity, and can be represented by a variable ranging between zero and one. The action of temperature, on the other hand, probably cannot be represented by such a variable, because at high temperatures activity is elevated above what would be expected from the animal's "hunger" alone, as the isopod attempts to escape from unfavorably hot conditions.

Environmental disturbances may act to interrupt signals in the system, as considered above, but they may act directly on the parameters of the system as well. My work to date has dealt primarily with one input variable, temperature, and its effects on the parameters of the biological rate processes in *Armadillidium*. In particular, I shall consider adaptive parameter control by the isopod in the process of temperature acclimation of respiration rate.

Although it is well known that the rate of biochemical reactions is exponentially related to the inverse of absolute temperature and can be described by the Arrhenius equation (Johnson *et al.*, 1954), no general mathematical model which adequately describes temperature acclimation by organisms has been developed. Typically the temperature dependence of biological rate phenomena is, itself, dependent on the organism's history of exposure to temperature. Thus, the response of respiration rate to temperature is nonlinear, both because of the exponential Arrhenius relationship and because of the dependence upon prior temperature conditions. To construct a nonlinear model for this system would require the explicit modeling of effects on respiration rate of all possible past temperature regimes, a manifestly impossible task. Therefore, we have built a model of respiration which is linearized with respect to temperature, while at the same time attempting to retain the essential features of the dynamic behavior of the nonlinear system.

According to the Arrhenius equation, the natural logarithm of respiration rate is proportional to $1/K$, a nonlinear relationship to absolute temperature. In order to obtain a linear relationship between log respiration rate and temperature, it was assumed that

$$R' = \log \dot{R} = c_1 + c_3(\mathrm{C}), \tag{41}$$

where c_1 and c_3 are constants. Note that this is still a nonlinear equation by the definition given in Section V; however, the nonlinearity introduced

by the constant c_1 is of a very simple sort which can easily be handled mathematically. Note also that the equation is nonlinear in R. This "linear" approximation to the Arrhenius equation is only adequate for relatively small temperature ranges. The temperature range of interest to the biology of *Armadillidium* is 273–303 K, small enough so that our assumption of linearity introduces an insignificant error. This equation, then, can be used to account for the temperature-proportional responses of respiration rate; it does not, however, account for temperature acclimation.

Temperature acclimation in the respiration rate of *A. vulgare* has been described by Edney (1964). Apart from the effects of specific dynamic action on respiration rate, which he apparently did not take into account, his results have been largely confirmed by me (Hubbell, in preparation). Acclimation in the standard metabolic rate is most obvious when an isopod is kept at a constant temperature for some time, and then suddenly exposed to a step transient to a different constant temperature. Rather than shifting more or less instantaneously to a new steady-state level, as Eq. (41) predicts, respiration rate overshoots the new steady-state level if the new temperature is higher, or undershoots the new level if the temperature is lower. This overcompensation in the acclimation responses of animals is, of course, well known (Prosser and Brown, 1961; Precht *et al.*, 1955).

Overshooting and undershooting is characteristic of a system which is responsive to both an input variable and its derivative (or other higher-order terms). In the present case, the logarithm of respiration rate is sensitive both to temperature and to the rate at which temperature is changing. The simplest differential equation which has these properties is the first-order equation,

$$R' = c_1 + c_3\left(k\frac{d(\mathrm{C})}{dt} + (\mathrm{C})\right), \tag{42}$$

where c_1, c_3, and k are constants. This equation, however, predicts that respiration rate becomes infinite when the animal is exposed to an instantaneous step change in temperature, an absurdity resulting from the instantaneous response of respiration rate in Eq. (42) to the rate of temperature change. Actually, of course, there is a lag in the response, which means that the logarithm of respiration rate is not perfectly proportional to the derivative of temperature. This lag has been included in the model as

$$T\frac{d(R')}{dt} + R' = c_1 + c_3\left(\alpha T\frac{d(\mathrm{C})}{dt} + (\mathrm{C})\right). \tag{43}$$

The constant T is the time constant of the exponential decay of log respiration rate to the new steady-state level. The constant α determines the type of response exhibited by respiration rate to temperature changes, as shown in Fig. 15: If $\alpha = 1$, acclimation does not occur, and respiration

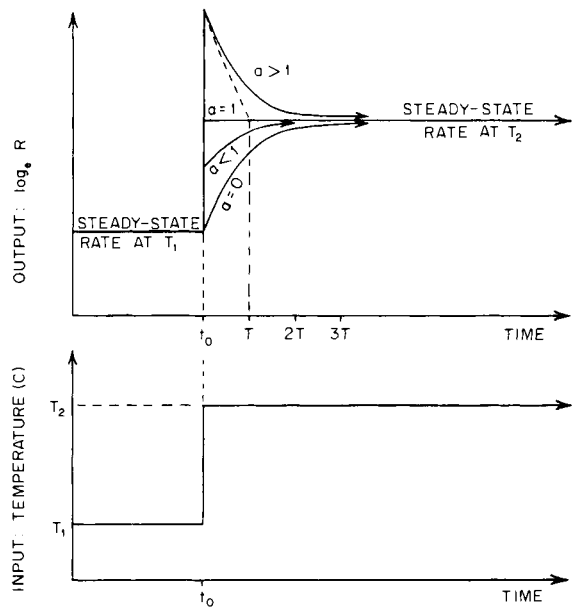

FIG. 15. Possible responses of a biological rate to a step in temperature. See text for discussion.

rate responds stepwise to a step change in temperature; if $\alpha < 1$, acclimation occurs, but respiration rate responds with a lag to a step change in temperature; if $\alpha > 1$, the most commonly observed type of acclimation occurs, viz., respiration rate overshoots or undershoots the new steady-state level. In the latter case the equation describes a "first-order lead–lag" system.

Respiration rate changes also in response to changes in body size. As is generally true, in *Armadillidium* the logarithm of respiration rate is linearly related to the logarithm of weight (Edney, 1964; Hubbell, unpublished). This relationship can be accommodated by further modification of the equation, to make it read

$$T\frac{d(R')}{dt} + R' = c_1 + c_2(\log P) + c_3\left(\alpha T\frac{d(\mathrm{C})}{dt} + (\mathrm{C})\right), \qquad (44)$$

where c_2 is the proportionality constant for the body size component. The caloric content of the isopod P changes so slowly that it has no influence on $d(R')/dt$. In *A. vulgare* the empirical estimates of the parameters for this equation are: $T = 96.4$ hr, $c_1 = -1.91$ log cal, $c_2 = 0.234$, $c_3 = 0.013$ log cal/C, and $\alpha = 1.68$ (Hubbell, in preparation).

As an illustration of a test of this lead-lag model of respiration rate, a simulation of the response in the respiration rate of a 50-mg isopod to stepwise changes in temperature is compared to actual results of respiration measurements in Fig. 16; the values are scaled for a 50-mg

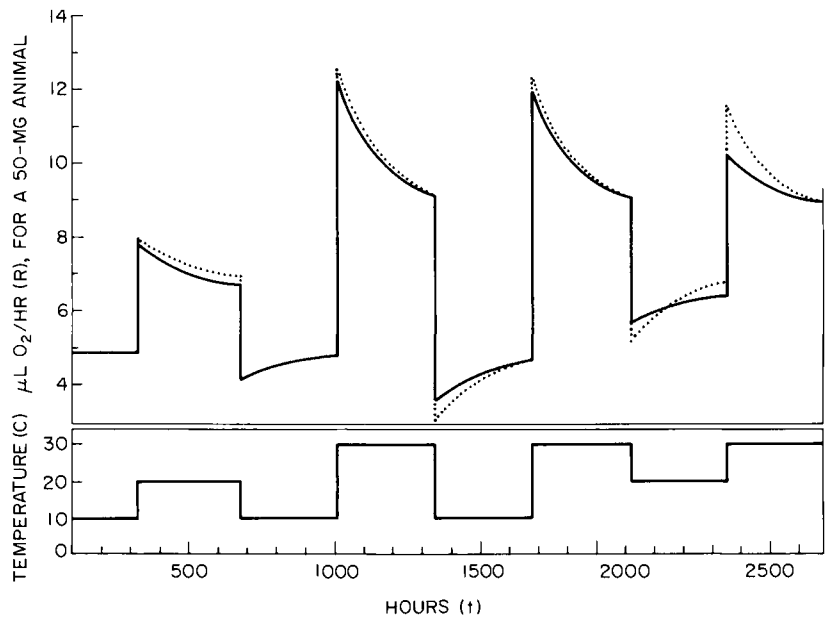

FIG. 16. Simulation of response of respiration rate (upper graph) to a hypothetical square wave temperature input (lower graph). The solid line is the model's linearized prediction. The broken line is based on actual results, scaled for a 50-mg isopod, of the nonlinear step response of standard metabolic rate to temperature. The calculations are based on the equation $T\,d(\log R)/dt + \log R = c_1 + c_2P + c_3[\alpha T\,d(C)/dt + (C)]$, where T is the time constant, R is the respiration rate (microliters per hour), c_1, c_2, c_3, α are constants, and P is body caloric content (log).

animal. The solid line in the upper graph is the output from the model, and the dotted line presents the performance of the animal. The curve of temperature inputs is shown in the lower graph. In this simulation, the caloric content (weight) of the animal was held constant to illustrate

more clearly the effects of temperature change on respiration rate. The model predicts the logarithm of respiration rate as a function of temperature, but in the graph respiration rate is plotted against temperature, because our interest is in the number of calories dissipated per unit time by the isopod. Thus, having solved the linear approximation of the response of log R to temperature and body size, we have returned to the nonlinear relationship between respiration rate and temperature by taking the antilogarithm of log R.

With this linear differential equation to model effects of temperature on respiration rate, it becomes possible to compute respiration rate given any conceivable history of temperature exposure of the animal. The equation has built-in lags which, in effect, give the model a "memory" of acclimation history. Because the model is linear, inputs are additive so that short-term cycles (e.g., diurnal) can be superimposed on long-term cycles (e.g., seasonal), and the model will predict the appropriate acclimation response to the combined effects of these temperature fluctuations. Even though the values for the parameters in the model were derived from laboratory experiments with *Armadillidium* this model can predict with satisfactory accuracy the fluctuations in standard metabolic rate (in calories) for an isopod of a specified size under field conditions, provided that the temperatures which it experiences are known.

Although we have been directly modeling effects of temperature and body size on respiration rate, it should be clear that it is the respiration rate *parameters*, such as *KRP*, *KRA*, and *KRE*, which are, in reality, being directly affected. This fact cannot alter our conclusions from the model, however, because the parameters must respond to temperature and body size in a manner similar to respiration rate; otherwise, they would not produce a signal (respiration rate) with these response properties.

The dynamic behavior of this first-order lead–lag model can be fully described by evaluating the frequency response of the system. If an isopod is exposed to a sinusoidally varying temperature as, for example, in a diurnal cycle, its respiration rate will also vary sinusoidally with time. This response is represented graphically in Fig. 17, which is a classical Bode diagram of the relative amplitude and phase of the input and output waves of a system, plotted for different frequencies of the input signal. The upper graph shows the logarithm of the ratio, (amplitude of the log R sine wave): (amplitude of the temperature sine wave). The lower graph shows the phase of the log respiration wave relative to the temperature wave. As the frequency of the input signal becomes greater, the logarithm of the amplitude ratio (log AR) increases in a

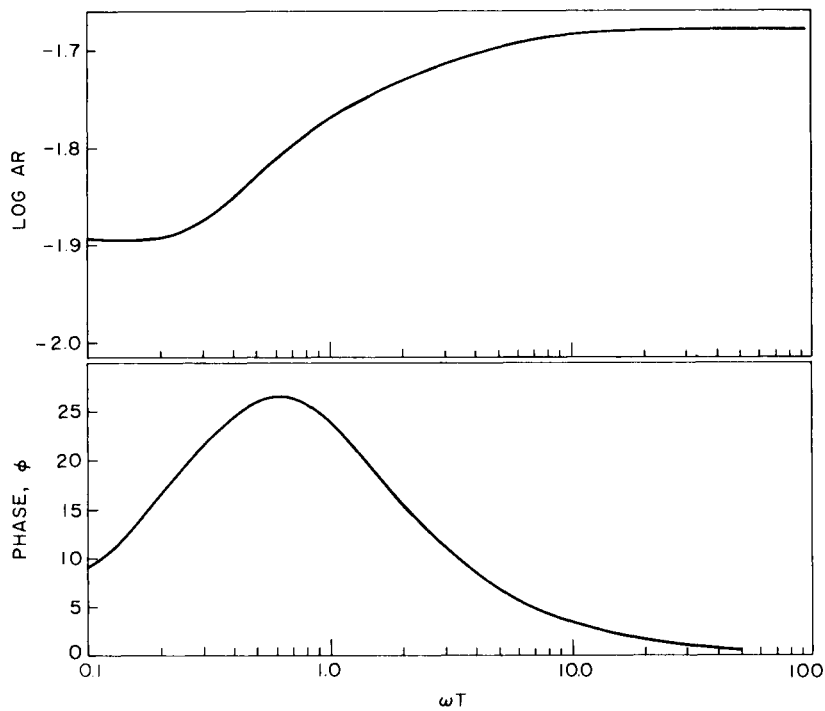

FIG. 17. Bode diagram illustrating frequency response of respiratory acclimation to temperature with $H(j\omega) = k \cdot [(j\alpha\omega T + 1)/(j\omega T + 1)]$, where $T = 96.4$ hr, $\alpha = 1.6844$, $k = 0.01266$, and ω is in radians per hour. See text for discussion.

sigmoid fashion from a low to a high plateau. This increase reflects incomplete respiratory acclimation to temperature at higher frequencies, because respiration rate is overshooting and undershooting with each rise and fall in temperature. At still higher frequencies (not plotted), the curve would again fall because respiration rate would no longer be able to follow the very rapid changes in temperature. When $\omega T = 0.28$ rad, where $\omega = 0.00291$ rad/hr, a complete cycle of temperature occurs every three months. Thus, for seasonal temperature cycles having a period of three months or more, the isopod is essentially completely acclimated at all times. Partial acclimation occurs when the period is one week ($\omega T = 3.59$ rad and $\omega = 0.0374$ rad/hr). Finally, for cycles with a 24-hr period ($\omega T = 25.3$ rad and $\omega = 0.2618$ rad/hr), the isopod shows very little acclimation.

Note that the sine wave of the logarithm of respiration rate is ahead, in phase, of the temperature sine wave. The lead in phase is a result of

partial acclimation to temperature: at low intermediate frequencies, the animal has longer to acclimate as temperature changes than it has at higher frequencies. This results in a large phase lead. At very low frequencies (not plotted), respiration follows the temperature curve exactly (complete acclimation), so that there is no phase lead. At very high frequencies, respiration has no time to develop a phase lead because no acclimation takes place before temperatures change.

All of the parameters of the model discussed in Section VI, with the exception of *KSC* and *KGE*, are influenced by temperature; and all but *KGE* are also probably exponential functions of body weight. We are currently investigating the effects of temperature on the parameters of the digestive system, and our tentative conclusion is that they exhibit lead–lag responses to temperature similar to those of the parameters of the respiratory system. Growth rates, on the other hand, do not seem to exhibit overshoot, not is there any apparent tendency for growth rates to be accelerated by cycling temperatures (Hubbell, in preparation), as has been found in a number of insects (Cook, 1921; Parker, 1929; Ludwig, 1928). The frequencies in the temperature cycle tested so far range from 0.5 to 0.0625 cycles/day. It is possible, however, that still higher frequencies could have an accelerating effect on growth rates.

Although we have been considering primarily the nonlinearity of environmental disturbance inputs, obviously this is not the only class of nonlinearities in the bioenergetics model, because even in a constant environment the system is nonlinear. As mentioned above, most of the system's parameters are log–log functions of body caloric content (weight). Moreover, desired growth rate is a nonlinear process. In *Armadillidium*, we have seen that linear models of desired growth rate suffice, both in the juvenile when the isopod is growing exponentially, and in the adult, when it is growing arithmetically. The nonlinearity is introduced by the switch from the juvenile to the adult linear model, with the opening of the desired growth rate feedback loop. In animals which do not grow continuously throughout life or have otherwise different growth patterns, we may expect to find different types of desired growth rate nonlinearities.

Unfortunately, less is known about the nonlinearities in other components of the system. In the case of the digestive system, however, some educated guesses can be made about what types of nonlinearity to expect. According to both of the linear models presented earlier, isopods eat continuously in the presence of food. Continuous feeding, of course, is not observed in isopods; like all other animals, they have essential occupations in addition to eating. Clearly, then, animals must have

built-in mechanisms for terminating currently inappropriate types of behavior, and initiating others which are more appropriate for the animal's present condition. Such mechanisms are often described abstractly in terms of "threshold" switches (Holling, 1966b). Depending on whether the value of a criterion variable is above or below some threshold value, different types of behavior are exhibited. The effect of thresholds in a storage-and-flow model is, of course, to produce discontinuous rates. Some indication of the discontinuous nature of feeding in *Armadillidium* is evident from the oscillation in average daily ingestion and assimilation rates of unstarved isopods (Fig. 9), although a finer time resolution is needed to see the actual discontinuities (Hubbell and Paris, in preparation). One way that the threshold effect on ingestion could be easily modeled would be to assume that the animal does not begin to eat until some fraction of the current gut capacity has been emptied. In the model, then, SE would have to reach a value, $KSE \cdot SC$, where KSE is a constant, before feeding would commence. Such a model appears to be adequate for a variety of predators (Holling, 1965, 1966b), but whether it is appropriate for isopods remains to be determined.

Another type of nonlinearity found in the digestive system of isopods is adaptive parameter control. We know for certain that KD, and probably also KC and KA, are under the partial control of the system. When *Armadillidium* is without food, or when food availability is low, the isopod exhibits a greater assimilation fraction. This results in part from a slowdown in defecation rate, which means that the food remains in the gut for a longer period of time. Isopods typically assimilate a rather small fraction of what they ingest; however, when food is scarce, they may digest components of the food that are unnecessarily costly to assimilate otherwise (i.e., when food is abundant) (Hubbell *et al.*, 1965).

Clearly, much remains to be done on the nonlinear model. A major problem requiring attention is how animals respond to the spatial heterogeneity of their environment. Note that the models presented here have no space dimensions. There are two main courses of action open. One is to model explicitly the spatial attributes of ecological events by including distance as an independent variable in the model. The problem with this, of course, is that it would greatly increase the complexity of the model because we would then have to deal with partial differential equations in a "distributed" system. A less satisfactory, but possibly more practical approach is to attempt to describe how spatial properties alter the model's time-dependent functions, without explicitly modeling the space dimensions themselves. This was Ivlev's (1961) approach in describing how the dispersion of food affects the ingestion rate of fishes.

In conclusion, the objective of this chapter has been to underscore the importance of control in the ecological bioenergetics of animals. To treat organisms as passive, open-loop, energy-partitioning devices is to obscure a basic characteristic of living systems: the adaptive control of energy and growth in the face of a limited and varying potential energy supply. To illustrate some basic energy-regulating properties of animals generally, and of the terrestrial isopod, *Armadillidium vulgare*, in particular, I have presented two linear bioenergetics models of differing physiological detail, and aspects of a more realistic nonlinear model now under development. If the value and necessity of treating organisms as active, energy-controlling systems becomes more widely recognized, the objective of this chapter will have been achieved.

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Computer Analysis of Predation Energetics in the Largemouth Bass

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I. Introduction

Predation is often studied from the viewpoint of time spent by the predator in various activities such as searching for, pursuing, or capturing prey organisms, etc. (Holling, 1959a, b, 1965, 1966; Ivlev, 1944; Salt, 1961, 1967). While the time that a predator devotes to different aspects of living is important, time itself is only an indirect measure of the critical commodity which all predators, indeed, all organisms, must obtain from their environments. Energy is the essential resource, and measures of time—while of direct value in some determinations of population dynamics—actually serve only as indices of the relative rates of energy acquisition and dissipation of individual predators. It is not

time per se which determines success or failure of a predator but rather optimization of the balance which must be struck between rates of energy acquisition and expenditure. Predators, like businessmen, survive over the long term not so much because of time spent in various activities but rather because energy debits and credits are in balance or show a net surplus.

Individual animals (Brett, 1965a; Glass, 1968a; Ito, 1964; Ivlev, 1939a, 1960, 1961; Smith, 1935a, b), populations (Slobodkin, 1960, 1962; Englemann, 1961; Richman, 1958), trophic levels (Golley, 1960; Lindeman, 1942), communities (Odum, 1957; Teal, 1957) and ecosystems (Patten, 1959) have been investigated from an energetics point of view. It is apparent that the study of energetics at any level of ecological organization from single individuals to communities or geographic regions encompassing more than one ecological community can be of great value (Slobodkin, 1968; Watt, 1968). An understanding of the energy relationships which exist within a single individual or between two or more individuals of the same or different species facilitates solution of practical problems in applied ecology, such as biomass production (Brocksen *et al.*, 1968; Gerking, 1962; Paloheimo and Dickie, 1966a, b). Similarly, energetics studies may contribute to ecological theory (Brocksen *et al.*, 1968; Warren and Davis, 1967; Engelmann, 1966) and provide a basis for comparison, which is ubiquitously applicable to all levels of organization from the individual to the ecosystem (Odum, 1968).

Energy, or caloric flux, was, therefore, employed to explore some aspects of a problem in predation arising from an apparent discrepancy between predator–prey relationships in nature and corresponding laboratory systems. The disparity between these two situations can be summed up as follows. In nature, most predators and their prey coexist in the same general environment for indefinite periods of time without the annihilation of the prey and subsequent starvation of the predator. There must be some explanation for the reasonably long-term survival of both organisms. That this relative stability does not obtain in the laboratory for the majority of experimental predator and prey populations is well known. In the classical case of laboratory populations (Gause, 1934; Gause *et al.*, 1936), it was shown that predators and their prey would survive only under the special circumstances of providing refuges for the prey by denying the predators access to some part of the environment or by introducing additional prey into the environment when there was a reduction in prey abundance. In a more recent study, Huffaker (1958) examined two more possible explanations: First, large environmental size allows the dispersal of prey into parts of the habitat unoccupied by predators with the result that prey survive as fugitives; Second,

prey survive because of partial (not restrictive) refuges which result from an increase in environmental complexity. There are, therefore, at least four potentially testable hypotheses and their various combinations, which might serve to explain prey survival and/or predator success.

(1) Prey reproductive rates or immigration of prey from areas outside of the normal habitat of the predator might be high enough to prevent extermination of the prey.

(2) Environments might by virtue of sheer size lower the probability of encounters between predators and prey and thereby allow the continued existence of the prey.

(3) Refuges may exist within the environment which are accessible to prey but totally exclude predators.

(4) Refuges in the habitat may provide partial protection for prey by making access by predators difficult due to some behavioral phenomenon (Johannes and Larkin, 1961) or by creating a partial physical barrier which reduces predator efficiency.

In practice, it is somewhat difficult to separate the effects of these four possibilities although the first represents a more or less discrete hypothesis. The fourth hypothesis can be examined in the laboratory by working in an experimental universe which is small enough for the predator to see all parts of it from any point and which is designed so that there are no complete refuges for the prey.

Predator survival is, of course, intimately related to prey survival. If prey are exploited by a predator at a rate which is in excess of the maximum sustained yield, then prey abundance will decline to zero, and this will be followed very shortly by predator extinction. On the other hand, if prey survival is excessively high (e.g., due to a low predator attack rate), then the predator will also experience the same fate although the proximal causes and the effect on the prey are different in the two cases. In short, predators and prey must coexist in an environment which does not permit over-exploitation of prey and, at the same time, allows the predator to acquire food at a level concomitant with its energy requirements. Therefore, the hypothesis explored by the present research work is the fourth possibility listed above. This will be examined by performing a predator energetics analysis, developing a mathematical and computer model of the various means by which a predator dissipates energy acquired through feeding, and, finally, an analysis of filmed feeding sessions. The various inputs for the model will be derived from a study of metabolic requirements of the largemouth black bass (*Micropterus salmoides*) and from a description of the environ-

ment in which the bass is pursuing and capturing a small prey fish (*Lebistes reticulatus*).

The analytical approach which was adopted is the experimental components analysis technique of Holling (1963, 1964, 1965, 1966) since this method is ideally suited to the solution of problems of this general type. Accordingly, the processes of energy intake and utilization can be fragmented, separated into basic and subsidiary components in the sense of Holling (1963), analyzed individually, and given a mathematical description, and then the entire process reconstructed from these submodels. As the whole energetic process is rebuilt from submodels or sub-submodels, and interactions between the various components can be included, the end product should then be a reasonably accurate and realistic systems model of predator energetics which can be used for descriptive, analytic, and predictive (through computer simulation) purposes. In principle, it should be possible to model from an energy point of view a bass feeding on a small prey fish given certain input information such as the temperature, physical description of plant densities characteristic of the environment, prey density, and predator weight. Furthermore, it should be possible to determine which of numerous factors all affecting energy dissipation are most important in determining the rates of food acquisition and utilization.

With due awareness of the existence of various feedback loops which exist between components, the general model of energetics adopted here is similar to those developed by Ivlev (1939b, 1960) and further elaborated by Rashevsky (1959) and Ursin (1967). Basically, the model will be viewed as a series of additive components

$$E_t = E_w + E_r + E_a + E_g, \tag{1}$$

where E_t is total energy requirement (food), E_w is energy wasted due to incomplete assimilation, E_r is energy required for routine metabolism, E_a is energy required for active metabolism, and E_g is energy required for growth and reproduction. Some data pertaining to E_w (Blackburn, 1968: p. 7) have been collected for the largemouth bass. Blackburn found digestive efficiency

$$\frac{\text{calories ingested} - \text{calories defecated}}{\text{calories ingested}} \times 100$$

to be approximately 90%. This value is somewhat higher than those of other investigators and was based on a rather small number of observations. Accordingly, until data in the literature or indications from further experiments suggest a more realistic alternative, a value of

85% for assimilation efficiency determined by Brocksen *et al.*, (1968), Warren and Davis (1967), and Winberg (1956, p. 156) will be assumed to be correct. Similarly, E_g may be derived from the net difference (positive or negative) between energy intake in the form of food and energy dissipated according to the formula

$$E_g = 0.85E_t - (E_r + E_a). \tag{2}$$

Therefore, only two components (E_r and E_a) will be presented here in detail. Furthermore, E_r and E_a are assumed to be independent and additive basic components.

II. Materials and Methods

To determine the parameter values, structure, and relative contributions of E_r and E_a to the bioenergetics and possible environmental limitations dictating survival or local extinction of largemouth bass, three types of experiments were conducted. First, a physiological study of routine metabolic requirements was performed by varying the weight, environmental temperature, and time of food deprivation. The dependent variable measured was oxygen consumption. Data obtained from this set of experiments were then analyzed and assembled into a mathematical description of the E_r component. The precise method of modeling this component is set forth in Section III. Second, an experiment was conducted to reveal the energetic requirements of largemouth bass at various swimming speeds. The dependent variable measured was again oxygen consumption. A detailed mathematical description of this component (E_a) along with its derivation appears also in Section III. With data from, and a mathematical description of, the above two experiments, results from the third experiment can be interpreted and better understanding of predation and its bioenergetic implications obtained. The third experiment involved determining the amount of food actually captured by the bass at four levels of environmental complexity and consists of movie films taken during feeding bouts. A detailed description of the experimental methods used in all three of the above investigations appears below under the appropriate subheadings.

A. Experimental Animals

The prey fish were female guppies (*Lebistes reticulatus*) varying in weight from 0.5 to 1.0 g (av = 0.6 g) which were collected by dip net

at intervals not exceeding five days from the University of California at Davis sewage-treatment plant. Females of this size range were used because of their abundance and also to minimize possible variability of predator attack behavior which might result from using males with widely varying colors and color patterns. In addition, since the predator's gut capacity is approximately 6–8 g, determined both from the feeding studies of Wells (1968) and direct autopsy data, the predator would have to eat a number of prey during each feeding session to become satiated. This provides a measure of the variability in attack velocity during a filmed feeding session, thereby reducing the amount of film to be analyzed.

Largemouth black bass, *Micropterus salmoides*, were obtained from two sources. The majority came from the State of California, Inland Fisheries Division fish hatchery at Elk Grove, California, through the generosity of Dr. Alex Calhoun. These bass were seined from holding ponds, transported approximately 30 miles to Davis, where they were held in either 10-ft diameter plastic swimming pools or in 250-gal holding tanks. The other source of bass was Lake Berryessa in Napa County, California, from which they were seined and transported to Davis. The bass were maintained in the laboratory on a diet of guppies, *Gambusia*, and young green sunfish and bluegills. No attempt was made to control either light regime or water temperature between experimental runs. Before using any fish experimentally, they were moved to different tanks and acclimated to desired temperatures as outlined below.

B. Routine Metabolism Measurements

Before each run, the bass were fed to satiation every day for at least two weeks (satiation was assumed if excess food was present two hours after feeding). Since data on six fish could be collected during each routine metabolism experiment, all six were placed in a 75-gal tank and fed an unmeasured but excess supply of food during the acclimation period. It was therefore necessary to assume that each individual received a maximum ration, and observations indicated this to be valid.

Beamish (1964a) measured oxygen consumption after a temperature acclimation time of two weeks following a gradual change in temperature of ± 1 C/day until the desired temperature had been attained. Brett (1964) included an extra week of acclimation at 5-C intervals above 10 C in raising the temperature of young sockeye, but this was not considered necessary for bass, a warm-water fish. Therefore, the acclimation regimen of Beamish was employed to avoid confounding effects of the previous thermal histories of the fish (Fry, 1957). Some fish were

maintained more than eight weeks at the experimental acclimation temperature.

Following the above acclimation procedure, fish were fed to satiation (as defined above), weighed individually and placed in respiratory chambers of one of two sizes, depending on size of the fish. The chambers were cylindrical, 15 cm in diameter by 15 cm long (approximately 2.5 liters) for the smaller fish, and 15 cm in diameter by 30 cm in length (approximately 5 liters) for larger fish. The chambers were made of $\frac{1}{8}$-in. Lucite, painted black to reduce visual stimulation, and provided with a 7.5-cm diameter hole at one end to allow introduction of the fish. This hole was sealed by inserting a No. 14 rubber stopper. Other environmental stimuli (Fry, 1947) and vibrations were minimized as much as possible by performing the experiments in a concrete block laboratory isolated from other buildings. Low intensity vibrations were no doubt present since an air conditioner was in operation during the summer months and piston type air pumps were operated continuously to aerate various aquaria and holding tanks. However, even if slight vibration was present, it was at least continuous.

Data on oxygen consumption were collected by means of a galvanic cell oxygen analyzer (Precision Scientific Co.) which operates on the principle of O_2 diffusion through a thin polyethylene membrane. Measurement of dissolved oxygen (milligrams of O_2 per liter) was accomplished by reading parts per million (ppm) O_2 directly on a meter calibrated in 0.2-ppm intervals with the capability of estimating 0.03 ppm with reasonable accuracy. Dissolved oxygen determinations were made on water flowing into the respiration chambers from a constant temperature water bath in which the chambers were immersed. The amount of dissolved oxygen was then determined in the water flowing out of the respiration chambers from a $\frac{3}{8}$-in. o.d. Tygon siphon tube. The flow of water through the chambers was regulated by means of a screw clamp on the siphon hose and was set at a flow rate such that the change in dissolved oxygen resulting from extraction by the fish was at least 1 ppm. The error in interpolating the second decimal place was thereby reduced to approximately 3%. The rate of water flow was measured by using a stop watch to find the time required to fill a 100-ml graduated cylinder. Galvanic cell readings were taken either visually at selected time intervals (approximately 3-hr intervals, night and day, for the first 24 hr of each run) or were monitored continuously by dc microammeter recorders (Esterline-Angus Co.).

The oxygen analyzer was calibrated daily, checked periodically by the unmodified Winkler titration method, and the probe renewed as required to maintain a sensitivity of at least 0.5. Sensitivity is determined

by dividing the meter reading in ppm dissolved oxygen by the actual dissolved oxygen concentration determined either theoretically for that temperature and salinity, or directly by Winkler titration

$$\text{sensitivity of probe} = \frac{\text{dissolved } O_2 \text{ (meter)}}{\text{dissolved } O_2 \text{ (actual)}}.$$

Comparisons between the oxygen analyzer and Winkler titrations were always within $\pm 1\%$.

Variation in the temperature of water flowing into the respiration chambers did not exceed ± 1 C for any experimental run at any of the three acclimation temperatures. The three experimental temperatures were 12 ± 1 C, 20 ± 1 C, and 25 ± 1 C. These were maintained by thermostatically controlled submersible 150-W heaters. The 12-C experiments were conducted during winter to coincide with prevailing thermal trends experienced by fish in nature and to minimize seasonal effects on routine metabolism (Wohlschlag and Juliano, 1959).

C. Active Metabolism Measurements

The apparatus used for determining oxygen consumption at various swimming speeds was essentially a combination of that used by Wohlschlag (1957), and Wohlschlag and Juliano (1959), and that described by Fry (1957) and Fry and Hart (1948b). The chamber was a circular torus constructed of $\frac{1}{8}$-in. clear Lucite with an outside diameter of 92 cm, an inside diameter of 61 cm, square (15 cm $\times$ 15 cm) in cross section, and containing a total volume of approximately 54 liters. Water was siphoned out of the torus by means of a Tygon outlet with flow rate controlled by a pinch clamp. Water removed for dissolved oxygen measurement was replaced by allowing water to enter the chamber from the 250-gal constant temperature water bath in which the torus was immersed. The rotating chamber was suspended by three wires fastened to one end of a mandrel, the other end of which was fitted with a series of reducing rubber V-belt pulleys. The chamber was driven by a 5-hp electric motor, and by varying the combinations of pulleys on the mandrel and on the motor the velocity of rotation could be varied between 5 and 70 cm/sec. In addition to pulley selection, a variable voltage transformer was connected to the electric motor and virtually any swimming speed within the above limits could be selected and maintained. It was found, however, that at velocities below 5 cm/sec, it was difficult to maintain a constant torus speed, apparently due to slight fluctuation in line voltage.

A mechanical counter was attached to the torus to count the total number of chamber revolutions. This number divided by the total minutes elapsed time equals revolutions per minute (rpm). By multiplying rpm times mean circumference (260 cm) and dividing by 60 sec/min, velocity in centimeters per second was determined.

To be sure that each bass maintained its position in the chamber during the run, pairs of 20-cm stainless steel electrodes were installed inside the torus at approximately 15-cm intervals around the inside and outside walls. The inner circle of electrodes was wired together and 4–6 V (60 cycle ac) were passed between the inner and outer electrodes each time the outer electrode made contact with a fixed brush mounted on the side of the water bath. With each contact between an electrode and the brush, a pulse would result, and since this pulse would always be detected by the fish at a fixed location with respect to the water bath, an avoidance of this region was quickly learned. After a few mild shocks, an inexperienced fish would maintain a position slightly in front of the electric field until fatigued.

The method of temperature acclimation for active metabolism measurements was the same as that described for the routine metabolism experiments. Following acclimation to 20 $\pm$ 1 C, each bass was fed to satiation (as defined above), then starved for 24 hr, weighed to the nearest 0.1 g, introduced into the torus through a 7.5-cm hole, and allowed 12 hr to become accustomed to the chamber. Each fish was thereby kept for 36 hr (24 + 12) without feeding. This deprivation period has been considered adequate by other investigators (Brett, 1964, 1965b), and should be sufficient to assure a postabsorptive state (Beamish, 1964a). Even though routine metabolism in largemouth black bass has been observed to require four to five days before approaching approximately standard metabolic levels (Glass, 1968a), the first 36 hr accounts for the majority of oxygen uptake due to specific dynamic action of food (SDA), digestion and assimilation of food, etc.

Following the 12-hr habituation period, the hole used for introduction of the fish was sealed by inserting a No. 14 rubber stopper, the ppm dissolved oxygen in the torus was measured, the revolution counter was reset to zero, and the torus was set in motion at a low velocity. After the first few fish had been run, it was possible to estimate the approximate time required, at a particular velocity and weight of fish, for extraction of about 1 ppm of dissolved oxygen. This was done to minimize the error in reading the oxygen meter, as mentioned above and to avoid respiratory dependence which might result from low dissolved oxygen concentrations. The torus was then stopped, and a dissolved oxygen reading was taken along with a determination of probe sensitivity. The

torus was then flushed by circulating water from the constant temperature water bath through it for at least an hour. The torus was then sealed, ppm dissolved oxygen determined, and rotation initiated again at, generally, a velocity higher than that of the previous run. This process was repeated at several velocities so that a full day was often required to complete work on one fish. After each bass had been run in the torus, it was placed in a separate holding tank and a new fish was introduced into the chamber and held for 12 hr for testing the next day.

All active metabolism experiments were performed at 20 ± 1 C. A total of 48 bass was used, some of which were tested individually; others were run in groups of two or three. The weight of test fish ranged from 21.5 to 294.0 g.

D. Filming Experiments

Feeding sessions were filmed in July, August, and September of 1967. Sixteen-millimeter movies, using a Bolex Rex 16H camera equipped with a 16-mm (moderately wide-angle) lens and electric drive motor were taken with Eastman Kodak tri-X film at an *f* setting of 4.0. Rolls of film 100 ft in length were used throughout the filming experiments since this amount of film represents 4000 frames, and with a time of 1 sec between frames, 100 ft lasts approximately 1 hr. A filming speed of 1 fps was chosen as a compromise between accuracy in recording movements of the bass and time required for frame-by-frame analysis. A time lapse of 1 sec was obtained by using a timer and solenoid (Sample Engineering Co., MC-5 movie control) which could be set for intervals ranging from 1 fps to fph.

The films were taken from overhead through a 2-ft square hole in the celling of a 9×12-ft filming room illuminated by eight 150-W bulbs. The light bulbs were located at ceiling height and were positioned so that there was no reflection from the surface of the filming tank onto the film. The camera was located 4.15 m above the filming tank, the distance at which, with the wide angle lens, the entire frame of film was occupied by the tank, thereby giving optimal resolution.

The filming tank consisted of two parts, a holding or maintenance area divided into three sections to keep the fish separate during nonfeeding times. This separation guaranteed several objectives. First, each predator was isolated from the others, and aggressive behavior which normally exists between largemouth bass in confinement was eliminated. Also, maintaining each bass in the tank in which filming takes place ensures acclimation to the proper temperature, eliminates excessive handling by the experimenter, and allows time for habituation to the filming

tank and filming room. Therefore, the fish is not disturbed when the sliding doors are raised to allow its entry into the filming arena, and film as well as film analysis time is not wasted while habituation to new surroundings occurs. In addition, little fecal material accumulates on the bottom of the filming tank, lessening the possibility of confusion with a prey fish during analysis of the film record.

The second part of the filming tank is used for filming of feeding bouts. This arena is 4 × 6 ft, made of $\frac{3}{8}$-in. exterior plywood which has been fiberglassed at each seam and corner to prevent leakage; all surfaces were coated with fiberglass resin and painted with white exterior house paint to enhance contrast between the fish and the background. The white background was necessary to accurately identify prey fish, which appear quite small when the film is projected on a screen or viewed in the film analyzer. The bottom of the filming arena was covered with a 4 × 6-ft × 18-in. piece of white Lucite in which $\frac{1}{4}$-in. holes were drilled every 2 in. on 2-in. centers. Any predetermined pattern or density of $\frac{1}{4}$-in. wood dowels could then be inserted into these holes and a range of environmental complexity or cover density could be easily established (see Fig. 1). By changing the density of dowels ($\frac{1}{4}$ × 6 in. in length), it was then possible to alter experimentally the density of partial refuge for the prey fish and, thereby, force the predator to pursue and capture prey in an environment which is more or less complex.

Initial analysis of the movie film was performed on a Vanguard motion analyzer and consisted of locating the head of the bass in each frame of film. This was accomplished by aligning cross hairs on the head of the bass, recording the X- and Y-coordinate values on data sheets and later punching these coordinate values on punch cards for computer processing. Each set of coordinate values represents the position of the predator and, by knowing that the time between frames was 1 sec, the velocity of the bass from frame to frame could be readily calculated. Accelerations and times spent at various swimming speeds were computed, and by knowing the energy requirements of different swimming speeds from the active metabolism experiments, it was possible to calculate energy utilization for each feeding bout. The information obtained from each feeding session consisted of the weight of the bass, prey density, water temperature, time of food deprivation, number of successful and unsuccessful pursuits, cover densities, and number and weight of prey eaten.

Films were made of three individual bass at a temperature ranging from 21 to 27 C with a minimum of two films at each of four cover densities. This is a very small sample size but in the absence of automatic film-reading equipment the long times required for film reading would

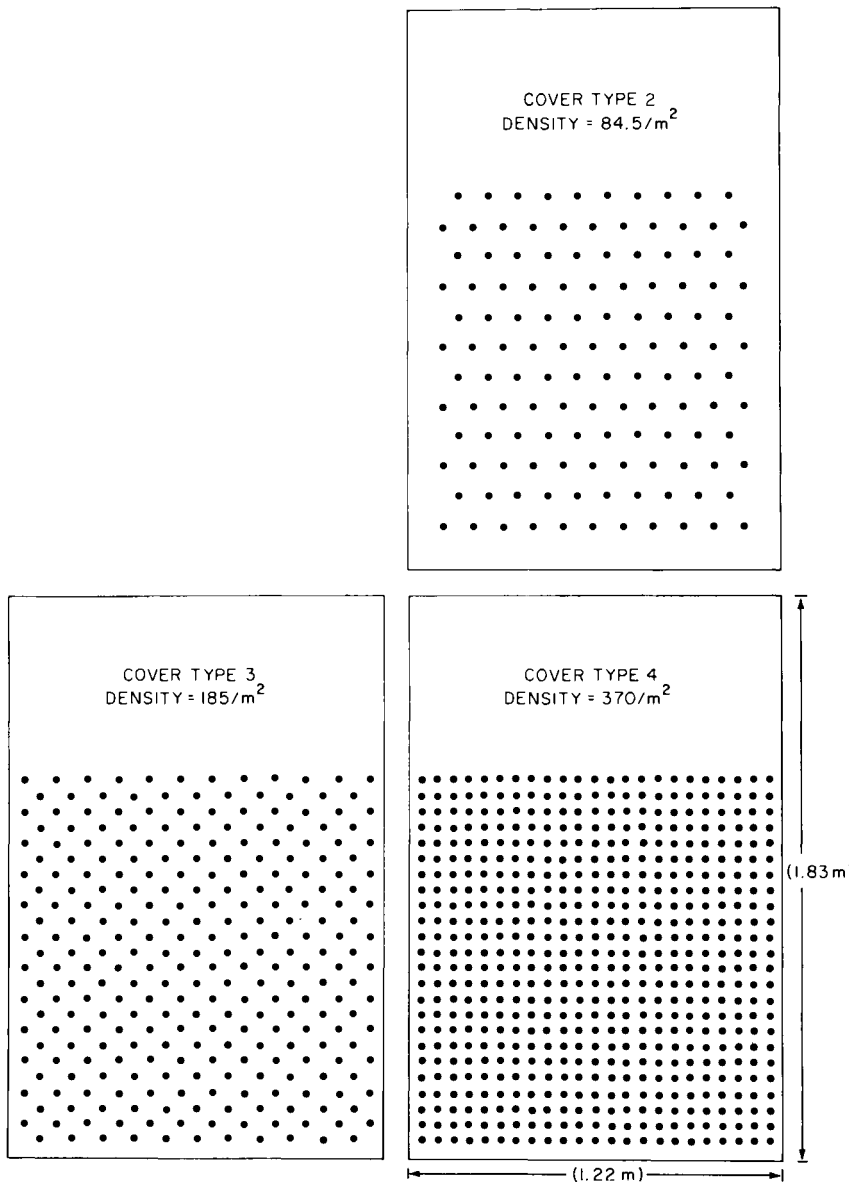

FIG. 1. Density and arrangement of cover in the filming area of the filming tank. Each dot represents the location of a $\frac{1}{4} \times 6$-in. wood dowel inserted into the tank bottom and extended to the height of the water level. Cover type 1 has no pegs anywhere in the tank. Cover type 3 is approximately double the peg density of type 2, and cover type 4 is approximately twice as dense as type 3 (not to scale).

have been prohibitive. The four densities of wooden doweling (see Fig. 1) were:

(1) no pegs inserted in the tank bottom, a completely open and unobstructed feeding area,
(2) 84.5 pegs/m^2,
(3) 185 pegs/m^2,
(4) 370 pegs/m^2.

Water depth in the filming tank was maintained at only 6 in. to avoid, as much as possible, the effect of three-dimensional movement of the predator by permitting only searching and pursuit which approximated a plane. This makes the use of only one camera, filming from overhead (instead of two cameras at right angles) a reasonably accurate method of recording swimming distances and velocities, and correspondingly reduces the time required for film analysis.

Each bass was maintained in the holding area of the filming tank for at least two weeks before feeding sessions were filmed to allow time for habituation to the tank and to become accustomed to feeding in the filming arena. Before introducing fish into the filming tank, they were kept in another similar room in an identical tank. This was done to reduce the time required to become sufficiently used to surroundings in the filming room so that film and filming time would not be wasted on an animal which would not perform "properly." When a fish was placed in the filming tank, it was given an identification number, weighed and allowed one to two days to recover from handling and weighing. Each fish was kept in the filming tank for approximately four to six weeks during which time it was filmed 15–20 times. This resulted in more films taken per fish than will be analyzed here. The reason for this is that initial taking of movie films is less time consuming than retrieving the data from the film record. Therefore, additional films were taken in case more "within fish" replication was required, but these were not analyzed due to the excessive time required.

III. Results and Discussion

A. Routine Metabolism

Figure 2 shows graphical representations of some of the pooled data as this was used to develop a computer model of the routine metabolism (E_r) component of Eq. 1. Table I gives a summary of routine metabolism data.

TABLE I

SUMMARY OF ROUTINE METABOLISM DATA, FOR LARGEMOUTH BLACK BASS *(Micropterus salmoides)* DEPRIVED OF FOOD FOR 24 HR

Temperature (C)	Weight group (g)	Av. weight ± 95% con. int.[a]	Av. mg O_2/hr ± 95% con. int.[a]	Av. mg O_2/hr ± 95% con. int.[a]	Number of observations	Number of fish
12	10.1–20.0	13.4 ± 1.701	2.08 ± 1.76	164.1 ± 148.5	6	3
	20.1–40.0	25.3 ± 1.44	4.64 ± 2.79	196.1 ± 123.3	12	4
	40.1–80.0	67.5 ± 3.58	4.68 ± 1.22	71.5 ± 21.5	22	6
	80.1–160.0	100.2 ± 1.68	7.27 ± 2.49	72.6 ± 25.0	15	3
	160.0–320.0	227.1 ± 1.45	17.78 ± 7.63	78.5 ± 33.8	7	2
20	2.5–5.0	4.0 ± 0.00	1.22 ± 0.24	305.1 ± 60.8	14	1
	5.1–10.0	8.9 ± 0.00	2.30 ± 0.32	258.3 ± 36.4	14	1
	10.1–20.0	14.7 ± 1.26	2.58 ± 0.28	182.0 ± 23.1	34	3
	20.1–40.0	27.1 ± 1.43	3.74 ± 0.40	138.6 ± 13.2	82	7
	40.1–80.0	46.9 ± 1.14	6.35 ± 0.66	134.2 ± 12.7	58	5
25	0.0–2.4	2.0 ± 0.14	0.72 ± 0.14	362.8 ± 66.8	24	17
	2.4–5.0	3.0 ± 0.07	0.81 ± 0.07	262.0 ± 22.7	142	69
	5.0–10.0	6.9 ± 0.75	1.99 ± 0.22	299.3 ± 34.4	25	11
	10.1–20.0	15.0 ± 0.43	3.48 ± 0.32	233.9 ± 21.8	67	11
	20.1–40.0	28.3 ± 0.89	5.53 ± 0.64	194.4 ± 20.1	102	14
	40.0–80.0	58.3 ± 2.08	8.93 ± 1.09	156.0 ± 19.8	92	11
				TOTAL	716	168

[a] con. int. = confidence interval.

Confidence intervals and/or standard errors of means are given to demonstrate some of the statistical characteristics of the data. The confidence interval is calculated on the basis of small sample size ($n < 30$). This was done to avoid overinterpreting the data and to minimize the importance of considering n the number of individuals tested or the number of observations (regardless of the number of individuals). All statistical computations were made on the basis of formulae in Bennett and Franklin (1966). With n as the number of fish, Student's t was calculated to determine any significant differences between mean values of mg O_2/hr in Table I for each comparable weight group at each temperature. The formula used was

$$t = \frac{m_1 - m_2}{\sigma_1^2 \sigma_2^2}$$

with $n_1 + n_2 - 2$ degrees of freedom. No significant differences ($t_{.05}$) between weight groups were found.

In Fig. 2 it may be readily seen that oxygen consumption for all weights and temperatures declines with increasing time of food deprivation. This is an important independent variable which has been overlooked by many investigators for two main reasons. First, it is difficult, if not impossible, with our present knowledge of physiological processes and existing techniques of studying respiratory metabolism to determine the separate effects of food assimilation, specific dynamic action of food (SDA), and lipogenesis during times of high blood glucose immediately after feeding. As a result, most investigators have simply determined routine metabolism at some fixed time of food deprivation (usually 24–36 hr). However, the effect of food deprivation time has been studied in trout and white suckers (Beamish, 1964b), a limpet (Berg *et al.*, 1958), lungfish (Smith, 1935a, b), largemouth black bass (Glass, 1968a), and a few other poikilotherms. The second reason why starvation time has been neglected seems to be that, apart from being just one more aspect of oxygen consumption for physiologists to examine, the need for data of this particular type is greatest if a model of a dynamic process such as the energetics of predation is to be developed.

Elsewhere (Glass, 1968a) the form of the function describing the decay in oxygen consumption with increasing time of food deprivation has been established using data from largemouth black bass, data on white suckers and trout (Beamish, 1964b), and data on five breeds of domestic animals (Brody, 1945). This relationship was best described by

$$Y_i = a + b \exp(-cX_i), \tag{3}$$

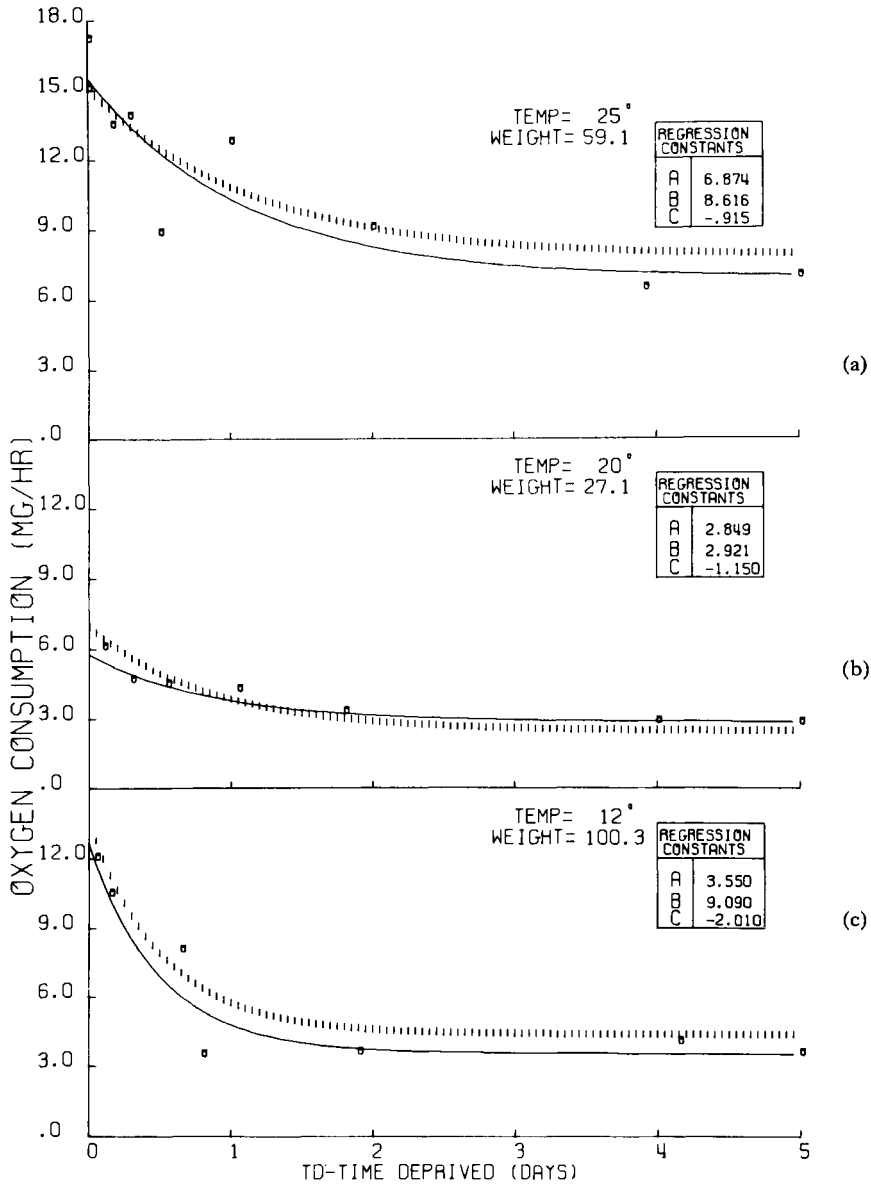

FIG. 2. Oxygen consumption (milligrams per hour) as a function of time of food deprivation at three experimental temperatures and three levels of weight. (a) temperature = 25 C, weight = 59.1. (b) temperature = 20 C, weight = 27.1. (c) temperature = 12 C, weight = 100.3. The solid line is the line of best fit through the data and was determined by an iterative least-squares calculation of best parameter values for the function $Y = a + be^{cX}$. The dashed line represents the prediction of the model [Eqs. (11), (12), or (13)] for the stated weight and temperature. Best parameter values for each weight and temperature are given in the accompanying tabulation.

where Y_i is oxygen consumption (mg O_2/hr), X_i is time of food deprivation in days (TD), and a, b, and c are considered constants for any weight and temperature.

In Fig. 2 the values for these three constants which give the best fit of the equation to the data appear [based upon minimum sum of squares, $\sum (Y_i - Y_c)^2$]. An inspection of the values for the constants reveals that they are actually not constants, but vary in a systematic way. It is this variation which will be exploited in development of the computer model and, as will be shown, the variation can be explained in terms of the weight of the experimental animal and its acclimation temperature. Inspection of Fig. 2 shows that oxygen consumption varies with time of food deprivation as a family of curves whose intercepts, asymptotes, and rate constants all vary as functions of at least weight and temperature.

The simplest and most thoroughly studied parameter in Eq. (3) is a. This obviously corresponds to and approaches $Y_{\min}$ or standard metabolism, which is known to vary with the body weight of the organism (Zeuthen, 1953; Kleiber, 1947, 1961) and also with temperature (Winberg, 1956, 1961; Beamish and Mookherjii, 1963; Fry, 1957).

The most widely accepted mathematical description of the effect of weight is

$$Y_i = \alpha X_i^{\beta} \tag{4}$$

where Y_i is oxygen consumption (mg O_2/hr), X_i is weight (W), and α and β are constants. Figure 3 shows plots of oxygen consumption as a function of body weight at each of the three experimental temperatures. An inspection of these figures reveals two items of interest. First, the slope β is in the range reported by other investigators (Job, 1955; Zeuthen, 1953; Winberg, 1956; and many others). Second, α varies with temperature. A plot of α appears in Fig. 4 and is graphed as a straight line in the absence of enough data to demonstrate clearly any other functional relationship, although an exponential function could probably be rationalized if the origin were considered a valid intercept. Since at 0 C there would be very little oxygen consumption, the line should pass almost through the origin. For this reason the intercept in Fig. 4, even though it was derived from the best least-squares fit to the data, will not be incorporated into the model. The slope was found by least squares to be 0.021 and will be included as

$$\alpha = 0.021T, \tag{5}$$

where T is temperature in degrees centigrade. By taking the average value for the slope in Fig. 3 to be 0.77 [close to the two-thirds propor-

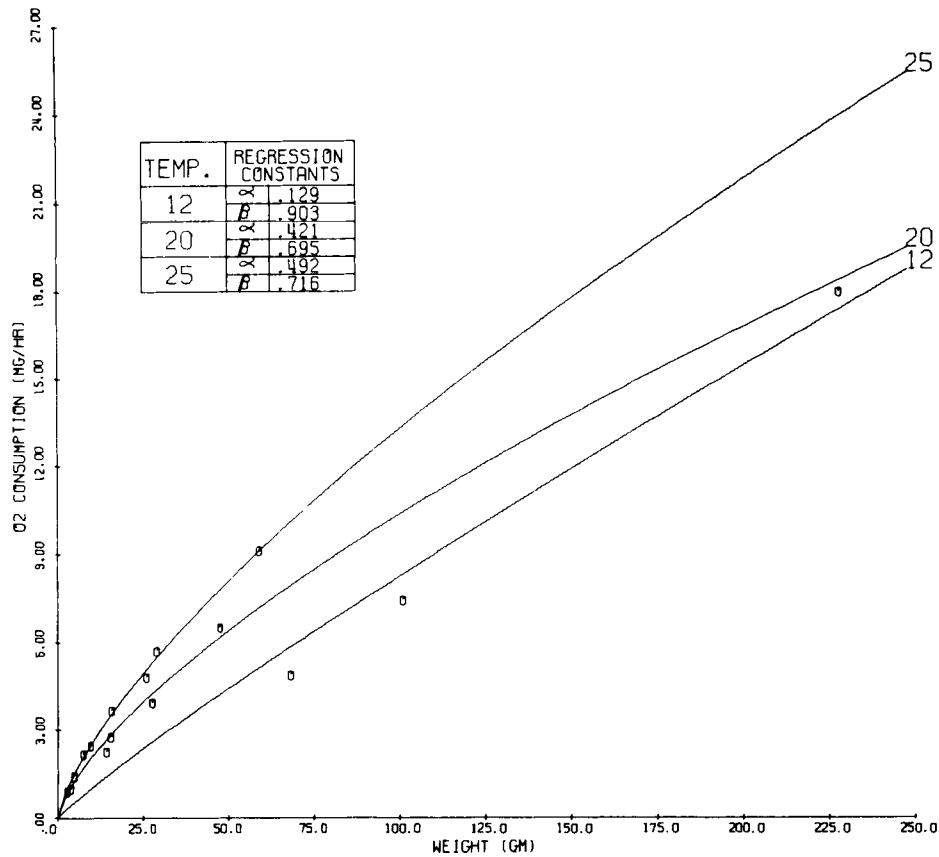

FIG. 3. Oxygen consumption as a function of weight for three experimental temperatures. The equation $Y = \alpha X^{\beta}$ was fit to the data (from Table I) by an iterative least-squares method. The α and β yielding the line of best fit for each temperature appear in the box.

tionality from the so-called surface area-to-volume proportionality, which is probably slightly low (Fry, 1957)], Eq. (4) can be refined by substituting Eq. (5) into it as

$$Y_i = \alpha W^{\beta} = 0.021 T\, W^{0.77}. \tag{6}$$

By then substituting Eq. (6) back into Eq. (3), the result is

$$Y_i = a + be^{-c\,TD} = 0.021 T\, W^{0.77} + be^{-c\,TD} \tag{7}$$

which expresses oxygen consumption in milligrams O_2 per hour in terms

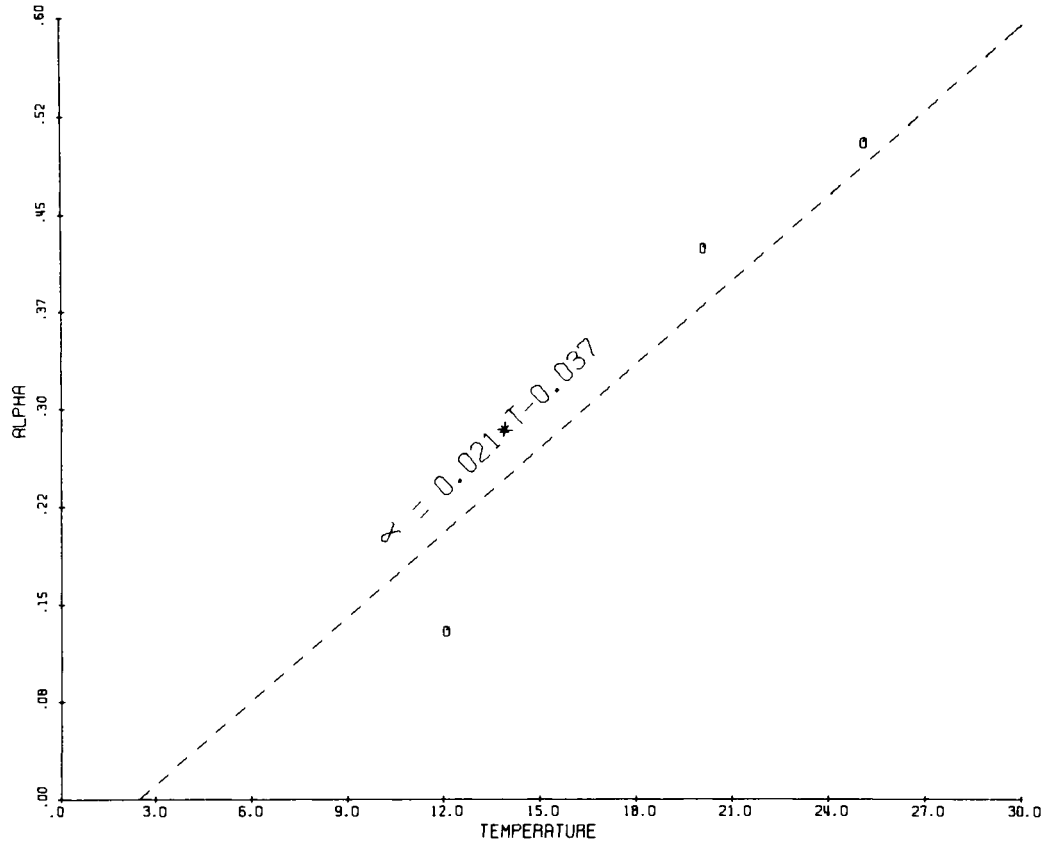

FIG. 4. Alpha ($\alpha = 0.021\ T - 0.037$) from Fig. 3 as a function of temperature (degrees centigrade). A straight line was assumed in the absence of more data over a wide range of temperatures.

of temperature, weight of the fish, and duration of food deprivation. This kind of data is available from some respiratory metabolism studies, and the biological bases of oxygen consumption become more evident when a step-by-step derivation can be shown.

It is more difficult to establish a logical biological basis for the parameter b in Eq. (7), but this can be accomplished by the following reasoning: b represents the difference between $Y_{\max}$ at zero time of food deprivation and $Y_{\min}$. This difference, of course, is due to food in the gut (i.e., SDA, active transport, if any, for assimilation of some food materials, and perhaps gut motility) and/or other processing of this food. The more food in the gut, the larger will be the difference between $Y_{\max}$ and $Y_{\min}$. By analyzing a large quantity of feeding data collected on *M. salmoides* by Wells (1968), which reflects the influence of feeding behavior as well as the morphological relationship between body weight and gut capacity, each body weight could be assigned a gut capacity. A comparison between feeding data and direct autopsy data showed a consistent tendency for feeding data to underestimate the maximum gut capacity of the fish. Nevertheless, if this underestimation is consistent for all weight groups, a plot of maximum gut capacity ($G_{\max}$) as a function of the animal's weight should yield the correct shape of the functional relationship between these two variables, and the true parameter values will only differ from the derived parameter values by a constant (C). Therefore, since

$$Y_{\max} - Y_{\min} \propto b \propto G_{\max} = f(\text{weight}),$$

then

$$b = f(W) \pm \text{C},$$

assuming a consistent difference between feeding and autopsy data. Figure 5 shows the functional relationship between b and $\log_{10} W$ which proved to be the transformation producing a linear relationship. By linear regression the line of best fit was found to be

$$b = 8.25 \log_{10} W - 7.31. \tag{8}$$

By substituting Eq. (8) into Eq. (7), the computer model can be developed one step further

$$Y_i = 0.021 T W^{0.77} + (8.25 \log_{10} W - 7.31)\, e^{-c\,TD}. \tag{9}$$

The rate constant c is the only remaining parameter to be explained. This parameter will be influenced primarily by three variables—the amount of food in the gut at any instant during digestion, the type of

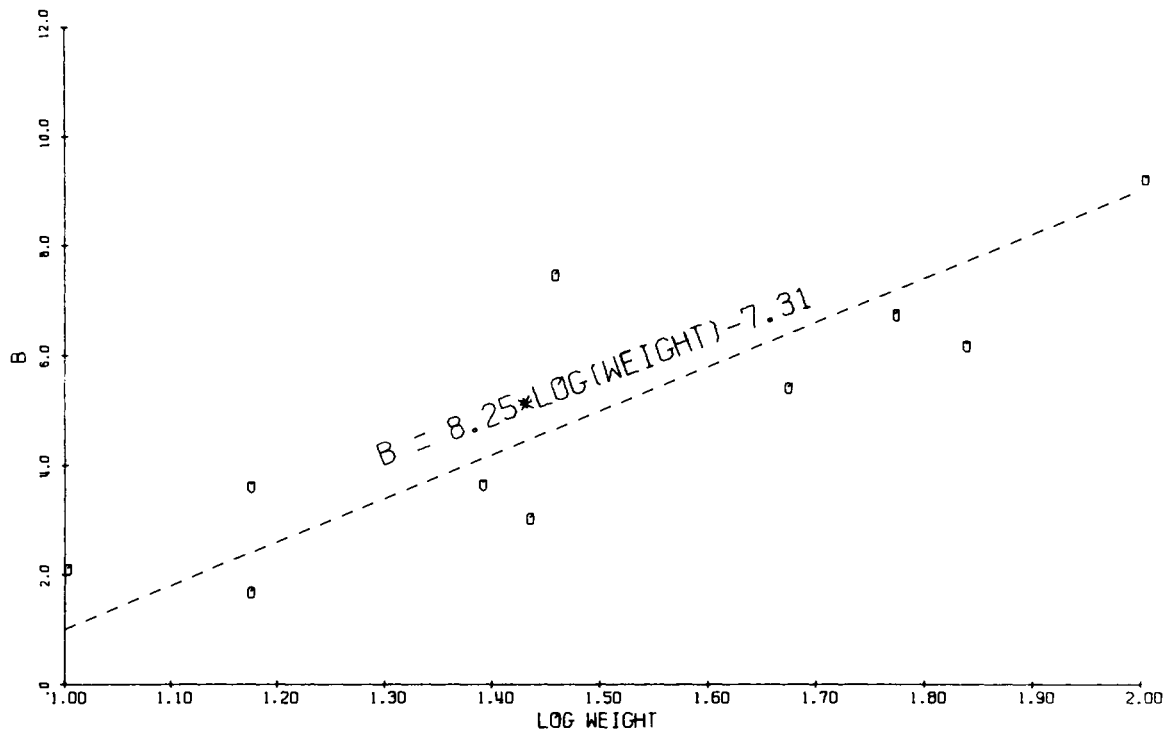

FIG. 5. The parameter as a function of $\log_{10}$ weight ($B = 8.25 * \log(\text{weight})-7.31$). The dashed line was fit by linear regression to data from Figures 8–17 in Glass (1968b).

food eaten (i.e., protein, carbohydrate, or fat), and temperature. Perhaps G_{max} will also have an effect since this will determine the absolute quantity of the gut contents. An increase in gut contents might slow the rate at which the gut is emptied, but no data which might describe this relationship were collected. The type of food being ingested was not varied due to the effect that this might have on other parts of the experimental program. Also, different food types would have added one more dimension to the experimental design, and time and facilities prevented this. The relationship between c and temperature could be derived from existing data but would be confounded as a result of at least the two above-mentioned variables. Therefore, c was simply set in the computer model by three Fortran logical IF statements, depending upon the experimental temperature, as

$$\begin{aligned} &\text{IF} \quad (\text{T.EQ.12.}) \quad c = -1.97 \\ &\text{IF} \quad (\text{T.EQ.20.}) \quad c = -1.10 \\ &\text{IF} \quad (\text{T.EQ.25.}) \quad c = -0.90 \end{aligned} \tag{10}$$

It may be readily seen from (10) that $\Delta c/\Delta T \to 0$ as temperature increases. This is not unexpected since intuitively the rate at which the gut empties should approach a finite maximum. One implication of this is that the error introduced into the model as a result of errors in the value selected for c will decrease at higher temperatures. This observation negates to some extent errors which might arise in interpreting the filming experiments since some of these were conducted at temperatures slightly in excess of 25 C.

The model developed in this section will be implemented later in analyzing the film records. It consists of three equations, one for each temperature at which routine metabolism experiments were conducted. These three equations are

$$Y_i = 0.021 T W^{0.77} + (8.25 \log_{10} W - 7.31) e^{-1.97 TD} \tag{11}$$

$$Y_i = 0.021 T W^{0.77} + (8.25 \log_{10} W - 7.31) e^{-1.10 TD} \tag{12}$$

$$Y_i = 0.021 T W^{0.77} + (8.25 \log_{10} W - 7.31) e^{-0.90 TD} \tag{13}$$

which differ only in the rate constant c which is set in the computer program by (10).

B. Sensitivity of the Model

Table II consists of the matrix which results from perturbations in each of the constants or variables in Eq. (12). For a given percent change

TABLE II

RESULTS OF THE SENSITIVITY TEST OF THE COMPUTER MODEL[a]

% Deviation	α	β	b	a	c	T	W	TD
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	6.03	17.15	8.30	−4.33	−2.13	6.03	5.81	−2.13
20	12.05	39.17	16.61	−8.66	−4.14	12.05	11.33	−4.14
30	18.08	67.46	24.91	−12.99	−6.04	18.08	16.59	−6.04
40	24.11	103.80	33.22	−17.32	−7.85	24.11	21.62	−7.85
50	30.13	150.48	41.52	−21.65	−9.55	30.13	26 46	−9.55
60	36.16	210.43	49.82	−25.98	−11.17	36.16	31.13	−11.17
70	42.19	287.45	58.13	−30.32	−12.70	42.19	35.64	−12.70
80	48.21	386.37	66.43	−34.65	−14.14	48.21	40.00	−14.14
90	54.24	513.44	74.74	−38.98	−15.51	54.24	44.24	−15.51
100	60.27	676.67	83.04	−43.31	−16.81	60.27	48.36	−16.81

[a] The results were taken from Eq. (12) at 20 C for an arbitrarily selected weight of 50 g and TD of 0.5. Each variable or constant was varied individually and the resulting percent change in routine oxygen consumption appears in the appropriate column.

(0–100%) in each variable or constant taken individually, the resulting percent change in the value of routine metabolism can be found in the appropriate row and column. It should be noted that if the variable values were different from the particular ones that were selected, the relative sensitivity of each variable or constant might be expected to change. In addition, the absolute change in Y would be somewhat different if other variate values, for example, $W = 10.0$, $TD = 5$, $T = 12$, were initially chosen. Obviously, many tables similar to Table II could be generated, each based upon different values of T, W, and TD, to demonstrate how the sensitivity of Eq. (12) changed as a result of altering the input variables. This was not done since several pages of related tables would yield information of minimal utility for present purposes. The equation for the computer model,

$$Y = (\alpha\, T\, W^{\beta}) + [(b \log_{10} W - a) \exp(c\, TD)], \tag{14}$$

indicates which column of Table II is representing each of the constants or variables, and is analogous to (12).

There are several points revealed by Table II. First, the most dramatically influenced column is that headed by β (column 3). This

parameter enters the computer model as the fractional power to which the weight of the animal [see Eq. (6)] is raised to give routine oxygen consumption. The constant β is probably one of the most frequently measured parameters in studies of respiratory metabolism in fish (see Winberg, 1956). However, it is probably not actually a constant, as can be seen from Fig. 3. Very likely, β is influenced by interaction between time of food deprivation, weight, and probably temperature as well (Job, 1955). Various values for β have been reported in the literature. Fry (1957) has discussed them, and it would be redundant to repeat that discussion here. It is sufficient to say that most values reported for β approximate the well-known surface area-to-volume relationship.

Since β is the most critical parameter, it follows that a great proportion of experimental effort should be allocated to its determination. The sensitivity of the model to perturbation in β was not known at the beginning of the experimental work reported here, but this "constant" was determined on the basis of 716 observations of 168 animals and this should be more than adequate statistically. With this number of degrees of freedom, the variance (assuming $\sigma/\sqrt{n} = 10\%$ of the mean value for β) would have to exceed 0.69 ($\sigma^2 = 168 \cdot 0.0041 = 0.69$) before additional sampling would be called for. To produce a variance of this magnitude would obviously require fluctuations in the data such that more than 33% of the experimental observations would yield a value for β of $-0.19 \leqslant \beta \leqslant 1.47$. This is clearly not true since values of β in these ranges would indicate wildly different values and variances in oxygen consumption than are evident in Table I. It is therefore safe to conclude that more than enough samples were taken. It should be noted, however, that while accuracy in β has probably been attained, the criterion of realism in describing processes influenced by and influencing β has not been achieved. For purposes of showing how β affects metabolic processes, it should properly reflect interactions between at least weight, temperature, and time of food deprivation. That it does not arises from the magnitude of the experimental program necessary to incorporate these interacting variables, so a reasonably accurate mean value was accepted as tolerable for present purposes.

The parameter which causes the second greatest fluctuation in the model is b, a linear multiplier of $\log_{10} W$. That this is true emphasizes the need for studies of feeding behavior in order to provide realism and accuracy as well as completeness in any model purporting to describe metabolic processes in fish. It is, of course, the behavioral aspects of fish feeding which dictate how closely the amount of food in the gut approximates maximum gut capacity, morphological limitations and

capabilities of the gut notwithstanding. Therefore, it is evident that significant improvements in the accuracy of b must await quantitative investigations of feeding behavior.

That α and T constitute the third most sensitive components (as well as being identical) should not come as a surprise. They are multipliers of each other, and in addition exert an influence on the calculated value of routine metabolism which is even less than the induced change in their initial values. It is important to realize that if T were to be incorporated into the model as a functional part of the rate constant c, the effects on Eq. (12) caused by small changes in T would be expected to increase substantially.

The actual weight of an experimental animal is apparently less critical to the performance of the computer model than was anticipated. Column 8 of Table II reveals a slightly diminishing, but nearly constant, change in the output from the model with increasing percent deviations in W. It should be pointed out that with W, as in the explanation of T, the expansion of certain model components (such as c) to include the effect of body weight might well result in an increased sensitivity to perturbations in W. However, that the model is somewhat resistant to variability in both W and T is an advantage since in a later section Eqs. (11), (12), and (13) will be employed to determine theoretical values for oxygen consumption during filming experiments. Although this apparent damping effect becomes important to the film analysis since fish weights were not taken every day and environmental temperatures were variable, the reasons for the lack of sensitivity to W and T are not known.

The low sensitivity of the model to a can be explained by the manner in which it exerts its effects. Since it is simply a linear addend in the functional relationship shown in Eq. (8), it might be expected to be of small importance.

Deviations in c and TD are equal in their alteration of the output from the model because they are multipliers of each other. Resistance of the model to changes in TD are low, but this results largely from the level of the variate values initially chosen. It is obvious from the relationship between oxygen consumption and TD (see Fig. 2) that at low (less than one day) values of TD this variable becomes very important in determining oxygen uptake. Conversely, after a long period of food deprivation the importance of TD to routine metabolism is quite minimal. The same argument applies to c. However, c is seen from Table II to be one of the least important parameters for another reason. Changes induced in all the constants and variables was directional, as can be seen from the following set of Fortran statements which show the method of creating deviations in c.

```
      A = 1.0
      DO 1 I = 1,10
      C = C * A
C     Calculate the value of Y by Eq. (12).
C     Calculate and write the percent change in Y resulting
C     from the deviation in c.
      A = A + 0.1
    1 Continue
```

Since the shape of the curve generated by the computer model changes from the form seen in Fig. 2 to a straight line as $c \rightarrow 0$, it follows that if c were made more positive instead of more negative in (14), it would be more critical to model sensitivity than Table II indicates. Therefore, resistance of the computer model to changes in c depends upon at least two factors, TD and the direction of the imposed deviation. The lower the value of TD, the more the model output is altered by deviation in c, particularly if that change results in a more positive value of c.

C. Active Metabolism

The results of active metabolism experiments in summary form appear in Table III. The raw data were pooled in two different ways. First, using standard cgs notation, work per milligram of O_2 consumed as a function of velocity, and efficiency (defined as centimeters traveled $\times 10^4$ per milligram of O_2 consumed) were calculated and plotted (see Fig. 6). This figure reveals two experimental problems that arise in determining oxygen consumption for different velocity levels. One is that at higher velocities (above 30–35 cm/sec) it becomes difficult for the bass to maintain high swimming speeds, long enough to ensure adequate reduction in dissolved oxygen concentration (refer to Section II). This increases error resulting from limitations of the experimental apparatus, thereby decreasing confidence in data points at high velocities. In addition, provision for the oxygen debt incurred at high swimming velocities has not been included in the data points. This is especially important where total swimming time is relatively short. The combination of these two factors therefore increases the uncertainty of the form of the function which should be chosen to describe work or efficiency of energy utilization at different velocities of swimming. Consequently, the following simple empirical relationships were used in Fig. 6:

TABLE III

SUMMARY OF ACTIVE METABOLISM DATA BROKEN DOWN BY WEIGHT[a]

Weight (g)	Velocity (cm/sec)	$\sigma\sqrt{n}$	mg O_2/hr	$\sigma\sqrt{n}$	mg O_2/cm traveled ($\times 10^4$)	$\sigma\sqrt{n}$	Number of observations
30.50	7.35	0.62	6.98	0.35	2.67	0.36	2
34.14	15.76	0.95	10.45	0.99	1.91	0.23	10
39.07	26.29	1.08	12.26	0.95	1.37	0.14	6
33.99	34.66	0.84	16.20	5.97	1.53	0.43	7
35.50	44.60	2.08	29.23	6.66	2.22	0.82	3
49.13	8.44	1.39	12.38	0.71	4.46	1.15	3
46.87	13.78	0.72	10.67	1.06	2.01	0.16	13
50.49	25.93	0.78	16.62	2.13	1.56	0.17	11
45.99	34.99	1.22	14.83	3.75	1.44	0.27	7
45.90	51.41	4.86	24.94	5.68	1.38	0.36	4
69.55	6.90	1.03	11.38	0.51	4.65	0.48	2
69.40	14.81	1.21	10.81	1.24	2.05	0.22	5
70.64	23.50	0.76	16.61	1.70	2.00	0.25	8
68.32	34.88	0.65	23.28	6.48	1.84	0.52	5
64.80	45.93	0.41	40.07	9.94	2.43	0.62	2
93.73	6.93	1.53	20.99	7.60	3.71	0.94	3
88.33	14.12	0.79	17.30	1.87	3.39	0.30	6
88.44	26.38	1.18	22.89	3.23	2.43	0.38	8
87.75	36.07	3.76	33.47	21.19	2.44	1.37	2
94.60	45.21	3.38	31.52	3.84	1.93	0.09	2

[a] Each $\sigma/\sqrt{n}$ column corresponds to the variable column immediately to the left.

For 20.0- to 60.0-g fish,

$$\begin{aligned} \text{work} &= 0.077 + 0.244X_i^{0.746} \quad \text{for} \quad 0 \leqslant X \leqslant 31.4 \\ \text{work} &= 3.45 - 0.0145X_i \quad \text{for} \quad X \geqslant 31.5, \end{aligned} \tag{15a}$$

and for 60.1- to 100.0-g fish,

$$\begin{aligned} \text{work} &= -0.486 + 1.823X_i^{0.245} \quad \text{for} \quad 0 \leqslant X \leqslant 28.4 \\ \text{work} &= 5.05 - 0.0526X_i \quad \text{for} \quad X \geqslant 28.5, \end{aligned} \tag{15b}$$

For 20.0- to 60.0-g fish,

$$\begin{aligned} \text{efficiency} &= 0.0935 + 0.326X_i^{0.892} \quad \text{for} \quad 0 \leqslant X \leqslant 31.4 \\ \text{efficiency} &= 1.22 - 0.0147X_i \quad \text{for} \quad X \geqslant 31.5, \end{aligned} \tag{15c}$$

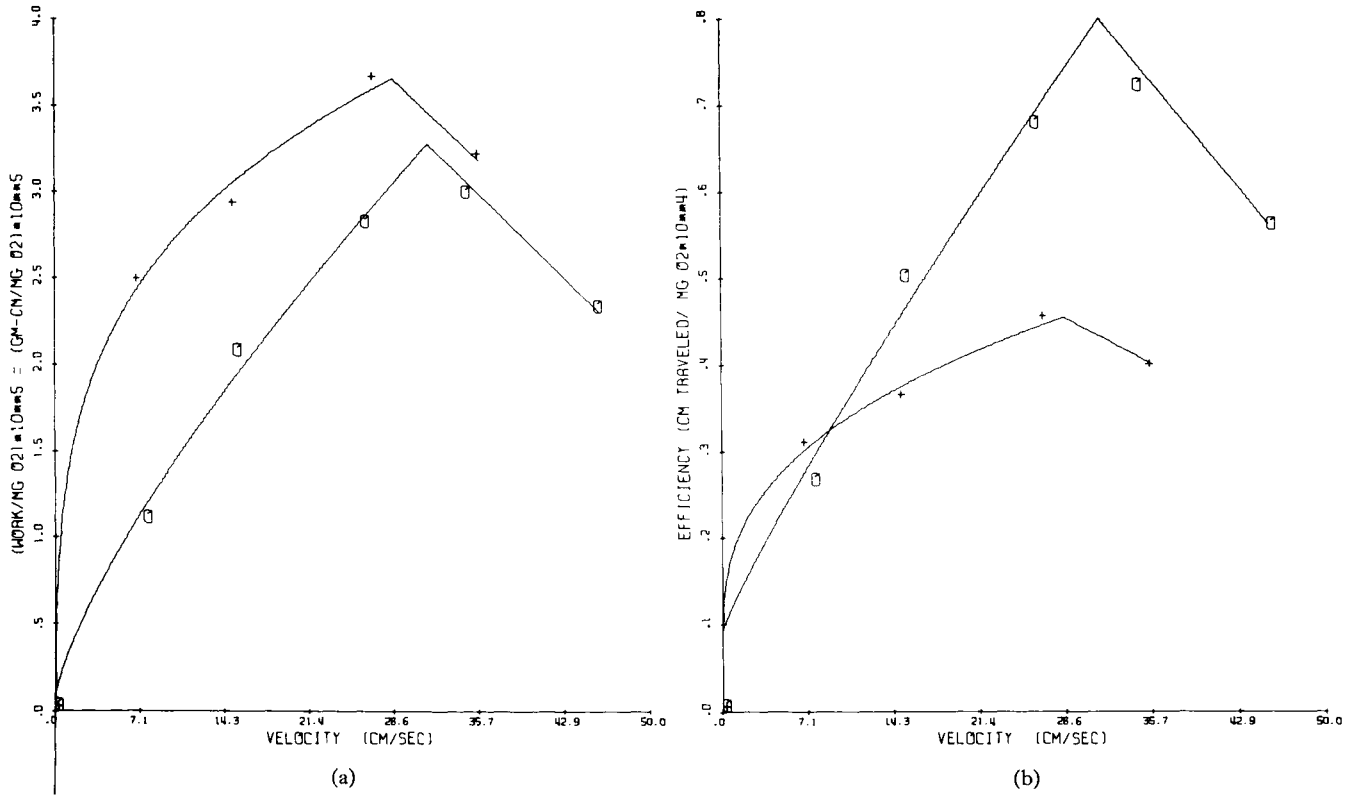

FIG. 6. Graph (a) shows the relationship between work per milligrams of O_2 consumed $\times 10^5$ and velocity (in centimeters per second) for two weight classes of fish. Results for 60.1- to 100.0-g fish are given by a plus (+), 20.1- to 60.0-g fish are plotted as an open circle. Graph (b) shows a plot of distance traveled per milligrams of O_2 (efficiency) with 60.1- to 100.0-g fish represented by a plus (+), and results for 20.1- to 60.0-g fish shown as open circles. All measurements were made at 20 $\pm$ 1 C.

and for 60.1- to 100.0-g fish,

$$\begin{aligned} \text{efficiency} &= 0.0811 + 0.1078X_i^{0.3711} \quad \text{for} \quad 0 \leqslant X \leqslant 28.4 \\ \text{efficiency} &= 0.62 - 0.0065X_i \quad \text{for} \quad X \geqslant 28.5, \end{aligned} \tag{15d}$$

where constants were determined either by linear regression or by an iterative least-squares technique (Marquardt, 1963; Glass, 1967, Conway *et al.*, 1970).

The second method of pooling data was by weight and velocity (see Fig. 7). This relationship is, of course, subject to the same qualifications as Fig. 6. The value of routine metabolism was calculated from Eq. (12), using as input, $T = 20.0$, $W =$ average weight, and $TD = 1.5$ days (see Section II). An equation of the form $Y = a + bX^c$ was fitted to the active metabolism data, where X represents swimming velocity and a, b, and c are fitted constants.

Figure 8 is the result of pooling the data of Spoor (1946) for several intervals of activity. Many investigators of respiratory metabolism in fish have regarded Spoor's graph (his Fig. 4) as evidence for a linear relationship between oxygen consumption and activity. Figure 8 shows that this presumption is probably invalid and, in the case of Spoor's data, results in an underestimate of standard metabolism by about 50%. Two lines of reasoning render the assumption of linearity improbable. First, the residual sum of squares is approximately twice as high for the straight line of best fit as it is for the curve. Second—and probably most convincing physiologically—increasing swimming velocity has a greater than linear effect upon oxygen consumption (see Fig. 7). Furthermore, the exponent of the curve in Fig. 8 has a value of about 1.5. This is not entirely unexpected since it is approximately the reciprocal of the well-known surface area to volume relationship. It would seem reasonable to hypothesize that use of muscle mass ($\propto$ volume) facilitates swimming or level of activity, and that water resistance ($\propto$ surface) hinders swimming or level of activity. Logically, then, if the surface area to volume relationship is physiologically sound, the idea of swimming velocity (or activity) raised to the 3/2 power being approximately proportional to oxygen consumption should also be true.

Complete description of active metabolism by a mathematical model was not possible since data for a wide range of temperatures and weights of fish were not collected. However, a partial model based upon the data that were collected was constructed since the weight and temperature ranges involved in the filming experiments were not too different from those of the active metabolism experiments. The model was

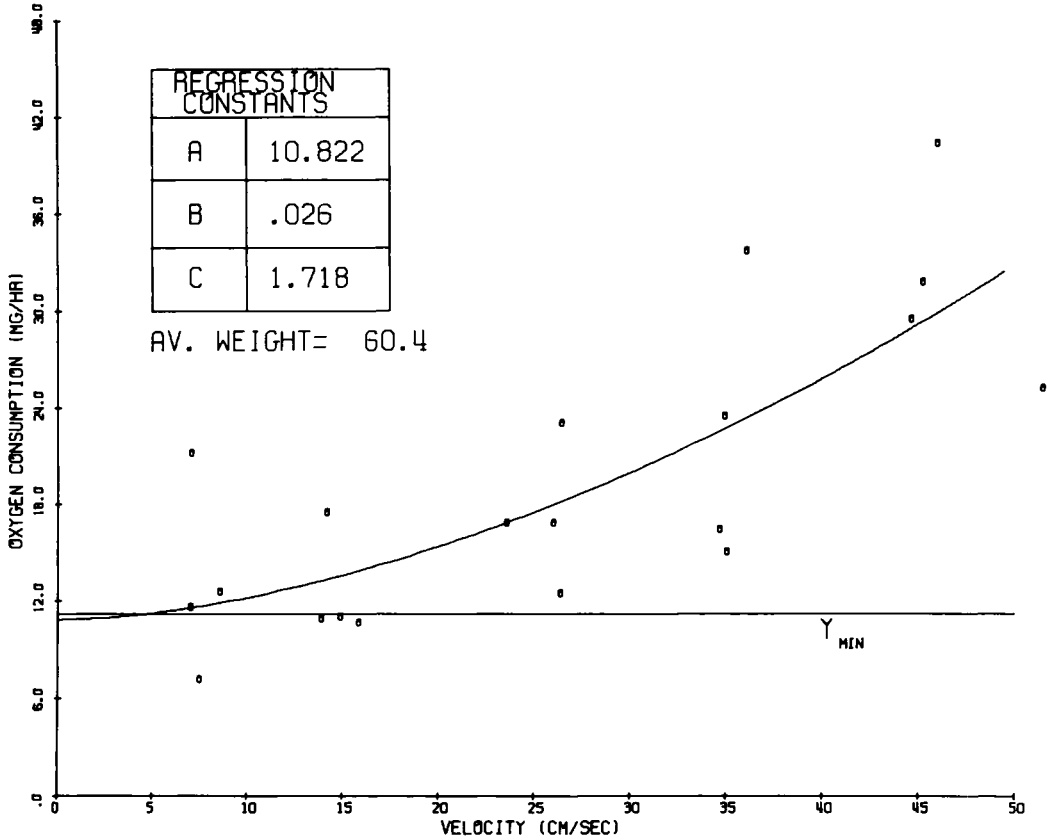

FIG. 7. Oxygen consumption as a function of velocity (in centimeters per second). Data from Table III. The equation $Y = a + bX^c$ was fit to the data by iterative least-squares. The straight line labeled $Y_{\min}$ represents the prediction of Eq. (12) for 1.5 days of deprivation time, 20 C, and a weight of 60.4 g. The fitted parameter values appear in the accompanying tabulation.

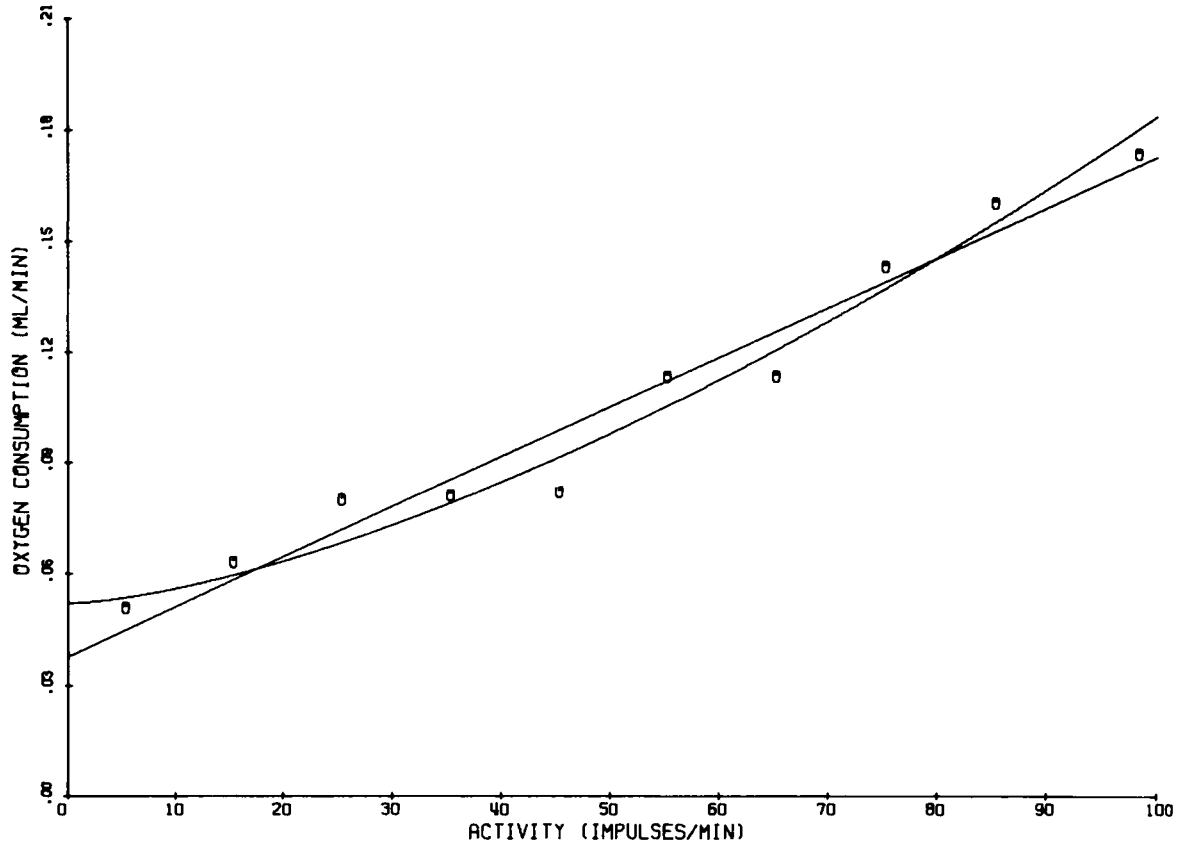

FIG. 8. Data from Spoor (1946) pooled by activity level. The points are unweighted and estimated from a graph of original data. The straight line is given by $Y = 0.0377 + 0.00135X$ and yields a residual sum of squares of 0.00046. The curve represents the fitting of $Y = 0.052 + 0.00012X^{1.52}$, and yields a residual sum of squares of 0.00028.

developed using Eq. (12) in place of the fitted constant a (the Y-intercept) in Fig. 7 since at zero velocity oxygen consumption should approach routine metabolic levels ($Y_{\min}$). Substituting RM as the output from Eq. (12), the equation for active metabolism becomes

$$Y = RM + bV^c \tag{16}$$

where Y is oxygen consumption in milligrams per hour, V is velocity in centimeters per second, and b and c are fitted constants (see Fig. 7).

D. Filmed Feeding Sessions

Analysis of movie films of feeding sessions was accomplished by means of a computer program which computed velocity, acceleration, location of the predator in the filming tank, and both routine and active metabolic expenditure through time during each feeding session. The number of attempts by the predator to capture prey, the number, time, and location of prey captures as well as the predator's velocity and acceleration during attempts and captures were monitored also. Some of the output from this program appears in summary form in Fig. 9 and Table IV. It is obvious that the complexity of analyzing film records is not great but does require a prodigious amount of bookkeeping. Once the scheme of analysis has been developed, however, memory capabilities of a moderately sized digital computer such as the IBM 7044 are adequate.

Both high and low cover densities (cover type) or environmental complexity fail to optimize long-term energy input and expenditure, although for quite different reasons. At low cover densities the predator has the capability of annihilating its food source which, of course, ultimately leads to local extinction of both species. At the low cover density, therefore, maximal energy input to the bass may be realized but this will result only in short-term predator success, and the evolution of an animal which crops lower trophic levels in any but a sustained yield fashion is very unlikely. At high cover densities, the predator is subject to a double disadvantage. First, an apparently behavioral deterrent to initiating attempts to capture food is operating (see Fig. 9) in combination with both a high velocity required to capture food and a lowered maneuverability due to a more complex environment (Table IV). Second, column 5 in Table IV indicates a relatively low amount of work per unit energy expended at high cover densities, and column 6 shows a rapid decline in the distance traveled per unit energy input. Therefore, even though the probability that an attempt will result in a

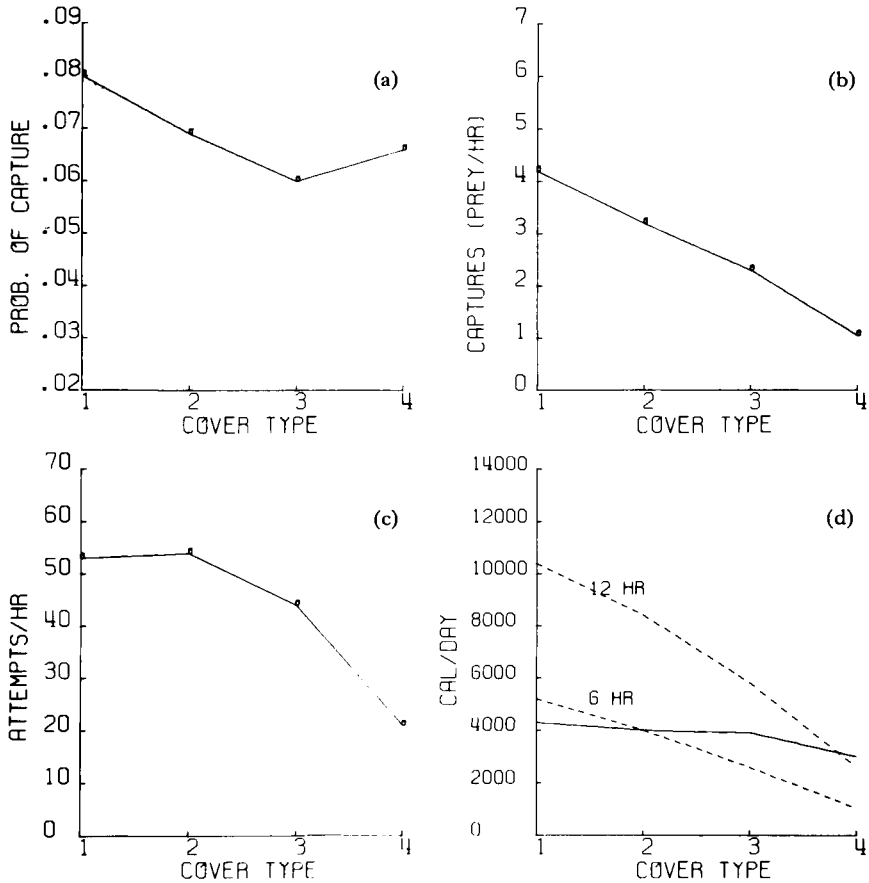

FIG. 9. Some summary information derived from analysis of filmed feeding sessions. Graph (a) shows the probability that an attempt will result in a successful capture at each cover density. Graph (b) shows how the rate of capture of prey fish by the predator declines with increasing cover density and represents the product of probability of capture and the attempt rate. Graph (c) gives the rate at which the predator attempts to capture prey at each level of cover density. Graph (d) shows the calories per day expended (solid line) by the predator and the calories per day acquired (dashed lines) by the predator at each cover density for 6 hr/day spent feeding and 12 hr/day spent feeding.

capture increases slightly at high cover densities as opposed to the probability of capture at intermediate cover densities, the number of attempts initiated declines and the energy expenditure per attack increases rapidly. Stated simply, the rate of capture or food intake

TABLE IV

SUMMARY OF DATA DERIVED FROM FILM RECORDS OF FEEDING SESSIONS[a]

Cover type	Average velocity at attempt (cm/sec)	Average velocity at capture (cm/sec)	Level of significance	Work/mg O_2 at capture (g-cm/mg O_2) $\times 10^{-5}$	Cm traveled/mg O_2 at capture $\times 10^{-4}$	Probability of successful capture	Cal/hr expended during feeding	Cal/hr captured during feeding	Physiologically useful cal/hr captured during feeding
1 (23)	57.01	23.68	0.001	2.67	0.642	0.0795	179	1845	864
2 (12)	51.35	23.12	0.01	2.62	0.630	0.0596	159	1448	677
3 (7)	57.01	50.12	0.1	2.72	0.480	0.0510	153	1043	487
4 (8)	42.29	69.59	0.01	2.44	0.194	0.0541	131	495	231

[a] Each column is derived from analysis of approximately 100,000 frames of movie film. Level of significance is from Student's *t*-test for the difference between mean velocity at attempt and mean velocity at capture. Numerals in parentheses are degrees of freedom.

must be substantially higher than observed, or more than 12 hr/day must be devoted to feeding at the experimentally observed rates before the effects of high cover density (such as decreased efficiency of energy utilization) can be overcome.

In the case of environmental complexity and its effects on predator or prey success (or both), the criterion for continued existence is optimization rather than maximization. To maximize the energy input, a predator would be most successful if it could feed in a simple environment for an unlimited time. This would permit a maximum energy input, but would also result in extermination of prey. Optimization of energy acquisition and utilization requires that the predator, through behavioral or physiological means, be adapted to an environment requiring slightly higher energy expenditure to acquire food and, at the same time, one which provides an energy dividend in the form of increased efficiency of energy utilization. In the present context an environmental complexity approximately intermediate between cover types 2 and 3 appears to be optimal in this respect. It would be interesting to know if this level of environmental complexity is also compatible with other aspects of prey survival, but this would be difficult to determine in the laboratory using the present predator–prey system. One tentative conclusion drawn from the filming experiments could be tested. If a cover density intermediate between cover types 2 and 3 is optimal for largemouth black bass from an energetics point of view, then assuming Eq. (2) to be valid, growth of bass in the 20–50 g weight range under these conditions could be determined and checked for correspondence with growth curves in the literature. No denial of complicating factors such as prey density or schooling of predators is implied, but such a growth experiment could provisionally confirm or deny the validity of the metabolic model presented here. A simulation model designed to test the hypothesis that the energy acquisition and dissipation rates discussed here will result in growth rates comparable to published growth rates has been developed by the author and is currently being refined.

Figure 9 shows the daily theoretical energy budget for a 50-g bass at 25 C. By multiplying the rate of attempts at each cover density by the probability of successful capture at that cover density, it is possible to determine the theoretical number of prey captured per hour. By multiplying the rate of prey capture by the average prey weight (0.6 g), the grams of food ingested per hour were determined. Assuming 85% assimilation efficiency and 750 cal/g wet weight, the calories assimilated per hour spent feeding were calculated. Using the concept of "primary heat," Ivlev (1939b) found that 45% of assimilated calories were unavailable to the organism for physiological purposes, and therefore

approximately 55% of assimilated food was "physiologically useful." Caloric intake was calculated by

$$\frac{\text{caloric intake}}{\text{hr}} = \frac{\text{g of food captured}}{\text{hr}} \times 750 \quad \text{cal/g} \times 0.85 \times 0.55.$$

To apply this hourly rate of caloric intake to a 24-hr day would introduce error for a number of reasons. For example, prey accessibility, abundance, and density are probably not uniform over an entire day. In the immediate vicinity of a predator, bass engage in activities other than feeding for a variable proportion of any given day, etc. Since the number of hours per day spent feeding at the experimentally determined hourly rates is not known, 12 and 6 hr/day were assumed. Figure 9, graph (d), shows the results of these two assumptions. It is important to note that the hours spent in feeding were selected arbitrarily and that regardless of time spent feeding, increases in cover density result in a more than linear decrease in energy captured.

The effects of cover or environmental complexity on an aquatic predator–prey system are several. From the preceding paragraphs, it is possible to conclude tentatively that cover dampens (stabilizes) predator–prey interaction by affecting the predator's energy cost per capture (see Table IV, column 5), reduces the rate at which prey are attacked and captured, and that these combined effects decrease the energy available for growth. This conclusion implies that not only are predator and prey survival influenced by cover density but that the rate of predator biomass production is related to cover density as well. For this reason, from the viewpoint of trophic ecology, it appears reasonable that cover will influence the sustained yield of predator biomass to other predators (including man). Hence, from the standpoint of a resource manager attempting to maximize both stability and production of a predator–prey system or an ecologist investigating the predation process, a study of the effects of cover and predator energetics deserves central consideration.

E. Summary

A computer model of the routine and active respiratory metabolism of the largemouth black bass (*Micropterus salmoides*) was developed using data from laboratory experiments. Sensitivity of a model of

routine metabolism to various perturbations in variate and parameter values was tested. The slope of the line relating log oxygen consumption to log weight was tentatively determined to be the most critical parameter in the model. The two components of respiratory metabolism in fish that were under study (routine and active metabolism) were combined into a more complete model used to describe some aspects of largemouth black bass energetics. The energetics model was then used to explore some implications and consequences of environmental complexity on the predation process. To do this, approximately 100,000 frames of movie film taken of feeding sessions were analyzed individually. By incorporating the energetics model into the computer analysis of film records, it was possible to discuss the energetic consequences of predation by largemouth black bass in environments with different cover densities. It was tentatively concluded that both prey survival and predator success would occur at levels of cover density intermediate between a completely unobstructed (no refuges for prey) environment and one in which cover density was high (370 units/m^2). The optimality of intermediate cover densities was found to be based upon energetic considerations. Although efficiency of energy utilization by the predator was found to be high in completely unobstructed environments, it is well known that simple laboratory environments result in prey extinction. Therefore, lack of cover was considered to be suboptimal for long-term predator survival. At high cover densities it was found that a reduction in energy utilization efficiency occurred. It was concluded that for long-term predator survival a balance between energy acquisition and energy dissipation could be achieved at intermediate levels of environmental complexity (cover density). One characteristic of an optimal environment for largemouth black bass was therefore deemed to be an intermediate or moderate cover density.

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PART III

THE ECOSYSTEM: SIMULATION

Webster's Unabridged does not inspire confidence in *simulation* as a prospective new tool of science. It's definitions are mainly pejorative: "act of assuming an appearance which is feigned, or not true; pretense or profession meant to deceive ... a counterfeit ... a fraud." John McLeod reacted unbelievingly with an article, "Simulation is wha-a-at?" (1968. "Simulation, the Dynamic Modeling of Ideas and Systems with Computers," p. 3. McGraw-Hill, New York). It is, of course, in modern usage, the dynamic modeling of ideas and systems with computers, and this section brings together a group of papers describing various aspects and philosophies of ecological simulation, with ecosystems the center of attention.

Chapter 6 provides a transition from Part II by starting with a general population model at the single-species level. Drs. Lassiter and Hayne believe that behavior of big systems can be mimicked by combining detailed submodels, and further, that mathematical parameters of the latter should be restricted to those which correspond to known or postulated biological processes. As Hubbell does, in Chapter 4, they recognize that feedback control may not be directly related to specific recognizable structures or physiological functions, but that regulation may come out of a dynamic interplay of processes when systems are complex enough. And ecosystems, they say, have the requisite complexity and dynamism.

Their model emphasizes the identity of the individual organism as mediator of all transactions in coupled ecosystems. The focus is on energy, particularly details of consumer energy budgets and their mechanisms of regulation. The equations are presented in finite difference form for digital computer implementation, neatly simplified by using a time step of unit length. The final result is a Fortran program and description of a number of simulation trials, providing a basis for discussion of population control in relation to the well-known Hairston, Smith and Slobodkin (1960. *Am. Natur.* **94**, 421) generalizations.

Chapter 7 considers a number of broadly encountered problems in ecosystem simulation. The framework is the cryptozoan subcommunity of the forest floor, a complex system embracing hundreds of populations and trophic interactions. Dr. O'Neill addresses the problems of simulating temporal fluctuations, quantifying energy and material flows, and compromising mathematical perfection to data imperfections.

Noting that constant coefficient models are inadequate to represent seasonal dynamics, a practical method of determining time-varying coefficients is described and applied to a millipede energetics example. Population simulation is illustrated with Collembola. Parameter estimation in complex food web models is approached through a conditional probability method related to Bayesian statistics. The method is applied to centipede and spider multiple-prey microcosms to determine dietary compositions. Interaction of radiotracer methodology and mathematical modeling in unraveling food webs is discussed. As an illustrative example, steps in the preparation of a digital computer model of radiocesium kinetics on the forest floor are described, with point-by-point discussion of difficulties as they arise. Finally, simulation runs are presented, illustrating the value of models, even inadequate ones, in concept formation and research planning.

Chapter 8, by Bledsoe and Van Dyne, poses the interesting question whether or not some of the newer methods of systems ecology might not be used in connection with some of

the older data and observations of traditional synecology. The notion is to seek new insights from past literature, and to preserve and extend the usefulness of semiquantitative and even qualitative data.

Two descriptive studies are recast in terms of simulation models, both on old-field succession, one in Oklahoma and the other in North Carolina. The methods and problems of making such conversions are systematically described, and example outputs from the models provided and discussed. Comments about appropriate uses of different kinds of hardware, both analog and digital, at different stages of model development are offered, and manpower requirements for such studies are also outlined. As to uses of such models, the authors suggest both sensitivity and perturbation analysis, stating that successional effects of fire, draught, erosion, pesticides, etc. can be given at least preliminary evaluation.While this paper may not bring the original idea to its ultimate utility, it does demonstrate clearly that qualitative information is not necessarily incompatible with modeling.

Chapter 9 is an analog computer study of three energy models of the plant–moose–wolf food chain on Isle Royale. Details of the programming are given, following the steps outlined in Chapter 1. All non-feeding flows are represented as constant fractional transfers from the donor compartments, and feeding flows only are varied in the three models, being linear, nonlinear "uncontrolled," and nonlinear "controlled," respectively.

Behavioral characteristics of the models are compared in terms of free and forced responses, steady states, and recovery from steady-state displacements. The uncontrolled nonlinear system was generally unstable. The controlled nonlinear model gave results similar to the linear one, with some improvement in realism based on considerable improvement of the biological rationale. Since little is gained operationally, however, Rykiel and Kuenzel suggest that linear models may be the more appropriate for studying general dynamic characteristics of ecological systems, particularly if the latter are in near-steady states where linear theory is known to apply.

Chapter 10 is a simulation study of Lindeman's classical investigations of Cedar Bog Lake. Probably no work of recent times has had the impact of this single effort, and a retrospective look at it through the developing eyes of systems ecology is thus quite instructive. Dr.Williams tries faithfully to preserve Lindeman's ideas in developing a hiearchy of models from the general to the specific. The data requirements of the models, however, quickly expose numerous gaps in the original information.

Four models are developed and explored. The first, a linear three-compartment cascade, failed to reproduce any of the significant behavior of the Cedar Bog Lake ecosystem when examined by an analog computer. The model was then expanded into a ten-compartment linear system with branching. Simulations of this and subsequent systems were performed with a digital computer, using a program that employs Euler integration. The model conformed generally to Lindeman's flow and standing crop data, but produced some unrealistic results due to dominance of the ooze compartment. The third model, a nonlinear "uncontrolled" version of the ten-compartment system, proved sluggish and unstable. Subsequent adjustments stabilized it and improved its responsiveness. The resultant "controlled" nonlinear system was then modified variously in efforts to produce a realistic simulation. One result was negating Lindeman's general hypothesis of increasing assimilation efficiency with increasing trophic level. However, Dr. Williams is quick to point out that this and other deficiencies revealed by the modeling study in no way detract from the original work, a milestone for its time. The value of modeling as an aid to structured thinking is thus underscored by its power to expose weaknesses in one of the best early examples of structured thought in ecological literature.

6

A Finite Difference Model for Simulation of Dynamic Processes in Ecosystems

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I. Introduction

This attempt to set up a rational model of an ecosystem has had two objectives. First, we wanted to examine the feasibility of such a task and identify the information needed; here we are encouraged by our results. Our second objective was to explore the results of changing parameters (within the model's limited ability). Here we have just begun.

There were two major questions when we started. First, can any finite model be realistic enough to be useful when any real ecosystem involves such great complexity and scope? Second, will we simply know enough within the near future to build a useful model? Clearly, much depends here on the point of view; although we disclaim any definitive answer to either question, we remain optimistic on both counts.

A. Point of View

Models are abstractions of real-world phenomena. They are used to frame concepts and organize knowledge to the end that the right questions may be asked. Some models are mathematical; these do not differ in any basic way from non-mathematical models. They are expressed in formal notation, tend to be more explicit, and proceed in natural sequence from the conceptual to the quantitative form.

In ecology, many of the modern conceptual models are inherently complex and difficult. Mathematical modeling may prove to be useful in several ways. First, it provides a means of systematic organization for what is known. The discipline of setting down a logical whole often forces attention to some relationship that hitherto has been ignored. If a model can be adequately quantified, then a test of the validity of general ideas may be possible. Systems analysis provides the basic ideas that may make possible the attack upon so complex an entity as an ecosystem. This is that the complex whole can be studied by modeling its separate parts and then combining these subsystems into the whole.

The nature of correspondences observed between the real system and the model is of fundamental concern to the ecologist. In the development of a mathematical model, when the biological rationale is discussed for a particular mathematical statement, in effect an isomorphism is being described (Hall and Fagan, 1956). The rationale amounts to a discussion of properties of the real system in relation to the mathematical expressions chosen. The fewer the constraints placed upon the model by the mathematics, the closer the situation is to an isomorphism, and the more realistic the results may be expected to be. It has been pointed out, however, that in practice, every model is a homomorphism (see Chapter 1). Simulation is the use of mathematical models to quantitatively reproduce some aspect of the real world. This model is used in simulation. The results, however, apply only very generally to the real world, for lack of many items of specific information required before simulation can be more specific.

As a guiding principle in developing the present model, we have, insofar as practical, admitted only algebraic components analogous to known or specifically postulated biological phenomena. To admit a mathematical function without any biological analog can often provide better curve fitting, but it explains nothing. On the other hand, if we construct a model analogous to the known or intelligently-postulated details of a system and find little correspondence to long-term system behavior, then we learn a significant fact: our hypothesis is too limited. We then must look elsewhere, and one way is to postulate a biological mechanism that may influence system behavior, introduce it as part of the simulated system, and try it. If it improves the results, then it may be worth studying in the real world. Such feedback between model simulation and the direction of field and laboratory research is the promise mathematical modeling can make in the advancement of ecological understanding. Such an approach is sound, however, only to the extent that the system model is built of components analogous to the real system as we comprehend it.

Differential equations have been most used in the development of ecological models, and computers have been employed (Garfinkel, 1962, 1967; Garfinkel and Sack, 1964; Patten, 1965; Wangersky and Cunningham, 1957; King and Paulik, 1967) as solutions have become more intractable. Solutions become more intractable as greater reality and resultant complexity are introduced. Thus, computer simulation, often meaning the solution of a set of simultaneous differential equations, has been employed of necessity in lieu of analytical solutions.

In the present work a recurrence or difference equation has been used as the basic population model. This approach is well suited to capabilities

of the digital computer, and when used with short computing intervals, it allows the statement of any action to reflect the influence of many other factors, all of which may be varying simultaneously from interval to interval. The characteristics of the method have been discussed in detail by Watt (1966, 1968). All results are conveniently available at the end of each computational interval. Because of the large number of biological parameters in any modestly realistic, multispecies model, and the very large number of computations, solution by computer is the only feasible approach.

B. The Ecological System

A definition of *system* that will be acceptable to ecologists may be similar to that used by Khailov (1967): A system is a collection of interacting objects together with their interactions. This definition omits the important concept of *holism* (Spanner, 1964; Watt, 1966). Spanner uses this idea alone in his definition of systems as "complex wholes." This means, too, that a system must be defined to include a meaningful set of objects.

In living systems as well as in others there are feedback control mechanisms, related to recognizable structures or physiological functions. But there is yet another type of regulation which von Bertalanffy (1956) has pointed out, namely those which result from a "dynamic interplay of processes." This type of regulation is possible only in systems which are sufficiently complex and dynamic to include great numbers of interactions. Conceptually, an ecosystem has the requisite complexity and dynamism, and therefore we should look for this type of regulation.

Khailov (1967) points out that systems are comprised of subsystems that are hierarchically subordinated. Subsystems may function suboptimally if that is the cost of whole-system optimization. An example of such "suboptimization" in ecology is found in the fact that populations of a community are restrained by competition for resources. Presumably the community system is optimized in the sense that there is maximum utilization of energy.

A system may be open or closed depending upon whether there is an exchange with outside systems. In constructing models of particular communities the simplification introduced by assuming a closed system, that is, no between-community interactions, makes this an attractive and practical approximation. There is, however, some exterior exchange of matter or energy for every ecosystem, hence, all ecosystems are open systems (Spanner, 1964; von Bertalanffy, 1956; Botnariuc, 1966).

The statement of King and Paulik (1967) that ecosystems are "highly organized closed structures" presumably referred to the idea expressed by Slobodkin (1964) that the biotic community is characterized by a particular set of ecological interactions, i.e., that the biological processes occurring within the ecosystem are the significant ones.

The mathematical model in this chapter attempts to specify, and thereby provide a means for quantifying, some generally held ecological concepts about the dynamics of natural communities. The mutual interactions of the biotic populations, as influenced by abiotic factors, have guided the construction of the model. The biotic community is the main subsystem of interest, but it cannot be considered separately from the abiotic influences. The model contains some parameters which have been measured for some populations, and other parameters which have never been measured because, to our knowledge, they have not been proposed in a model.

Ecosystem processes are best understood if the identity of the individual organism is maintained. Energy budgets and changes in body energy stores must be calculated for the individual. The unit of predator-imposed mortality is the individual predator. Population interactions take place between individuals, although ordinarily the interactions of individuals within populations are distinguished from those between populations. On the other hand, some of the important measures of population dynamics are best understood as populational rather than individual phenomena; an individual lives or dies, but a death rate or a statement of probability of death is a population parameter. Further, it is often convenient to treat population biomass as an entity, growing or furnishing food to some other population.

Energy flow in biotic communities has come traditionally to be considered a process of trophic level transfer. But energy transfer and biomass changes result when individual consumers eat individual prey. To account the transfer one must identify the species, but need not explicitly name the trophic level. Thus the vexing problem of overlapping and indeterminate trophic levels does not arise in this model. Energy is transferred between individuals; the population flux is a matter of summation.

The absolute upper bound of energy transfer is set by availability. But when food is abundant, the operational upper bound is set by the energy needs of the individual organism. This point, widely appreciated by ecologists, has not generally been introduced into mathematical models. The present model considers the effect of satiation, as well as those of malnutrition and starvation, in computing individual energy budgets.

II. General Population Model

The form of the model will be stated in this section, then the parts will be examined in greater detail. Much of the paper is discussion of individual factors, biotic and abiotic.

A. The Equation of Population Dynamics

The familiar recurrence or difference relationship was used to represent population change. Thus, the population at time t is determined by (1) the population at time $t - 1$, and (2) the population rate of change during the interval $(t - 1, t)$. With time of unit value, certain familiar equations may be used without explicit statement of the variable Δt. The basic equation describes changes in a single population in response to all the biotic and abiotic factors allowed to interact. Thus, the basic building block is the sum total of interactions by the individuals of one species with the ecosystem, including members of the same or different species. The model of a community is built up from a set of these submodels, one for each species.

The form of the population model follows the Malthusian equation of change in population size proportional to size of the population

$$dN_i/dt = r_i N_i \,, \tag{1}$$

with

$$r_i = b_i' - d_i',$$

where

$$b_i' = b_i \left(\prod_{h=1}^{l} \varphi_{ih} \right)$$

and

$$d_i' = \sum_{k=1}^{m} \delta_{ik} \,,$$

so that

$$dN_i/dt = \left\{ b_i \left(\prod_{h=1}^{l} \varphi_{ih} \right) - \sum_{k=1}^{m} \delta_{ik} \right\} N_i \,. \tag{2}$$

N_i is number of individuals of the ith species; b_i is physiologically maximum instantaneous rate of population increase, or birth rate for animals; b_i' is adjusted or "ecological" instantaneous rate of population increase; φ_{ih} is the hth modifying factor, out of l such factors, for the rate of increase b_i for the ith species (always $0 \leqslant \varphi_{ih} \leqslant 1$); d_i' is the

instantaneous rate of total mortality for the ith species, or death rate; and δ_{ik} is the instantaneous rate of the kth mortality factor, out of m such factors, for the ith species. Any influence on population change is limited to an effect on the birth or death rates. Thus, the population rate of change is the difference, the rate of increase minus the rate of decrease, with the direction of change denoted by the sign of the difference.

Both rates of increase and decrease are modified through biotic and abiotic influences, as discussed later. The rate of increase starts with some maximum value b_i and is modified toward zero by various influences including crowding, energy deficit, and deviations of abiotic factors from optimum values. The rate of mortality starts at zero and is modified upward without limit through addition of instantaneous rates of mortality δ_{ik} from different causes. These include a value, constant for each species, that may represent here such unspecified mortality as that from disease or fighting. This mode of expressing the influence of environmental factors allows action of limiting factors, any one of which may, of itself, suppress increase or generate high mortality.

The working model is the integrated difference of Eq. (2), or

$$N_{i(t)} = N_{i(t-1)} \left\{ \exp \left[b_i \left(\prod_{h=1}^{l} \varphi_{ih} \right) - \sum_{k=1}^{m} \delta_{ik} \right] \right\}, \tag{3}$$

where none of the l birth-modifying factors or m death rates is made an explicit mathematical function of N. As will be pointed out, if any of the modifying factors or death rates is a function of N it is not always easy to use an integrated difference form.

In using this model, several approximations have been introduced in concession to both practicality and realism in simulation. A closed system is assumed, with two major exceptions. Unlimited energy is allowed as available to producers, and movement into the population is assumed to balance movement outward except for the case where action of mortality in one interval may reduce the population number to less than unity. Here the next interval is arbitrarily started with a single individual, simulating, in a sense, a continuous low-level exchange with surrounding populations. From interval to interval, the population number of each species is calculated, with species biomass following as the product of number and average weight. The average weight is accounted separately using a constant basic body weight of non-fat components and a fat weight varying by interval in response to the energy balance of the animal (for plants, a constant fat weight is used). Newly created individuals, animal or plant, are immediately accounted as of average size, with the energy expenditure of reproduction taken to

include any extra costs of growing the new tissue. The increase from reproduction (including growth of plants) is calculated each interval from the number of individuals and the modified rate of increase with no consideration of any distribution of individuals by age or sex. Seasonal patterns are imposed on both increase and mortality through effects of a seasonally fluctuating abiotic factor that simulates the combined effects of climatic factors. For the convenience of being able to divide a year into equal parts of several different magnitudes, a 360 computing-interval span is used, with 12 equal months (Fig. 1).

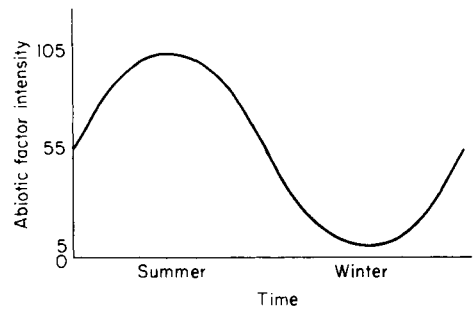


FIG. 1. Scaled and translated sine wave utilized as abiotic factor representing annual climatic changes.

This form provides for population change as a function of factors operative within the system. Regardless of what happens in the environment, only those influences that in some way affect the birth or death rates are allowed for here. Such influences are of two kinds, biotic and abiotic.

B. COMPUTER ROUTINE FOR POPULATION DYNAMICS

The Fortran IV computer program, ECOSYS, is presented in Appendix D together with a flow diagram of the subroutine sequence. The subroutine which is the counterpart of the species population model is ACTION. When this routine is to be entered, the factors which reduce birth rate or which add mortality rates have all been computed. These are used in computations analogous to Eq. (2). In Appendix A the symbols used in the computer program are matched with text symbols and defined, and in Appendix B the items required as input are listed, along with a typical set of values.

III. Biotic Factors

Biotic factors are considered here as crowding or competition effects, or as energy relationships; this distinction is only for purposes of discussion.

A. Crowding and Competition

The notion of crowding implies some resource in short supply. Often this is space, but the supply of energy is also finite. Other items are in limited supply; all may be grouped as resources for which there may be competition. Crowding and competition imply existence of some density-dependent factor.

The best known expression for a density-dependent modification of growth is the following statement of the logistic relationship

$$dN/dt = rN(1 - NK^{-1}), \tag{4}$$

where K is maximum possible population size. Andrewartha and Birch (1954) have interpreted this model biologically. Each individual organism, of which there are N, requires $1/K$ of the available ecological space. When $N = K$ individuals all the ecological space is used up, there is a zero rate of change, and a steady state results. The density-dependent factor is $(1 - NK^{-1})$; this becomes more restrictive of growth rate at higher population densities. The integrated form, as given for example by Andrewartha and Birch (1954), is

$$N = K[1 + \exp(a - rt)]^{-1}, \tag{5}$$

where $a = \ln(KN^{-1} - 1)$ when $t = 0$ and all other symbols are as previously defined.

A difference form is readily obtainable as well. Rewriting the differential form as

$$dN[N(1 - NK^{-1})]^{-1} = r\,dt \tag{6}$$

and integrating over the interval $(t - 1, t)$, we obtain

$$N_t = N_{t-1} \exp(r)\, K \{K - N_{t-1}[1 - \exp(r)]\}^{-1}. \tag{7}$$

This expression contains only r in the exponent and involves a density-dependent factor. This form would allow the influence of current environmental factors through changes in the upper asympote K, or in the maximum rate of increase r, or in both, but this manipulation is

more complex in concept and less easily handled in the difference form than in Eq. (3) which has the basic form

$$N_t = N_{t-1} \exp(b' - d'), \tag{8}$$

where exponents b' and d' are modified birth and death rates.

The simplicity of Eq. (3) makes it especially useful for computer simulation. The modifying factors for birth rate [φ_{ij} of Eq. (3)] and the mortality rates [δ_{ik} of Eq. (3)] may be changed as desired and readily inserted into the model. In comparison, while the difference form of the logistic [Eq. (7)] can be handled well enough with the single generalized factor r, it becomes difficult when generalized to l factors (only part of which are density-dependent) modifying birth rate and to m death rates (where also only some are density-dependent). But ease of use is not sufficient justification if Eq. (3) departs too far from reality. For density-dependent factors, the form of Eq. (3) may not strictly be applicable because the integration has not taken into account that adjusted birth and death rates b' and d' are functions of N. This question requires examination.

Cook (1965) has noted that if the logistic equation applies on a per generation basis, with the interval $(t - 1, t)$ representing one generation, and if "adult numbers in any generation are determined by the number of adults in the previous generation," the difference form may be written

$$N_t = N_{t-1} \exp[r(1 - N_{t-1}K^{-1})]. \tag{9}$$

A generation is too long an interval to be of use in simulation here, but the form of the equation is ideal. For a given value of r, the population size increases faster by this form because it is always one time interval behind in applying the density-dependent modifying factor whereas the difference form of the logistic adjusts continuously to the current population level. But the shorter the interval the closer the approximation. Further, it seems unlikely that populations instantaneously and with perfect precision adjust birth rates to accommodate to population size. When the lag period is actually known it can be used instead of a single interval.

The logistic form was not used here directly because of the need to separate the effect of density-independent and density-dependent factors. This model uses a logistic-like form as one of several modifiers of birth rate and uses a different method to treat mortality as a function of population size.

Most users of the logistic have held to a basic interpretation that the

rate of increase r is modified by the density-dependent factor $(1 - NK^{-1})$, with population growth rate going to zero as N approaches K. Now, r is ordinarily accepted as made up of two rates, b and d, so that the logistic may be written

$$\begin{aligned} dN/dt &= (b - d)\,N(1 - NK^{-1}) \\ &= bN(1 - NK^{-1}) - dN(1 - NK^{-1}). \end{aligned} \tag{10}$$

The latter form suggests that both birth and death rates are affected identically by the density-dependent factor. This implication may be questioned; it is not readily to be understood on a biological basis. One expects rather to find two types of response, a reduction of birth rate and an increase of death rate. In the literature on density-dependence, use of the logistic has been more general and directed toward describing the result that a larger population increases more slowly.

This model incorporates a direct density-dependent mechanism in the form

$$N_t = N_{t-1} \exp[b'(1 - N_{t-1}K^{-1}) - d'], \tag{11}$$

where b' and d' are as defined in Eq. (2). The density-dependent factor is stated explicitly here, but functions as one of a series of φ values [Eq. (2)], reducing the population birth rate in proportion to the fraction of the space taken up. In the computer program the operation of the density-dependent restraint on birth rate is optional for each species. Mortality rates are not made directly a function of population size, but indirectly so by increasing mortality when food is limited (discussed later).

Consider competition for all resources together. For a model in the present level of detail, it is immaterial what behavior causes competition for what resources. It is required, however, that at any time the total amount of resource can be specified and that the amount of resource needed by an individual be known. These values need not remain constant for longer than the basic computational interval. This view of "known" leaves open the possibility of further detailed modeling, for if the functional form of the requirement for a resource be found, it can be incorporated.

Let space, however, be used as the example of a resource for which there is competition. This may be root space for plants or territory for animals. If there are n species of organisms in a biological community and an individual of the jth species takes up an amount of space a_{ij} which an individual of the ith species cannot simultaneously utilize, we may construct a matrix $A_{n\times n}$ of these requirements. This matrix,

consisting of n^2 elements, is similar in appearance to the predation matrix discussed later, in that the effect of each species on every other is represented and may be addressed by its row–column index. Let row i represent the competitor species and column j represent the species being crowded, for which the competition effect is being calculated.

Thus far the elements have either negative or zero values. For example, in a very small community of three species, the competition matrix may be represented as

$$A = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}. \tag{12}$$

In this matrix, a_{ij} for $i = j$ is the amount of space required by an individual of a species for which contemporaries of the same species are in competition. This would be equal to unity as used in the logistic, but space might also be specified as units of space or volume uniquely occupied by an individual. Now, a_{ij} for $i \neq j$ is analogous to the "coefficient of competition" of Gause (1934). In general a_{ij} does not necessarily equal a_{ji} and, except where each is near zero, we may expect equality only rarely. Values near zero may be expected often for space, especially with animals, because territoriality is so often intraspecific.

As an example, consider the competition matrix for a community in which there are two competing plant species and three animal species that compete for space only intraspecifically. The competition matrix would appear as follows, where the plant species are indexed 1 and 2, and the animals are 3, 4, and 5

$$A = \begin{bmatrix} a_{11} & a_{12} & 0 & 0 & 0 \\ a_{12} & a_{22} & 0 & 0 & 0 \\ 0 & 0 & a_{33} & 0 & 0 \\ 0 & 0 & 0 & a_{44} & 0 \\ 0 & 0 & 0 & 0 & a_{55} \end{bmatrix}. \tag{13}$$

There is some amount of space available to each species, the same amount for each if we merely consider physical area. But there are more interesting meanings for available space. Say that the amount of available space could be different for each species. Then we could represent the community space as a vector for the n species

$$\mathbf{K} = [K_1, K_2, \ldots, K_n], \tag{14}$$

where **K** is the community space vector. For one species j, the modifying factor for the effect upon birth rate of crowding by all n species is

$$\varphi_{aj} = \begin{cases} \left(K_j + \sum_{i=1}^{n} a_{ij}N_i\right) K_j^{-1} & \text{for } \left|\sum_{i=1}^{n} a_{ij}N_i\right| \leqslant K_j \\ 0 & \text{otherwise.} \end{cases} \tag{15}$$

The sign change in the numerator reflects the negative a_{ij} values.

The presence of a species may be beneficial to another, and may even be required for survival, referring to space, not food, and carrying the discussion beyond the present program. This would be the inverse view of competition with the a_{ij} values, the "coefficients of competition," carrying positive signs in contrast to the negative signs thus far associated with all nonzero values. Volterra (1928) proposed an analogous formulation with what he called "the true coefficients of increase." His general statement of population rate of change for species j, in the presence of n species, becomes

$$dN_j/dt = \left(r_j - \sum_{i=1}^{n} p_{ij}N_i\right) N_j , \tag{16}$$

where Volterra's p_{ij} "are any constant whatever" and the rest of the symbols match those defined here. Volterra's form does not, however, discriminate the effect on birth and death rates.

This generalization of the competition matrix [Eq. (13)] to accept positive coefficients to indicate symbiosis would allow for all possibilities of interaction between two species with respect to a resource. These might then be for the ith and jth species any element of the set of relationships

$$\{(+, +),\ (+, 0),\ (+, -),\ (0, +),\ (0, 0),\ (0, -),\ (-, +),\ (-, 0),\ (-, -)\}.$$

This representation resembles that of Odum (1959, p. 226) but differs in that predation is excluded here.

If symbiosis were to be included in the model, Eq. (15) would have to be modified. The amount of the resource available to species j would, in effect, be increased due to the symbiotic species. One adjustment could be that in K_j' (next page), only positive values for a_{ij} be added to K_j, the measure of space present otherwise, changing Eq. (15) to

$$\varphi_{aj} = \left(K_j + \sum_{i=1}^{n} a_{ij}N_i\right) K_j'^{-1}, \tag{17}$$

where

$$K_j' = K_j + \sum_{i=1}^{n} a_{ij}N_i \qquad \text{for all} \quad a_{ij} > 0.$$

Note that K_j is not necessarily zero, but represents space available otherwise.

Ecological succession may be viewed as a long term result of symbiotic relationships. In the succession of an old field to a forest, there are many unidirectional changes (Daubenmire, 1947). The dry, sunny habitat is converted to a moist, shady condition, with species change both cause and effect of the shift in local climate. It is not inconceivable that succession may one day be modeled, and a competition matrix like Eq. (17) might be useful to represent some phases of the process. But the present model is far from such a capability.

B. Energy Dynamics

Analysis of how the biota uses available energy is basic to contemporary ecology. The ideas of Lindeman (1942) have stimulated much research on the energetics of species and communities, with some general work. But the trend has been toward studies of mass results, assuming a steady state, without much concern with mechanisms. For simulation, at least the results of mechanisms must be described, whether understood or not in detail.

In this model, energy influences a population only by changing rates of increase and death. But consideration of how this may happen quickly expands the inquiry to include questions of the sources, use, and storage of acquired energy, the kinds of energy expenditures, the natural controls exercised over rates of energy capture, consumption, utilization and storage, and the mortality imposed upon the prey species through food acquisition by the predator. Figure 2 presents a simplified view of this physioecological system.

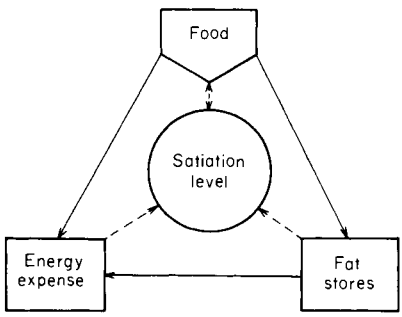


Fig. 2. Schematic representation of the control system for energy intake, storage, and expenditure. Solid lines indicate physical or chemical transfer; broken lines indicate physiological influence.

We will consider energy relationships in the sequence indicated below; this also presents the postulates upon which the conceptual model is built.

(1) Energy requirements of producers are assumed to be met in excess by the sun. Energy requirements of consumers are met by ingested food, with a constant fraction of stored fat mobilized in each interval, and in starvation by catabolism of body proteins. Excess energy is stored as fat.

(2) The effect of an altered energy supply comes about through modified rates of increase and death. For producers, no energy fluctuation is postulated. For consumers, when energy (food or stored fat) is abundant, then population changes are controlled by other factors. When energy is scarce birth rate may be depressed and death rate increased. For the population these changes commence before the average individual reaches energy deficiency.

(3) The energy expenditure budget of the individual consumer organism is quantified here with a basic component related to body size, plus a set of expenditures proportional to the deviations of abiotic factors from optimum levels, plus the costs of reproduction and growth, plus the costs of activity (for food gathering and escape from predators).

(4) Control of food intake, and thus of rates of predation, is by satiation, brought about through the glucostatic and lipostatic mechanisms.

(5) Predation has the dual aspect of food gathering by the predator, and mortality for the prey. Rate of prey capture by the individual predator is controlled by the numbers and vulnerability of the prey species, and under appropriate conditions by development of satiation. The prey mortality rate is the summation of instantaneous rates of mortality to all the predators on the species.

Presenting the problem this way will sometimes introduce a mathematical formulation ahead of its biological justification. We hope that the occasional awkward transition may be tolerated in the interest of maintaining continuity of biological thought.

C. Energy Intake

Producer organisms receive energy from the sun, and store it as new tissue. While the energy supply is considered unlimited, the rate of growth and storage of energy in tissue is made subject to modification by abiotic factors, by the grazing (predatory) action of consumers, and by the density-dependent limitations imposed by space. As a result,

the plants store energy in a varying tissue biomass that has a constant proportional composition of digestible carbohydrate, fat, protein, and bulk residue.

For consumer organisms, the energy content of ingested food becomes available through digestion, then the energy is used, with any excess stored in tissues. If there is a deficit of energy, there will be a drain on tissue stores. In the model it is assumed that all food ingested during an interval is disposed of physiologically during the same interval, that is, either digested or excreted, and if digested, either used or stored. Therefore, it is reasonable that an interval correspond to a feeding cycle. It would require a more elaborate accounting system to provide for lags in use of energy, or to describe better the case of the continuously feeding organism.

Assume that digestion is proportional to time within the computational interval, and set d_1 as the instantaneous rate of digestion for unit time. A constant proportion of food ingested will be digested. Then with f_t representing the amount of food taken in by an individual during the interval, we may state the amount digested as

$$f_t[1 - \exp(-d_1)],$$

with the amount excreted being

$$f_t \exp(-d_1).$$

The energy content of food depends upon amount ingested and proportions of carbohydrate, fat, and protein. The diet composition is calculated from the known body composition of the species eaten, and from the amounts eaten of each. Where plants are eaten, the proportions of dietary elements remain constant for any one species. Where animals are eaten, the proportion of fat in the prey changes with its energy status, with consequent changes of fat content in the diet of the predator. A running account of all fat stores is maintained and the fat content of each predator's ration of food is determined for each computing interval.

For each time interval, let a set of three partial digestion rates be calculated as a product of the overall rate d_1 and the proportional composition in the diet of the three nutritional elements. These partial rates will be d_{11} , d_{12} , d_{13} with the second subscript designating, in order, carbohydrate, fat, and protein, respectively, and with

$$d_1 = d_{11} + d_{12} + d_{13}. \tag{18}$$

The amount of each of the three elements available to the animal in digested form will be the corresponding fraction of the total digested; with carbohydrate, for example,

$$d_{11}d_1^{-1}f_t[1 - \exp(-d_1)].$$

For convenience we may identify the average amount of undigested food during the interval as

$$\bar{f} = d_1^{-1}f_t[1 - \exp(-d_1)]. \tag{19}$$

Further, our primary interest being in the energy contributed by digested food, let q_1, q_2, and q_3 represent the respective unit caloric equivalents of digested carbohydrate, fat, and protein. Then the separate sources of energy from digested food become

$$\begin{aligned} \text{from carbohydrate} &= q_1 d_{11}\bar{f} \\ \text{from fat} &= q_2 d_{12}\bar{f} \\ \text{from protein} &= q_3 d_{13}\bar{f}. \end{aligned}$$

It seems to be accepted that animals preferentially catabolize carbohydrate over fat, and fat over protein (Guyton, 1966). This hierarchy utilizes carbohydrates when available, catabolizes some fat if not enough carbohydrate is available, and by the complementary mechanism, anabolizes the carbohydrate into fat when the energy available from carbohydrate exceeds the amount expended. Further, there is the energy from fat mobilized from storage.

The model assumes that a fixed proportion of the body fat store is mobilized in a unit time. Bates *et al.* (1955), studying various strains of mice, found that an amount of fat proportional to the amount present was mobilized daily. This occurred under experimental conditions where need remained constant, while recording a weight gain up to 70% due to increased size of fat depots. Apparently this mobilized fat is available as raw material to the lipolytic process which itself proceeds at a rate dictated by energy expenditure.

Using the idea of a constant proportion d_2 of the initial fat store F_{t-1}, being mobilized during the interval, the total amount of energy in fat available from ingested food and body stores becomes

$$q_2(d_{12}\bar{f} + d_2F_{t-1}),$$

and the total amount of energy available E_l may be written as

$$E_l = (q_1 d_{11} + q_2 d_{12} + q_3 d_{13}) \hat{f} + q_2 d_2 F_{t-1}, \tag{20}$$

assuming that all fat ingested in an interval will be available in the same interval.

The energy balance of an animal is reflected in changes in the body stores of fat. As the model is developed here,

$$F_t = \begin{cases} F_{t-1}(1 - d_2) + (E_l - E_w)\, q_2^{-1} & \text{for } E_l \geqslant E_w \\ F_{t-1}(1 - d_2) & \text{for } E_l < E_w, \end{cases} \tag{21}$$

where F_l is fat store at the end of the interval; F_{t-1} is fat store at the beginning of the interval; d_2 is the proportion of fat store mobilized during the interval; E_l is available energy, as in Eq. (20); E_w is required energy; and q_2 is energy equivalent per unit of fat. Fat stores are reduced unless the available energy exceeds the demand by enough to repay into storage the amount of fat mobilized. Any excess over this requirement increases the fat stores.

Starvation is defined here as the state when the demand for energy exceeds the total amount available; the deficit can be met only by destruction of protein. In the model, mortality is increased when starvaiton occurs. There is also a state of less severe undernutrition where the animal must draw upon its fat stores to exist; this lies between the starvation level, where demand exceeds supply, and the level where supply exceeds demand by just enough to maintain the body stores. In the model, this intermediate state is accompanied by a reduction of birth rate.

This model of energy intake, use, and storage uses approximations that will require more exact treatment in more sophisticated application. While the destruction of body protein is assumed with starvation, there is no allowance for a corresponding reduction in body protein weight. There is no explicit allowance for an energy cost of storing fat beyond the energy content of the tissue, though the energy needs for growing new animals are included under the energy expenditures for reproduction.

There is no specific model here for protein metabolism. There seems to be neither need, nor adequate information, to warrant its construction. Proteins may play a role in food intake; amino acid imbalance and excessively high proportions of protein in the diet are cited in situations where proteins affect food intake (Krauss and Mayer, 1963). These authors found that protein in the diet may affect food intake indepen-

dently of the homeostatic satiety mechanism, to prevent the excessive intake of protein.

The energy equivalents used in this work (q_1 , q_2 , q_3) are those given by Hawk *et al.* (1954) as 4.1 kcal/g for carbohydrates and proteins, and 9.3 kcal/g for fat. Other values for particular species may be obtained in Golley (1961), Slobodkin and Richman (1961), Watt and Merrill (1963), and Cummins (1967), among other sources. In computation, the energy derived from protein is combined with that from carbohydrate.

D. Effects of Energy Deficit

When the food supply is inadequate, an animal has increasing difficulty in maintaining physiological integrity. In the model, food shortage affects the birth rate or the death rate; any other impairment is an intermediate step toward one of these two results that in turn affect population size.

The reduction of birth rate is assumed to start when the individual commences to draw upon body reserves for energy, and increased mortality to commence at the point of further deprivation where starvation begins. But the population effect cannot be reasoned directly from the status of the average individual. When the average energy balance is at some threshold value, the population rates of birth and death will already have been affected, and perhaps to some important degree, because about half of the individuals will be experiencing greater than average deprivation. To calculate properly an effective rate for the population would require information not available, that is, knowledge of both distribution of energy status throughout the population, as well as the functional relationship between energy deficit and biological result. Not knowing this, we use an approximation, based upon the observation that the closer the population approaches the stressed condition (from the unstressed) the more individuals will be under stress. A constant value L between zero and unity, subtracted from the ratio of energy supply to energy needs will have the effect of calculating the average individual to be in somewhat greater stress than it is, a correction in the right direction to make an allowance for that part of the population in worse condition than the average.

That the birth rate is lower and the survival of young less when food is scarce has been reported often. Lack (1954) has summarized some of the information for birds and mammals; Slobodkin (1964) described the effect of starvation upon reproduction in *Daphnia*. But no general statement has been found relating birth rate to available energy; some such statement is required in a model.

We shall hypothesize that the birth rate of an individual begins to decrease when the energy in the food ration is no longer adequate to meet the energy demands, and that the birth rate becomes zero when none of the energy demands are met in the food. The effect is introduced into the model as one of the modifying factors φ for birth rate, with the inclusion of the constant L_φ inserted to reduce the population birth rate below the maximum as a result of undernutrition, at a time before the average individual is undernourished

$$\varphi_b = \begin{cases} \varphi_b' - L_\varphi & \text{for } L_\varphi < \varphi_b' \leqslant 1 + L_\varphi \\ 0 & \text{for } L_\varphi \geqslant \varphi_b' \\ 1 & \text{otherwise,} \end{cases} \tag{22}$$

where L_φ is a constant, $0 \leqslant L_\varphi < 1$ (in the model, $L = 0.10$) and

$$\varphi_b' = (q_1 d_{11} + q_2 d_{12} + q_3 d_{13}) \bar{f} E_w^{-1}.$$

Increase in mortality rate due to starvation reflects a more severe deprivation than reduction of birth rate. In the model increased mortality begins with starvation, at the point where the needs are not met by the energy taken in as food plus that mobilized from body fat. Here destruction of protein begins; an organism can tolerate some loss of protein but the probability of death increases as proteolysis continues. The severity of the stress is in some fashion inversely related to the proportion of the energy demand met by available energy. Designating this proportion as I, then

$$I = [(q_1 d_{11} + q_2 d_{12} + q_3 d_{13}) \bar{f} + q_2 d_2 F_{t-1}] E_w^{-1}. \tag{23}$$

The inverse relationship may be represented as

$$d\delta_s/dI = MI^{-1}, \tag{24}$$

where δ_s is instantaneous rate of mortality due to starvation and M is a constant. Integrating, we obtain

$$\delta_s = M \ln I + C, \tag{25}$$

and since $\delta_s = 0$ when $I = 1$, $C = 0$. In practice, the value of I, no matter how small, must exceed zero; and here, though not below, $\delta_s = 0$ for $I \geqslant 1$.

There is still the need to start increasing the population death rate while the average individual is not yet starving by subtracting a constant, L_δ from the ratio I. This constant L_δ serves a populational function similar to L_φ which reduces birth rate, though the two constants are not

necessarily equal; in fact, in the model, L_δ has the value 0.25. The model for mortality due to starvation becomes

$$\delta_S = \begin{cases} M \ln (I - L_\delta) & \text{for } L_\delta < I < 1 + L_\delta \\ M \ln I & \text{for } L_\delta \geqslant I \\ 0 & \text{elsewhere.} \end{cases} \tag{26}$$

The form of this model results in a time lag from the development of a food shortage in one interval to its effect on the population in the next interval. This lag offers a means for describing naturally occurring lags (Wangersky and Cunningham, 1957; Slobodkin, 1964); it could be increased if biological information warranted.

E. The Energy Expense Budget

Energy expenditures for an interval are calculated here as the sum of the separate items of the energy budget for an individual. The items accounted are cost of body maintenance as a function of body size, the energy drain imposed by action of abiotic factors, the costs of reproduction (and growth of young), and the energy demands of activity. No doubt other categories of energy expenditure exist, but it is likely that this model accounts for the major energy losses.

Studies in ecological energetics have usually been based on mass energy exchange over long intervals of time, with the budget of the individual set aside in favor of the large goals. McNab (1963), in contrast, has constructed an energy budget model for a wild mouse. In simplest form his model is a function of time, environmental temperature, and rate of metabolism; the term for metabolism includes several environmental factors. Porter and Gates (1969) have considered thermodynamic equilibrium in several species.

The possibility of interactions among energy-demanding activities presents questions that cannot be resolved without detailed biological study. There may be differential responses to changes in one factor at different levels of another, and with study algebraic functions may be found to describe these interactions. On the other hand, we anticipate that in magnitude the interaction expenditures are probably less important than direct effects. Thus for the initial model a simple algebraic summation is accepted for the components of energy expense after each is computed; this does not mean that any component is necessarily a linear function.

The commonly accepted relationship between energy use and weight of an animal is used here for energy needed for body maintenance

$$E_{1k} = u_{1k} W_k^{v_k}, \tag{27}$$

where E_{1k} is the energy expended which may be accounted for by body size for species k, and u_{1k} and v_k are constants, characteristic of the relationship for species k. Metabolism under standard basal conditions specifies the maintenance requirement for energy, to which other needs must be added. In the model the exponent v is given the generally used value of $\frac{2}{3}$ (Englemann, 1966, for example) even though there is biological evidence against the universal value (Prosser and Brown, 1961).

Departure of an abiotic factor from the optimum environmental value may require energy expenditure from an organism. Such abiotic factors include temperature, light, day length, precipitation, and humidity; in the model two abiotic factors are provided. It is assumed that the basal energy requirements E_{1k} have been determined for species k in the optimum zone for each abiotic factor, i.e., where energy expenditure due to the particular factor is at a minimum. Any departure from the optimum zone increases the energy need; here it is assumed that the energy consumption increases by the same amount per unit deviation regardless of direction. Hence the model

$$E_{2k} = \sum_{x=1}^{f} u_{2kx}\, \Delta_{kx}\,, \tag{28}$$

where

$$\Delta_{kx} = \begin{cases} \text{zero} & \text{for } O_{kx1} \leqslant \mathscr{F}_x \leqslant O_{kx2} \\ O_{kx1} - \mathscr{F}_x & \text{for } \mathscr{F}_x < O_{kx1} \\ \mathscr{F}_x - O_{kx2} & \text{for } \mathscr{F}_x > O_{kx2}\,. \end{cases}$$

E_{2k} is total energy demand due to f abiotic factors acting on species k; $\mathscr{F}_x$ is the current level of abiotic factor x; O_{kx1}, and O_{kx2} are bounds of the optimum zone for abiotic factor x with respect to energy expenditure by species k (subscript 1 indicates lower bound, subscript 2 upper bound); and u_{2kx} is a proportionality constant, the increase in energy requirement (kilocalories) per unit deviation of factor x from the optimum zone for species k.

Population increase demands large quantities of energy. Here this reproductive function includes the cost of growing the new individual of average size as well as the usual charges for gamete production, courtship, and care of the young. The cost of growth must include the work of elaborating the new tissues as well as the energy content of those tissues. We have provided for both costs by calculating the energy expenditures to be 1.5 times the energy content of the tissues produced. This factor falls within the range of values given by Needham (1964) for a number of species. We assume that energy is expended in proportion to the

number of new individuals produced per unit time, or, on the per-individual basis, proportional to the current value of the modified rate of birth b'. Thus, the amount of energy expended in reproduction is

$$E_{3k} = u_{3k} b_k' Q_k , \tag{29}$$

where E_{3k} is energy required for birth and growth of young by an individual of species k, u_{3k} is energy cost per new individual as a ratio to average energy content (value used here is 1.5), b_k' is modified birth rate for species k, and Q_k is average energy content of an individual of species k.

The final category of the energy budget model for animals is that of activity. Activity may be directed in many ways; the two considered here are food gathering and escape from predators.

Regarding food gathering, we may observe that (1) the more available the food, the less effort required to obtain it, and (2) the more food needed, the more effort required to obtain it. Thus, an expression proportional to need and inversely proportional to availability is suggested. The measure of food requirement is satiation level, to be given in Eq. (40). The measure of availability is the potential food ration, to be given in Eq. (50). Combining the two expressions as suggested

$$E_{4k} = u_{4k} S_k R_k^{-1}, \qquad \text{always} \quad E_{4k} \leqslant 2E_{1k} , \tag{30}$$

where E_{4k} is energy expended for food gathering in the interval by an individual of species k, E_{1k} is energy expenditure accountable to body size, or basal rate [Eq. (27)], S_k is amount of food required to produce satiation for an individual of species k in this interval, R_k is maximum amount of food that an individual of species k could gather during this interval, or potential food ration, and u_{4k} is energy needed to gather the amount of food required to just reach the satiation level for species k, under conditions where exactly this amount can be captured during the interval. Note that the fraction $S_k R_k^{-1}$ has a value of 1 when the food for satiation just equals that which can be captured during the period. Values for the fraction greater than unity will result here when food is relatively scarce, implying that under such conditions the expenditure of energy can be greater than for a full day of hunting (but with a limit here of twice basal metabolism). The implicit concept of hunting efficiency is unsupported; factual information on predator behavior and physiology is needed. Two reported values for the energy spent in food gathering probably set reasonable bounds for most species; Pearson (1954) showed that something less than one-third of the energy budget

is spent in food gathering by the hummingbird, while Lucas (1963) reported that a steer spends about 5% of its daily budget in grazing.

To develop a model for energy expended in escaping from predators, let us use the assumption that a prey species spends energy in an amount proportional to the energy that all predators spend in capturing that prey species. It will be shown later that the number of prey taken by an individual predator of species i from n prey populations is

$$\sum_{j=1}^{n} c_{ij}\bar{N}_j ,$$

with the amount taken by this predator from the kth prey population being

$$c_{ik}\bar{N}_k ,$$

where $\bar{N}_j$ is mean number of individuals of prey population j present during the interval, and c_{ij} is adjusted predation rate of predator i upon prey j. The proportion of the total amount of food taken by predator i that comes from the kth prey population is

$$c_{ik}\bar{N}_k \left(\sum_{j=1}^{n} c_{ij}\bar{N}_j\right)^{-1}.$$

Now, in order to find the amount of energy spent by an individual of the ith predator species in hunting food from the kth prey population, we may multiply the above fraction by the amount of energy the predator of species i used in capturing all its food and obtain

$$E_{4i}c_{ik}\bar{N}_k \left(\sum_{j=1}^{n} c_{ij}\bar{N}_j\right)^{-1}.$$

This expression describes the amount of energy expended by an individual predator of species i in capturing prey of species k. Considering that there are N_i such individuals of this predator species, and that we must account for the energy spent per individual of the N_k in the prey species, then multiplication by the fraction $N_iN_k^{-1}$ is required. Further, such quantities must be summed over a total of y predator species. Thus, the submodel to represent energy spent in escaping all predators by an individual of prey species k becomes

$$E_{5k} = u_{5k}\bar{N}_k\bar{N}_k^{-1}\sum_{i=1}^{y}\left[N_iE_{4i}c_{ik}\left(\sum_{i=1}^{n} c_{ij}\bar{N}_j\right)^{-1}\right], \tag{31}$$

where u_{5k} is a proportionality constant characteristic of prey species k.

The energy budget model may be written out in full for an individual of species k, as

$$E_k = E_{1k} + E_{2k} + E_{3k} + E_{4k} + E_{5k} . \tag{32}$$

Davis and Golley (1963) have pointed out that for mammals the energy cost of normal activity is about twice the resting metabolism, or in these terms, $E_k = 2E_{1k}$.

F. Regulation of Food Consumption

The control of energy balance through limitation of food consumption has attracted relatively little attention among ecologists considering the apparent importance of this phenomenon in governing the flow of energy through populations. A notable contribution is the experimental and analytical work reported by Holling (1965, 1966). Physiological investigations of the regulation of food intake have been made by several, notably by Mayer and his co-workers. The mechanisms have been studied most for mammals, but research by Rozin and Mayer (1961, 1964) on the goldfish and Dethier and Bodenstein (1958) on the blowfly indicate that the regulatory mechanisms for these widely divergent kinds of animals may be simpler versions of the mammalian mechanisms.

Food intake appears to be regulated by two mechanisms, termed glucostatic (sensing on blood glucose) and lipostatic (sensing on blood lipid) as well as the more obvious upper limit of intake set by the physical capacity for ingesting, or the "biometric limit." In discussing the regulation of food intake, Mayer (1964) emphasizes the development of a satiation level which is adjusted by the glucostatic mechanism according to the recent exchange of energy. This is termed a "short term" regulation in contrast to the lipostatic component of regulation, called "long term." In addition, there is biometric regulation, which refers to the physical (and other) limits on the ability of the animal to ingest food at one time; this clearly sets an upper level below which the average rate of energy expenditure must surely lie. Ivlev (1961) has identified this limit as the maximum ration and Holling (1965, 1966) as the maximum amount of food the gut can hold.

We now require a mathematical model to describe satiation level as a function of the variables mentioned above, viz., the biometric maximum food intake, the glucostatic mechanism, and the lipostatic mechanism.

The glucostatic mechanism is said by Mayer (1964) to function in short-term regulation by adjusting satiation level commensurate with the difference between recent energy intake and output. The satiety center, in the ventromedial area of the hypothalamus, contains gluco-

receptive cells that control the nearby feeding center. As the animal feeds there is an increase in glucose concentration at the satiety center, and its resulting activity inhibits further feeding. As blood glucose is metabolized, activity is decreased in the satiety center, releasing the inhibition on the feeding center. But in order for a satiation level to operate in large animals the satiety center must be activated much sooner than would be possible through increased blood glucose from digested food. This has been observed to occur and has been explained in at least two ways. Mayer and Thomas (1967) quoted observations showing that blood glucose is elevated at the onset of feeding by release of endogenous hepatic stores. Maller *et al.* (1967) suggested another possibility, metering of the intake via direct pathways to the brain from the oropharyngeal region. They were able to show that this was indeed the case not only for glucose, but also for several other compounds. Further, Mayer and Thomas (1967) point out that other receptors located in the stomach and perhaps elsewhere are complementary in the operation of the whole mechanism.

In such small animals as the blowfly the mechanism may be much simpler. Because of the small size a direct influence of the carbohydrate level in the body fluid could be exerted on a satiety center with time lags sufficiently small that oversupply could be prevented. This appears to be the case (Dethier and Bodenstein, 1958). Goldfish have been shown to regulate caloric intake to balance energy output, perhaps by a similar mechanism (Rozin and Mayer, 1961, 1964); the mechanism has not been elucidated for other poikilotherms. It does not appear, however, that the glucostatic mechanism can be the only one operative in all mammals, especially with predators for they often ingest only minimal amounts of carbohydrate.

Suppose that only the glucostatic component and the biometric maximum accounted for the satiation level. The effective satiation level can never surpass the biometric maximum. We postulate that satiation level may increase in response to an energy expenditure in proportion to the difference between the biometric maximum and the most recent satiation level. Thus satiation level could increase more, if it had recently been low, than it could if it had been high. Some type of memory, possibly physiological, is implied here. The model then, is

$$\partial S/\partial E = k(B - S), \tag{33}$$

where S is satiation level, E is energy expense, k is a proportionality constant, and B is biometric maximum food intake. After integration we have

$$S = B - C\exp(-kE), \tag{34}$$

where C is a constant of integration. As an initial condition to evaluate C, let $S = 0$ when $E = 0$; thus $B = C$, and we can rewrite as

$$S = B[1 - \exp(-kE)]. \tag{35}$$

The satiation level is set here by the total energy expenditure. It seems somewhat more reasonable to set satiation according to that amount of energy used above basal metabolism. Further, the constant k in the above expression for satiation level is a function of animal size and carries the units cal^{-1}. Both difficulties are corrected by standardizing the statement of energy expenditure above basal in terms of the basal value [which has already been calculated as E_1 in Eq. (27)]. Rewriting, the basic expression used is

$$S = B\{1 - \exp[-k_1(E - E_1)\, E_1^{-1}]\}, \tag{36}$$

where k_1 is the modified rate constant, now a unitless number. The standardized statement of energy expenditure above the basal metabolic expense may range in value from some high multiple, where the satiation level approaches the upper (biometric) limit, down to zero, where the satiation level is also zero. This last case implies that if no energy is expended beyond that required for maintenance, then no feeding will occur.

Figure 3 shows satiation level graphed against energy expenditure. For some values of energy expenditure, the amount of food the animal can ingest before satiation will exceed its energy expenditure, and fat will be stored (provided, of course, that availability of food is such that it will be possible for an animal to ingest a ration sufficient to satiate). These values of energy expenditure consistent with fat storage all lie below some critical point, while above this point it is not possible for the animal to pay for the expenditure by intake.

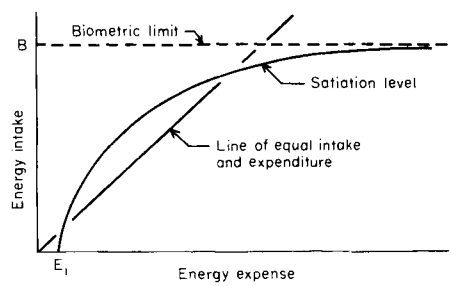


FIG. 3. Simple model relating energy intake to energy expense. The model assumes that all energy expenditures except basic bodily processes generate drive for energy intake.

The lipostatic mechanism is hypothesized by Mayer (1964) to function through some type of metering of blood lipids. The amount of fat mobilized in a given interval of time, and thus blood lipid level at any time, are proportional to the size of the fat depot (Bates *et al.*, 1955; Mayer, 1964). There is a "privileged body weight," i.e., an adult animal is said by Mayer to tend toward some body weight typical of the individual and this tendency involves adding or losing weight due only to changes in the size of the fat depot. The farther the animal's weight moves from this privileged weight in one interval of time, the more likely is an accommodating change in food intake during the next interval. Thus, if an animal has depleted his supply of stored fat somewhat, he will soon eat a larger than usual amount of food to replenish his supply; if on the other hand he has accumulated an excess, he will soon reduce intake to utilize some of the excess fat. Perhaps this is called long-term regulation because fat stores do not usually change much from the day-to-day energy fluctuations, and because the size of the fat depot exerts a continuing influence on the effective asymptote for satiation level.

It is interesting to speculate upon a possible mechanism for lipostatic control of satiety. Mayer and Thomas (1967) point out that the mechanism probably operates through some type of interference in the functioning of the glucostatic mechanism instead of as a completely independent process. Fats are converted to glucose to some extent in the gluconeogenetic process. If there are fats available there may also be glucose. Now if this gluconeogenetic glucose is in proportion to the amount of fat present, then the stored fat F can give rise to a background amount of glucose exerting an effect on satiation level, and this could occur independently of blood glucose levels which originated from ingested carbohydrates.

Whatever the mechanism, the effect of the lipostatic component upon satiation level is a function of fat depot. We expect the satiation level to remain high while fat stores are low, given that energy expense is such that the glucostatic component requires a large satiation level. But with larger fat stores the lipostatic component tends to subdue satiation level so that the privileged body weight is not exceeded. One simple model to approximate this component, given that energy expense is maximum, might be

$$\partial S/\partial F = -KF, \tag{37}$$

where F is the size of the fat depot. After integration this becomes

$$S = -KF^2/2 + C, \tag{38}$$

where C is the integration constant. When fat stores approach zero with energy expense high (as is assumed here) then satiation level is B; this supplies the initial condition: when $F = 0$, $B = C$. Substituting gives

$$S = B - k_2F^2, \tag{39}$$

where $k_2 = K/2$, a proportionality constant (associated units are gm^{-1}). This is the equation used for the lipostatic component of food intake regulation.

Since Eq. (39) sets the level of satiation when energy expense is high, it is in effect a modified biometric maximum level of food intake. Satiation is bounded by the value set by fat stores regardless of energy expense, in the interpretation of the model. This, and not the value of B, is the real limiting value for the glucostatic model. Combining the lipostatic with the glucostatic model, we may use the maximal satiation level as set by the lipostatic model, as the asymptotic value for the glucostatic model. The final model for food intake regulation becomes

$$S = [B - k_2F^2]\{1 - \exp[-k_1(E - E_1)\, E_1^{-1}]\}. \tag{40}$$

Under experimental conditions, with a rigidly controlled activity regime in a controlled temperature environment, a long-term regulation to a privileged body weight is observed. The model adequately mimics this observation. With a constant energy expense, the right-hand factor of Eq. (40) is a constant. Thus, satiation level may be computed as

$$S = C(B - k_2F^2). \tag{41}$$

If F could reach such high levels that $k_2F^2 = B$, then S would equal zero. But in practice this may seldom happen. When fat storage is high, part of the energy expense is paid for by food intake and part by mobilized fat. Thus, there is a continual drain on fat stores during periods of low satiation level resulting from a large fat depot.

Holling (1965, 1966) developed a model for hunger identical to that developed here for the glucostatic mechanism. Holling's experiment, designed to elucidate the effect of hunger in his predation model, was to starve his animals (mantids) for varying lengths of time after satiating them. The times varied from $\frac{1}{2}$ hr to 72 hr. Hunger was measured as the amount of food required to satiate after the planned period of deprivation. He postulated that hunger really was a measure of the amount of food left in the gut. From this he wrote, in the terminology used here,

$$dH/dt = d_1(B - H), \tag{42}$$

where H is hunger, t is length of time of food deprivation, d_1 is a constant, the rate of food disappearance from the gut (digestion rate), and B is maximum amount of food the gut can hold, or biometric maximum for the corresponding time interval. Integrated, this resulted in

$$H = B[1 - \exp(-d_1 t)]. \tag{43}$$

His experiments were conducted under controlled temperature and relative humidity with standard mantids. Assuming that activity was closely controlled, then energy utilization is a function of time; thus

$$E = ct,$$

and we can rewrite Holling's equation as

$$H = B[1 - \exp(-kE)], \tag{44}$$

where $k = d_1 c^{-1}$, and we have a form identical to that used for satiation level in the glucostatic model. No effect of energy storage is included in this model, although, as Holling recognized, there was evidence in his data that some type of energy storage existed. In testing his model against his data, departures were found which Holling recognized as biologically meaningful. He said,

> The most likely cause is a nutritional deficit acquired after long periods of food deprivation, a deficit that cannot be made up at one sustained feeding but shows its effects on subsequent feedings as well. Since long deprivation times tended to be followed by shorter ones, therefore the hunger measured at these shorter intervals tended to be higher than the actual deprivation time would warrant (Holling, 1966, p. 18).

This is a statement of much the same concept as Mayer's "privileged body weight." The "nutritional deficit" was created by utilization of the mantid's energy stores (which surely existed to permit survival for a 72-hr fast). With the deficit, just as Holling pointed out, the mantids tended to eat more until there had been a return to privileged body weight. It is likely that Eq. (40) here would better describe Holling's results.

G. Predation

Predation always has a dual meaning, for while it serves one species in food gathering, it imposes mortality on the other. The mortality rate on the prey describes the process, but is a property of the interaction of two species. It is true that any predator may capture and consume members of a number of prey species, and any species may be preyed

upon by several predators. Nevertheless the essential act is pairwise, one predator with one prey, in a process vital to both.

Consumption of plants by animals is predation, in terms presented here, not to be distinguished from the eating of one animal by another (except by the numerical content and context). In fact, the identification of discrete trophic levels, while convenient, is not necessary.

For complete generality let us say that any species may prey upon any species, including members of its own species. Then we may form a matrix P of predation rates. These are instantaneous rates of mortality that characterize, pairwise, all the predator–prey interactions. They state the mortality rate imposed on a prey population by a unit density of predators, and are thus implicitly specific for some time unit and for some area (for statement of densities). A predation rate may have any positive value including zero; the matrix may include very large and very small or zero rates at the same time. Any element p_{ij} of the matrix may be identified by its row–column index, where the row i pertains to the predator species and the column j to the prey.

For an example, consider the matrix representation of a simple, five-species food web with classical trophic structure, in the form

$$P = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ p_{31} & p_{32} & 0 & 0 & 0 \\ p_{41} & p_{42} & 0 & 0 & 0 \\ 0 & 0 & p_{53} & p_{54} & 0 \end{bmatrix}. \tag{45}$$

In this matrix, with the row indicating the eater and the column the eaten, species 1 and 2 are autotrophic and are eaten by species 3 and 4, but eat no species (rows 1 and 2 all zeros). Species 3 and 4 eat species 1 and 2 and are eaten only by the carnivorous species 5, which is eaten by none of the species. There is a discrete trophic structure here, with three levels, A_1, A_2, and A_3, as indicated by the predation matrix.

As a second illustration, we construct a predation matrix for a food web in which there are five species: (1) a completely autotrophic plant, (2) a carnivorous plant, (3) a small omnivore that is cannibalistic, (4) an herbivore, and (5) a top carnivore. Taking the species in the order mentioned, the predation matrix could be

$$P = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_{24} & 0 \\ p_{31} & p_{32} & p_{33} & p_{34} & 0 \\ p_{41} & p_{42} & 0 & 0 & 0 \\ 0 & 0 & p_{53} & p_{54} & 0 \end{bmatrix}. \tag{46}$$

Here though trophic structure may be unclear, it is still simple to show the feeding relationships in a predation matrix.

Predation rates used here are instantaneous rates of mortality; for these, two properties are used (Ricker, 1958). First, the instantaneous rate of total mortality, when several different kinds of mortality are acting independently, is the sum of the separate instantaneous rates; this property has been used previously in this chapter when summing death rates. The second property is especially useful when several mortality rates apply at the same time with a rate of increase during an interval. The "yield" to any one kind of mortality (in present context, to a predator) may be calculated as the product of the particular instantaneous rate and the mean population level during the interval. The mean population during the interval is calculated, in present context, following Ricker (1958, p. 32), as

$$\bar{N}_i = N_i \left[\exp\left(b_i' - \sum_{k=1}^{m} \delta_{ik}\right) - 1\right]\left(b' - \sum_{k=1}^{m} \delta_{ik}\right)^{-1}, \tag{47}$$

where $\bar{N}_i$ is mean population number during the interval; N_i is population number at the beginning of the interval; b_i' is adjusted birth rate for population i; and $\sum_{k=1}^{m} \delta_{ik}$ is the sum of m mortality rates acting on population i, taken at this point to include predation.

The predation rate p_{ij} is specific to the time interval and also to the unit area on the basis of which population densities are stated. Thus, the predation rate reflects home ranges, activity patterns, and behavior of both predator and prey. Further, predation rates provide an operational measure for the relative vulnerability of prey species to a predator, or for any "preference" exercised by predators among prey items.

To illustrate the use of predation rates, consider an elementary example. Suppose that in a unit area there are N_j individuals of prey species j, preyed upon by an individual (or, unit density of) predator of species i, with the resulting predation rate being p_{ij}. If this predation is the only kind of mortality experienced by the prey, and with no reproduction, then during the unit time interval the probability of death for any individual of the prey population will be

$$1 - \exp(-p_{ij}),$$

and the number of prey captured by the predator, on average, will be

$$N_j[1 - \exp(-p_{ij})].$$

Next, if there are two individual predators the effective predation rate is the sum of the rates for the separate predators, or $2p_{ij}$, and with N_i

individual predators, the prey is exposed to an instantaneous rate of mortality, or effective predation rate, of $N_i p_{ij}$. Here with the same assumption as above, the total number of prey captured becomes

$$N_j[1 - \exp(-N_i p_{ij})].$$

Under these conditions each of the N_i predators takes an equal share (on the average, N_i^{-1}) of the total prey captured. The amount of food ingested by an individual predator is the average weight of the prey, multiplied by the number captured. The potential ration R_i is the amount of food an individual predator of species i would consume, feeding for the interval at the maximum predation rate p_{ij}; under these conditions it would be

$$R_i = W_j[1 - \exp(-N_i p_{ij})]\, N_i^{-1}, \tag{48}$$

where R_i is the potential ration an individual predator of species i can capture in the interval under given conditions of prey abundance and weight; W_j is biomass (total) for prey species j at the beginning of the interval; N_i is the number of individuals of predator species i; and p_{ij} is the predation rate on prey species j, exposed to a unit density of predator species i. Other factors equal, R_i will decrease with increasing N_i, illustrating competition among independent mortalities. This is the so-called "law of diminishing returns" as encountered by sportsmen who are predators on game and fish populations.

Thus far this description of predation is greatly oversimplified, even in terms of our model. Other kinds of mortality, including other predators, compete for any one prey population, and during some intervals the prey populations increase through birth and some of the prey increase may be taken by predators. Further, any predator's food ration is made up of a number of components, one for each prey species that it exploits. Finally, satiation may stop a predator before he has consumed the potential ration.

Continue to consider the potential ration for an individual predator of species i. The whole ration is the sum of its separate components in the form

$$R_i = \sum_{i=1}^{n} R'_{ij}, \tag{49}$$

where R_{ij} is the component of the whole ration R_i for an individual predator of species i due to prey species j; these components are summed over all n prey species. Each component of the complete ration for any predator is calculated separately, species by species, for all prey.

Use is made here of the property of instantaneous rates, illustrated earlier, for calculating yield to one predator when there are several kinds of mortality and possibly increase during the interval. The form for a single component of the ration is

$$R'_{ij} = p_{ij}W_j \left[\exp\left(b_j' - \sum_{i=1}^{y} N_i p_{ij} - \sum_{k=1}^{m} \delta_{jk}\right) - 1\right] \times \left(b_j' - \sum_{i=1}^{y} N_i p_{ij} - \sum_{k=1}^{m} \delta_{jk}\right)^{-1}, \tag{50}$$

where b_j' is the adjusted birth rate for prey species j; $\sum_{i=1}^{y} N_i p_{ij}$ is the sum of effective predation rates on prey species j for all y predator species; $\sum_{k=1}^{m} \delta_{jk}$ is the sum of all m other instantaneous rates of mortality on prey species j, excluding any effect of predation which here is included in the previous term; and R'_{ij}, W_j, N_i, and p_{ij} are defined immediately above.

The total food that might be ingested by a predator in all components of its potential ration R_i may exceed the satiation level S_i that has already been set according to the biometric limit, the recent history of energy balance and the fat store. If this be true, the predator must cease to feed when satiated (or reduce the rate of feeding just to accomplish satiation within the interval), thus feeding at predation rate c_{ij} that is less than the definitive rate p_{ij}. At the same time, other predators may or may not operate with reduced predation rates. The new predation rates must reduce the ration to the satiation level, in the form

$$S_i = \sum_{j=1}^{n} S'_{ij},$$

where

$$S'_{ij} = c_{ij}W_j \left[\exp\left(b_j' - \sum_{i=1}^{y} N_i c_{ij} - \sum_{k=1}^{m} \delta_{jk}\right) - 1\right] \times \left(b_j' - \sum_{i=1}^{y} N_i c_{ij} - \sum_{k=1}^{m} \delta_{jk}\right)^{-1}, \tag{51}$$

where elements are as previously defined, except that $\sum_{i=1}^{y} N_i c_{ij}$ is the sum of adjusted effective predation rates on prey species j for all y predator species (including any such rates where adjustment was not necessary because $S_i \geqslant R_i$). The method is discussed later for changing each definitive predation rate p_{ij} to the corresponding adjusted rate c_{ij} needed to establish the above equality.

If, on the other hand, the sum of all components of the ration is less than or just equal to the satiation level for the predator ($R_i \leqslant S_i$) then the potential ration may be used without adjusting the predation rates; adjustment is required only with $S_i R_i^{-1} < 1$.

Calculation of a set of adjusted rates, or c_{ij} values, is accomplished for any one predator species by reducing all its definitive rates in some constant proportion. This adjustment implies that when near satiation an animal exercises the same relative degree of selection as when hunting at full capacity. This seems to us a reasonable approximation in light of limited knowledge on the point, though Holling (1965) reported that certain sizes of prey were favored when his mantids were near satiation. Murdoch (1969) has discussed "switching"; the model makes no provision for this phenomenon.

The calculation of adjusted rates is carried out by an iterative process, calculating trial c_{ij} values from the definitive p_{ij} values in the ratio of satiation to potential ration ($S_i R_i^{-1}$), substituting these as new p_{ij} values, recalculating a new R_i, and then repeating the process until the potential ration is suitably close to the satiation value.

To illustrate calculation of c_{ij} values, consider the first example given for a predation matrix. Suppose that we have calculated, for the three species of animals eating other organisms, both the satiation levels S_3, S_4, and S_5, and also the potential ration values R_3, R_4, and R_5. Then, as a first approximation, each c_{ij} element is the product of $p_{ij} S_i R_i^{-1}$

$$C^* = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ p_{31}S_3R_3^{-1} & p_{32}S_3R_3^{-1} & 0 & 0 & 0 \\ p_{41}S_4R_4^{-1} & p_{42}S_4R_4^{-1} & 0 & 0 & 0 \\ 0 & 0 & p_{53}S_5R_5^{-1} & p_{54}S_5R_5^{-1} & 0 \end{bmatrix}, \qquad (52)$$

where C^* is a C matrix conditional upon calculation (from its elements) of the food ration values that match the satiation levels. Where any of the $S_i R_i^{-1}$ values exceeds unity, a value of 1.0 is used in the adjustment process. Calculation of a single C^* matrix cannot be expected to give final c_{ij} values. It will be a first approximation. The second C^* matrix will be closer and with repetition the differences $(R_i - S_i)$ will all become less than a predetermined small value ϵ.

The effective predation on each prey species may at this time be calculated as the sum of effective rates for each predator, as calculated above for the c_{ij} values in the expression for satiation ration. This sum

will enter into the basic expression for population change of the prey [Eq. (2)] as one of the δ_{jk} values for mortality rate, as

$$\delta_{jk} = \sum_{i=1}^{y} N_i c_{ij} , \tag{53}$$

where k here denotes mortality due to predation.

To summarize briefly, this section concerns control of energy and food intake. The iterative computation of all elements of a predation matrix provides predation rates for the interval to be simulated. These rates are such that the predator's energy needs will be satisfied whenever prey levels are high enough that a full ration may be captured. There is a lag caused by basing energy need on the activity of the previous interval. This is realistic, but the amount of lag, one interval of time, is special to this model. If this period of lag proves too restrictive, it can be changed.

H. Subsystem of Computer Routines for Biotic Factors

The computer subsystem of routines which correspond to the mathematical models of this section is made up of four subroutines and one function subprogram. The four subroutines are, in the order that they are called in the main program: PRDAT, CALOR, FATLE, and SPACE. The function is SATIA. Note that with one exception computations for the entire biological community proceed for the values of a particular routine with one entry into the program. The exception is SATIA which is called once for each species.

PRDAT is a routine which iteratively finds a set of predation rates which satisfy satiation levels as computed in SATIA. SATIA is called with PRDAT. Following establishment of the matrix of predation rates, the energy expense part of the energy budget for the current interval is computed in CALOR. The predation rates for the current interval are required in order to construct the energy budget, because activity is largely a function of these rates. Based on the factors of food intake as determined by predation rates computed in PRDAT, the population sizes, the energy expense as computed in CALOR, and the residual fat depot, subroutine FATLE computes the energy expended from food and from residual fat stores. The size of the fat depot at the end of the interval is also calculated. Depending upon the energy balance, birth rates may be reduced. Subroutine SPACE handles the computations for competition and the logistic-like density-dependent adjustment of rates of increase.

Note the sequence of operation of the routines. SATIA computes satiation levels for the current interval based on the expenditure of energy and the fat depot at the end of the previous interval. The other

programs are sequenced in the order in which values are required. In this case we use the sequencing to take care of the time lag in satiation level by allowing computations to be based on the previous interval. These satiation values supply initial conditions so that the other values for the current interval may be computed.

IV. Abiotic Factors

A. Abiotic Factors of the Model

Abiotic, or physical, factors influence populations. This section concerns their direct effects upon birth and death rates. We have already discussed the less direct effects resulting from increased energy demands; if the total energy needed exceeds the caloric intake in food, the birth rate is reduced, and if the demand exceeds energy in food plus mobilized fat, starvation begins and the death rate is increased.

Although the mathematical model puts no limit on the number of abiotic factors, the present computer model contains only two. One of these is programmed to vary as a sine curve with a period of 360 intervals, simulating seasonal changes in climate throughout a year (Fig. 1). This cyclic factor is used for two reasons. First, it is a composite factor representing all influences that operate in a seasonal manner; it has been so-used here. Second, it allows the future inclusion of more specific seasonal effects where the sinusoidal factor may serve as an argument in describing natural processes that fluctuate with the earth's orbit and axial inclination. The second abiotic factor is not really used here; it is maintained at the value set, and represents some constant environmental influence. Neither factor is specifically identified as, for example, water, light, or minerals, the factors said by Clements (1949) to be important in terrestrial systems. Much could be done in simulation of abiotic factors for particular ecosystems; as a start the mathematical descriptions for a number of factors are considered in the volume edited by Van Wijk (1963).

B. Population Effects of Abiotic Factors

The effect of an abiotic factor upon population birth and death rates is made a function of deviation from the optimum range for the organism. This mode of action in the model derives from the ecological concepts of tolerance (Shelford, 1913) and of niche (Hutchinson, 1957). With respect to any one factor, an organism may exist within a range of values, or the tolerance range. Within this tolerance there is a shorter range, or perhaps only a point, where conditions are optimum.

Changes in birth or death rates are as yet unknown and probably complex mathematical functions of the deviation from optimum. Within a population, we may expect individual variation in precise physical definition of optimum and tolerance, and perhaps also in functional response to change. We know too little to approximate populational response more than roughly, except possibly in the specialized area of toxicology (Finney, 1952).

The model assumes a linear response to changes in an abiotic factor between the optimum zone and the limits of tolerance. As deviation from the optimum increases, both the birth rate modifying factor and the survival rate decrease from unity toward zero. The optimum range and the slopes of the linear responses are specified, thus implicitly defining the zone of tolerance.

The model provides the options for a different optimum range for each species, with different constants for response to deviation from the optimum (and for birth and death rates, different values for deviations above or below the optimum). Further, different sets of values and responses may be set for increase of energy expenditure (as already discussed), reduction of birth rate, and increase of death rate. Thus, any species may be given a unique set of optimum ranges and responses.

Reduction of birth rate by an abiotic factor is brought about through use of the modifying value φ which takes values only in the interval (0, 1). At the optimum, the modifier has a value of unity and hence no effect. In nature, the modifier decreases, probably monotonically, as the abiotic factor departs from the optimum. Here we assume the decrease to be linear to a zero value; all population increase is cut off outside the zone of tolerance (Fig. 4). The model permits different rates of change above or below the optimum. The model is thus

$$\varphi_{ix} = \begin{cases} 1 & \text{for } O_{ix1} \leqslant \mathscr{F}_x \leqslant O_{ix2} \\ 1 - \beta_{ix1}(O_{ix1} - \mathscr{F}_x) & \text{for } O_{ix1} > \mathscr{F}_x \geqslant O_{ix1} - (1/\beta_{ix1}) \\ 1 - \beta_{ix2}(O_{ix2} - \mathscr{F}_x) & \text{for } O_{ix2} < \mathscr{F}_x \leqslant O_{ix2} - (1/\beta_{ix2}) \\ 0 & \text{elsewhere,} \end{cases} \tag{54}$$

where φ_{ix} is the modifying value for birth rate of the ith species, for abiotic factor x, always $0 \leqslant \varphi_{ix} \leqslant 1$; β_{ix1} and β_{ix2} are slopes of decrease in the modifying value as abiotic factor x deviates from the optimum range (subscript 1 indicates deviation to lower values, and subscript 2 deviation to higher values, with a negative sign associated) for species i; O_{ix1} and O_{ix2} are bounds of the optimum zone for the abiotic factor with respect to birth rate of species i (subscript 1 indicates lower bound, and subscript 2 upper bound); and $\mathscr{F}_x$ is current value for abiotic factor x.

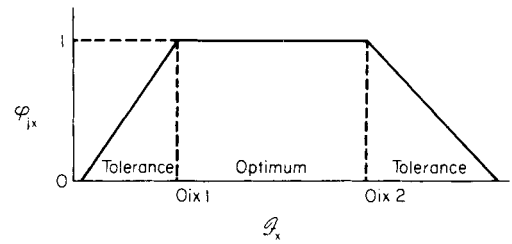


FIG. 4. Function relating current value of abiotic factor $\mathscr{F}_x$ to proportional modification of birth rate φ.

This model may be too simple to approximate nature in any real situation more than roughly, but it allows the specification of a seasonal pattern of reproduction with intervening periods of no increase, and the separate description of characteristics for each species.

Mortality rate increases as the abiotic factor deviates from the optimum. Complete survival to action of the particular factor is assumed in the optimum range (under the hypothetical condition of no other mortality), with survival decreasing toward zero as the factor departs from optimum. The corresponding instantaneous rate of mortality is the natural logarithm of this rate of survival, providing survival exceeds zero by some quantity no matter how small. This small quantity is here arbitrarily made exp(−4).

$$\delta_{ix} = \begin{cases} 0 & \text{for } O_{ix1} \leqslant \mathscr{F}_x \leqslant O_{ix2} \\ -\ln_e[1 - \lambda_{ix1}(O_{ix1} - \mathscr{F}_x)] & \text{for } O_{ix1} > \mathscr{F}_x > O_{ix1} - (1/\lambda_{ix1}) \\ -\ln_e[1 - \lambda_{ix2}(O_{ix2} - \mathscr{F}_x)] & \text{for } O_{ix2} < \mathscr{F}_x < O_{ix2} - (1/\lambda_{ix2}) \\ 4.0 & \text{elsewhere,} \end{cases} \tag{55}$$

where δ_{ix} is the instantaneous rate of mortality due to abiotic factor x, for species i; λ_{ix1} and λ_{ix2} are slopes of decrease in survival rates as abiotic factor x deviates from the optimum range (subscript 1 indicates deviation to lower values, and subscript 2 deviation to higher values, with a negative sign associated) for species i; O_{ix1} and O_{ix2} are bounds of the optimum zone for the abiotic factor x with respect to mortality of species i (subscript 1 indicates lower bound, and subscript 2 upper bound) and $\mathscr{F}_x$ is current value for abiotic factor x.

This model provides for virtually complete extinction of a species when an abiotic factor is outside the range of tolerance. This provides the capability of imposing as heavy a mortality as may be required; if the species is to remain in the community it must have tolerance ranges that include the values for all the abiotic factors.

C. Computer Routines for Abiotic Factors

The effects of abiotic factors are included in the two subroutines ABIMOD and ABMORT. Both routines require the operation of a function subprogram WEATHR that so scales a sine wave that its amplitude is the specified range (100 units, fluctuating 5–105), its period 360 intervals, commencing with the specified argument (0.65 rad), illustrated in Fig. 1. ABIMOD is a computation of modifying factor for birth rate, Eq. (54), for each species in the community, and ABMORT is a similar computation of mortality rate by Eq. (55).

V. Results and Discussion

A. Simulation Trials

The computer program for the mathematical model is listed in Appendix D. An example of the output is in Appendix C, and a listing of input data required, with a sample set of data, is in Appendix B. A glossary of symbols used appears in Appendix A.

The community simulated in the program had six species (two each of plants, herbivores, and predators). In selecting input values, we kept in mind two plants of small biomass, possibly perennials, two small herbivores like mice, and two predators of small body size like weasels or owls. Many values needed to implement the model were not available. These were approximated, often with little information. Surprisingly few trial sets of input data were required to find values that gave reasonable results. The first set tried was instructive in that heterotrophs became extinct in a few years due to starvation and repression of reproduction; predation rates were not high enough to transport sufficient energy through the food chains.

Four simulations are reported, each for a 30-yr span (Figs. 5, 7–9). Input data were similar for each, the runs consisting of a "standard" set of values and three variations. The standard data are those listed in Appendix B. Space limits, and thus upper limits on population growth, were imposed on the two producers, but not on heterotrophs. Maximum rates of increase were highest for the plants, less for herbivores, and still less for predators. Optimum climatic conditions were defined somewhat differently for each species (see Appendix B). The simulation based upon these standard data is shown in Fig. 5; setting an upper asymptote on herbivore growth produced Fig. 7; effectively removing predators yielded Fig. 8; and increasing the rates of herbivore increase to equal those assigned to plants resulted in Fig. 9.

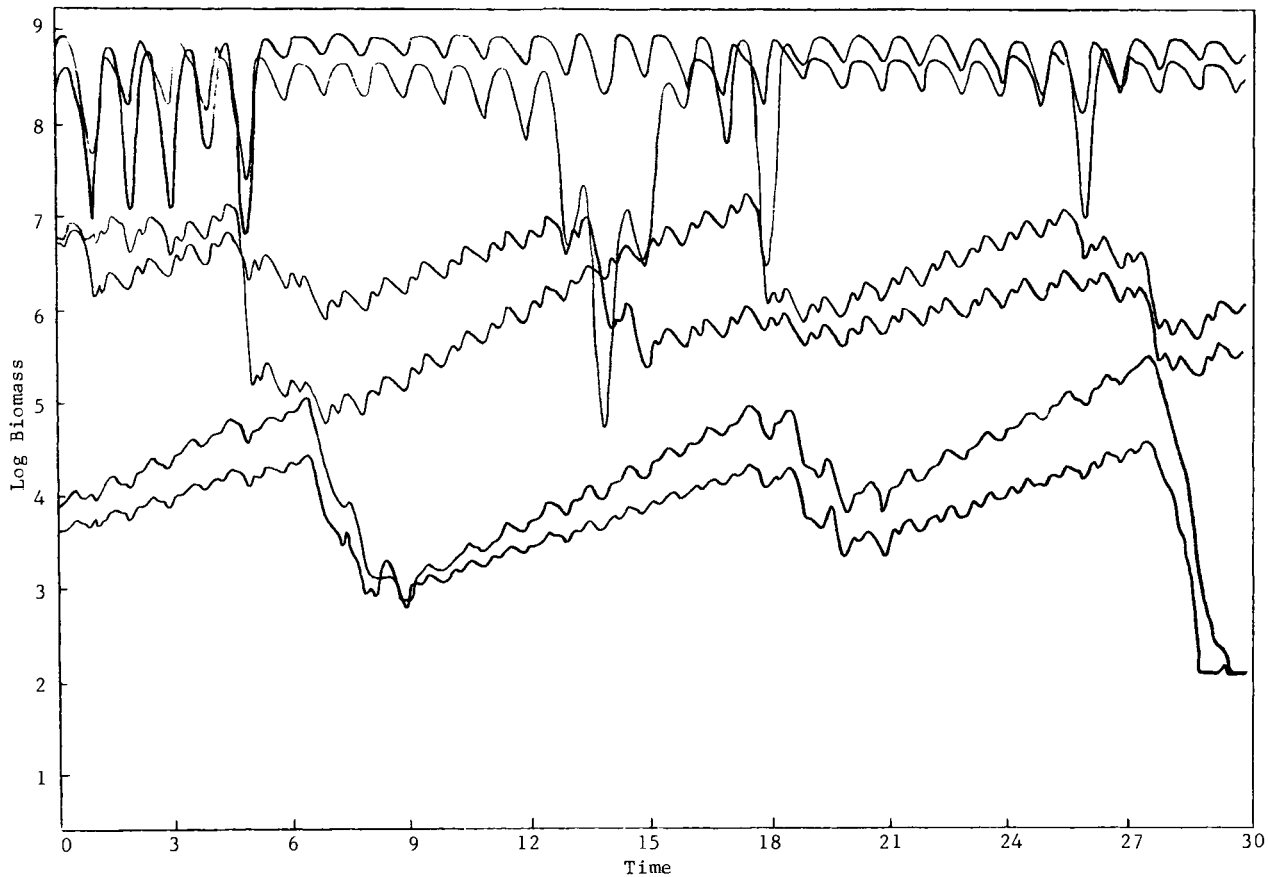


FIG. 5. Plot of biomass (logarithmic scale) of six species (from top down: two plants, two herbivores, two predators) for 30-yr simulation; input data as listed in Appendix B.

Each species (e.g. Fig. 5) clearly responded to the annual cycle of simulated climate, with a period of growth and a period of decline. This pattern reflects ranges set in the input for the climatic factor optimum. The heterotrophic species had two optimal periods each year, resulting in two peaks of increase, as shown diagrammatically in Fig. 6.

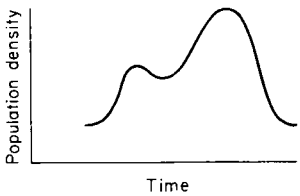


FIG. 6. Typical pattern of population size during year of no overall change, for organism with two periods of high rate of increase.

In Fig. 5 the climatic factor (Fig. 1) passed through the optimum range as it increased in spring and again as it decreased in fall. The two predators were almost eliminated (Fig. 8) by assigning them a zero increase rate (and starting them at zero level). Whenever any species count drops below unity, the program starts the next computing cycle with a single individual. Thus, predators were maintained at a very low level, and with minimal effect on the herbivores.

B. CHARACTERISTICS OF THE MODEL

The oscillations produced with the standard set of input data (Fig. 5) mimic generally the fluctuations of natural populations. Were these real observations, we might postulate long-term cycles for the heterotrophs, with nadirs occurring about 11 years apart on a somewhat irregular schedule. Like natural fluctuations, these would seem to be only generally predictable. Here, of course, the model is entirely deterministic, each fluctuation being absolutely predictable and any time sequence reproducible merely by starting the computer over with the same data. The oscillations result from species interactions; left to itself with an adequate energy supply, each would follow a smooth curve reflecting the seasonal effect. Thus, it is interactions that are responsible for observed irregularities.

Still referring to Fig. 5, the plant populations fluctuated in regular annual cycles, following the climatic pattern, until some herbivore population grew sufficiently that its plant consumption reduced the plants to a low level during the nongrowing season. When this happened, the plants usually returned almost to their normal summer maxima,

and thus they oscillated over a wider range when under herbivore pressure. When herbivores were reduced, however, either by lack of food, or by predator action, or both, the plants returned to their regular annual cycles. In the illustrated simulation both herbivore species were made selectively predatory upon the two plants, and consequently both plants and herbivores were permitted to oscillate with different time relationships.

Herbivore effects on the plant populations may be regulated by imposing upper limits on growth of each herbivore species. If these limits are beneath the point where herbivores constitute important mortality factors, then the producers fluctuate under climatic influence only. The data that produced Fig. 7 were so adjusted; other asymptotic herbivore limits would produce different results. Note that the variable period of oscillation caused by selective predation on plants disappears in Fig. 7.

In Fig. 5 herbivore populations oscillated under control of the available food level at some times, in response to predator pressure at other times, and under the combined influence of both these factors at still other times. When the predator effect was removed (Fig. 8) the herbivores oscillated somewhat as they do with predators present, but more often they reached levels high enough to reduce plant populations. When present (Fig. 5) the predators only occasionally reached levels high enough to reduce the herbivores; their effect in these trials seemed to be to lengthen the period between low values.

When there is an upper asymptote limiting herbivore growth, fluctuations may all but disappear, as seemed to be the case in Fig. 7, or else, where the upper limit for herbivores is set at a higher point, they may fluctuate under control of periodic predator increase. When herbivores were given higher birth rates, equal to those assigned to the producers, oscillations of the lower two trophic levels became more frequent and more violent, while the predators were almost eliminated (Fig. 9).

Predator species fluctuated here according to food availability. This response is clearly to a threshold level, above which predators may obtain food to reproduce and below which they starve. When herbivores are above the threshold, predators increase until the herbivores fall below threshold, either due to increasing numbers of predators, or starvation. At this point, the predator populations crash and remain low until herbivores again exceed the threshold level which allows predators to grow. Thus, in this model predators are entirely controlled by their prey levels.

The predators of the community simulated in Fig. 8 are kept at low

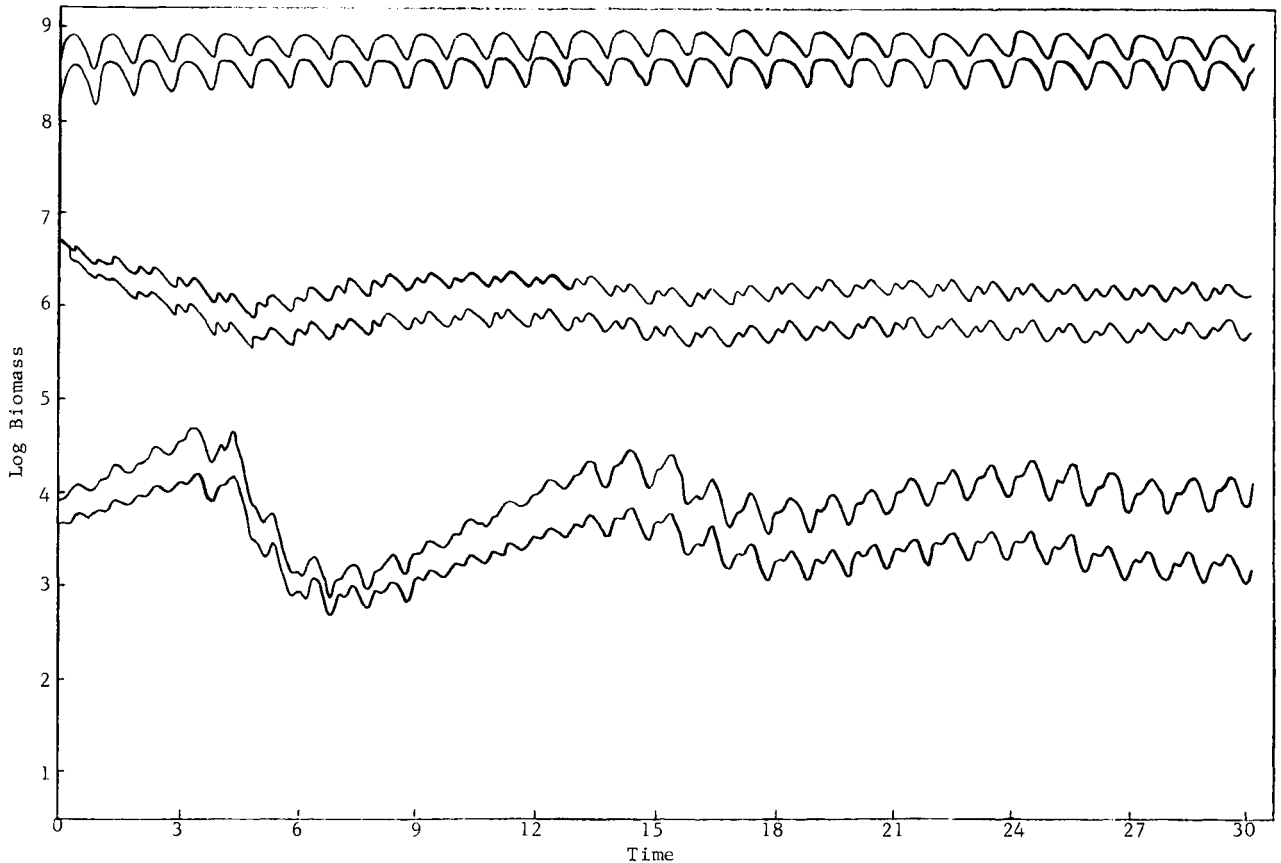


FIG. 7. Plot of biomass (logarithmic scale) of six species (from top down: two plants, two herbivores and two predators) for 30-yr simulation where herbivores have upper population limits; input data as listed in Appendix B except that herbivores are assigned limits for space and coefficients of competition.

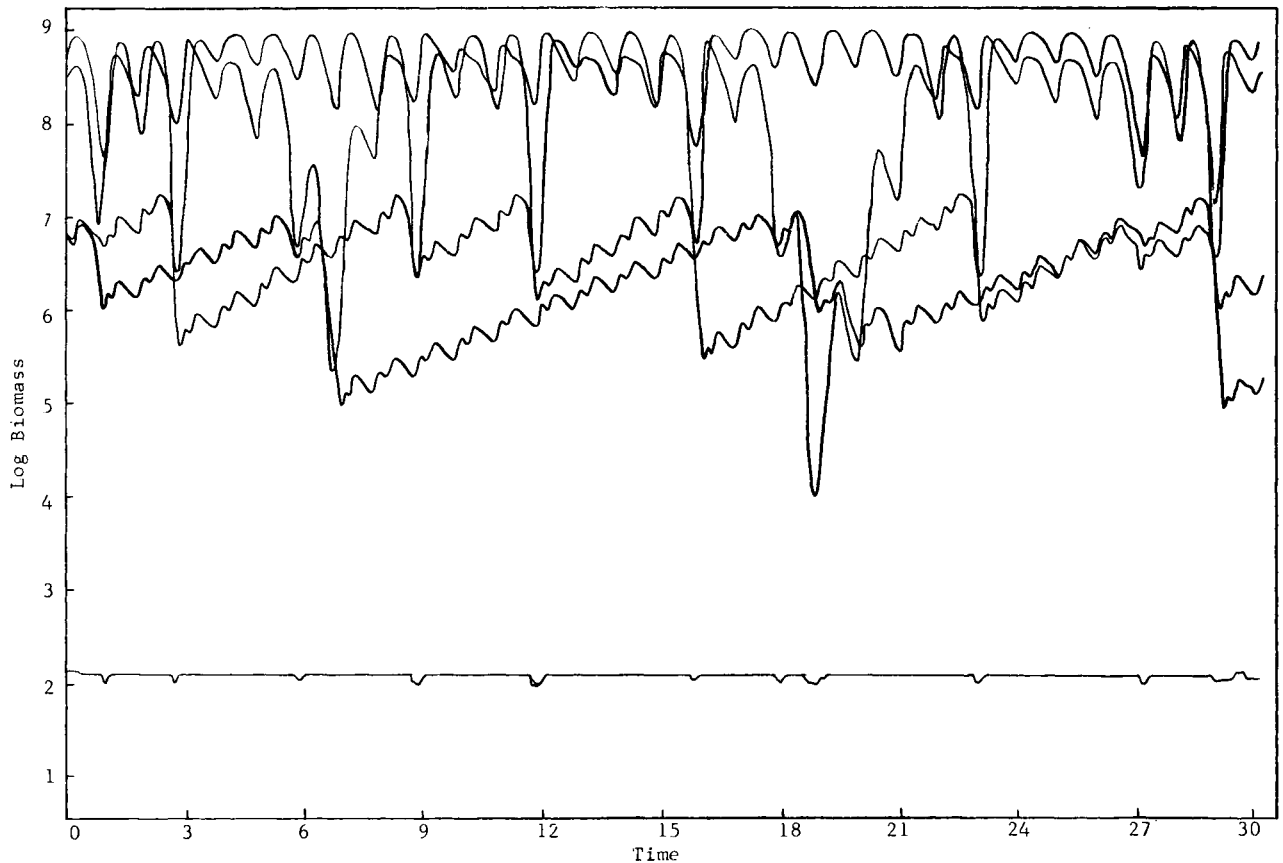


FIG. 8. Plot of biomass (logarithmic scale) of six species (from top down: two plants, two herbivores, two predators) for 30-yr simulation where effect of predators is eliminated; input data as listed in Appendix B except that predators are started at zero and assigned zero birth rates. Notches in lines representing predators represent periods of starvation and no weight gain.

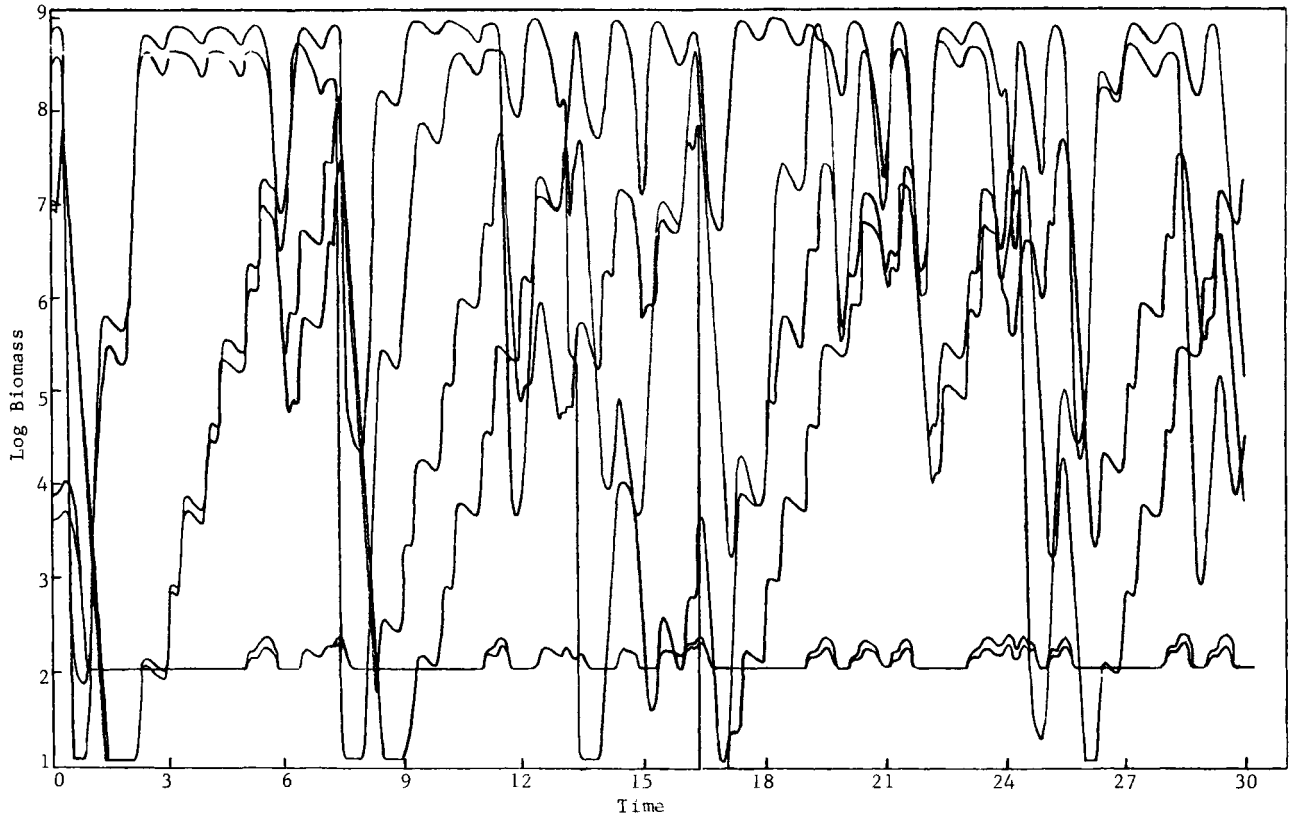


FIG. 9. Plot of biomass (logarithmic scale) of six species (from top down: two plants, two herbivores, and two predators) for 30-yr simulation where herbivores have higher rates of increase; input data as listed in Appendix B except that maximum birth rates for herbivores have been increased to equal the values assigned to the plants.

levels by the timing of fluctuations in their food supply. Here the herbivore populations, given high birth rates, oscillated rapidly and frequently dropped below the threshold that controls the predators. Thus, the predators never increased long enough to attain control of the herbivores.

The seasonal cycle built into this model clearly exerts an important influence on the oscillations. The most important population reductions occurred during nongrowing seasons. Starvation is most important then, though it may occur at any season. The ecology of the Temperate Zone is reflected in choice of optimum seasons and the adjustment to climatic fluctuation built into the model; therefore temperate or perhaps arctic conditions are simulated.

The effects of changing numerous biological parameters of the model is not yet explored. Results of changing one value suggest that interesting questions may be raised. In the standard set of data, the proportion of the fat store mobilized each day is set at 0.10 for species 4 (one of the herbivores). Reduction of this fraction to 0.018 resulted in virtual extinction of this species, but could be counterbalanced by raising its birth rate by half. Apparently, in this model a low rate of fat mobilization results in frequent undernourishment and reduced birth rate, even when an animal has a large fat store. Another compensating adjustment might have been to adjust control of the satiation level as exercised by the fat store.

Having a model that will simulate a hypothetical set of species, we now require a set of measurements to characterize real population histories. For example, it is clear that relatively minor changes, like altering the fat mobilization constant or the initial number of a species, will produce marked changes in biomass and numbers of all the species in a short time (10 yr). We now require useful measures to quantify such changes, an analysis of time series, not only by the usual mathematical techniques but also with parameters of more immediate biological meaning. There is need to program a running summary, perhaps over quarter years or full years, to record the energy consumed by each heterotroph, the organic production of each species, and the cumulated rates of mortality and increase.

There are certain obvious deficiences in the model. Most important is the absence of any age-class effect. The hypothesis of increased mortality in populations that exceed habitat carrying capacity should be incorporated. Some values now inserted into the program as constants should probably be made species-specific. Perhaps digestion rates should be variable among species. In earlier sections, comments were made at several points where increased sophistication might be introduced.

C. Discussion of the Model

It is apparent from this investigation that sufficient biological information to simulate a real community accurately is not available at the present time. Many specific data demands of this model cannot be met, and some of the variables have never been measured in natural populations. It is by no means clear that further development of this kind of model into a more sophisticated mathematical form is justified before we know more.

At the same time, we feel the model to be heuristically useful, in that it has required us to set down specific information and identify areas of greatest deficiency. The results appear realistic, and potentially able to give answers about effects of changing various parameters. Further, the work suggests certain general questions.

This model emphasizes contingency as determining population change. Population dynamics may be described as a set of potentials for action, with final action contingent upon the set of factors instantaneously influencing the population. What happens next is contingent on the present status. That this principle governs the model only means, of course, that we built it on this view of natural events. This seems a valid view for it places less emphasis upon supposed overall governing processes which can, after all, have effects only through influences exerted at the present moment. Any natural programming of future events must be through the setting up now of processes that will approach the future set of predisposing conditions step by step as time passes. As population growth follows some curve, this means that at each instant the population changes in response to the set of influences to which it is immediately exposed. One important influence is the population level itself; knowing nothing more we can expect it to be the same in the next instant. Other important influences are population characteristics like sex and age distribution (not included in our model), reproductive status, other characteristics of physiological well being, as well as the pressures of other biotic and abiotic factors. Of no real importance is the position the population should take at some future date on some mathematical curve of expected growth. Such a curve may have great descriptive and predicted usefulness; used with caution it can enhance understanding. But what the population does at the moment must be determined only by the set of influences at that moment.

In computer simulations of the model, whenever the same set of initial conditions, rates and characteristics, are provided the same output follows. But if a single effective condition is changed, the resulting series of population fluctuations differs to some degree. Even with the

vastly oversimplified description of nature illustrated in Fig. 5, it seems quite unlikely that exactly the same sequence of events will happen twice in a simulation. How much less likely is the enormously more complex natural system to return exactly to the same set of conditions, to predispose it to generate exactly the same set of responses. Any degree of predictability seems remarkable under these circumstances.

The population fluctuations in Fig. 5, sometimes of several orders of magnitude, seem too violent to be "natural," and those in Fig. 9 are even more so. Yet, in making such a judgment, we lack good standards for there is little real knowledge of the actual scale of local fluctuations for most natural populations year after year. Most series of records are for economic forms (game or pests) over large areas; local information is especially scanty.

D. Factors of Population Control

The factors which control populations are the most important and most interesting features of population study. In the natural world, no populations increase without limit and few decrease without limit. It has long been held that prey species are controlled in some manner by predators (and parasites). It has recently been suggested (Murdoch, 1969) that a logical requirement for control by predation is the phenomenon of "switching," or an increased efficiency of predation upon the more common species. Holling (1959, 1965) has pointed out the importance of satiation in limiting predation effectiveness. Other influences stabilizing numbers below some asymptotic upper limit are density-dependent factors acting within populations. One density-dependent mechanism, not modeled here, is the postulated increase in vulnerability to predation as numbers exceed the carrying capacity of the habitat. This may be another aspect of "switching," mentioned above. Finally, there is much speculation currently about the possibility that interrelationships among many species in a community impart stability not to be found in communities of few species. Our model is restricted to few species, and so this last factor is not included.

The effect of the predator–prey relationship in the model is clearly control of the predator populations by prey density; control in the reverse direction is less clear. When prey availability is above a certain threshold level the predators may increase. Otherwise they decrease under mortality pressure of several kinds, to which starvation is added when prey become low enough. What has been called a threshold is actually a zone of rapid change with decreasing numbers of prey, the predator passing from adequate food through undernutrition to

starvation. This comes about because an individual predator cannot capture enough food to meet his energy requirements unless the prey population is at a certain level [Eq. (50)]. When the prey animals exceed this level, they can support the well-being of any number of predators, but below this level they can fully support none.

As a control factor for prey populations, this threshold of predator well-being is density-dependent. When the prey reaches a certain density, the predators increase and so does prey mortality due to predation. Of itself, this may not be able to reduce an increasing prey population, but this density-dependent factor may be combined in effect with others, like a decreasing food supply of the prey, or perhaps a graded series of similar releases of other predators, to control the prey numbers.

Satiation of the predator tends, however, to reduce the effectiveness of any prey control. When the prey population exceeds that level which the predator needs for capture of a satiation ration, then the effective predation rate is reduced [Eqs. (51) and (52)] more and more as the prey increases (and with predator numbers constant). The food intake per predator remains constant beyond a given point of prey density (Fig. 10). This phenomenon has been discussed by Holling (1959, 1965)

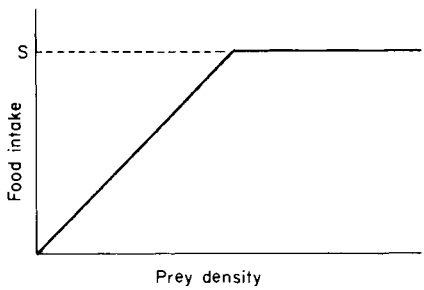


FIG. 10. Food intake as a function of total prey density (biomass). Below a critical density, satiety (S) is not reached, above this level food intake is constant regardless of prey density.

for several conditions. If it is allowed that predators will increase when food is abundant, then in the long run satiation would seem only to slow, rather than prevent, the ultimate overtaking and reduction of the prey in coordination with other factors. Further, at the point where prey no longer satisfy food needs of the predators, the mortality rate experienced by the prey increases disproportionately as each predator now hunts with full effectiveness.

Switching is supposed to increase the effectiveness of predation as a population control when a prey species becomes abundant (Murdoch, 1969). But under these conditions, in the view taken here, the effective predation rates are set at the reduced levels needed to just achieve

satiety; changes in the definitive rates may have relatively little effect. Switching can only increase the portion of the ration, already predominant, that is drawn from the abundant prey species, by substituting it for some of the food otherwise to be drawn from the rare forms. The total amount of food will not increase. This would seem less important in controlling the abundant form than in sparing rare species (the buffer species concept).

An asymptotic upper limit of population growth can provide stability of numbers when adjusted to the correct level. To both achieve stability and retain a community of species, such upper limits must be set high enough that the species transmits enough energy to sustain those organisms that feed upon it, yet low enough that the species cannot generate important predatory pressure on its prey. A stable community can be achieved by postulating enough of such limits; the interesting question seems to be whether realistic stability can be achieved without them.

Hairston *et al.* (1960) concluded that producers are resource limited, herbivores predator limited, and predators food limited. Regarding producers, this model agrees; a space limit was built in although energy was assumed to be unlimited. Regarding predators, agreement is also complete because predators are here provided with a capacity to increase unless food is limiting. Regarding herbivores, however, we observe that in this model their control comes about both by predator action and by limitation of their food supply. Even when predators are effectively removed from the model, the herbivores are eventually limited by food.

We raise the question of whether herbivores may not be limited, at least in part, by food supply. The remarks of Hairston *et al.* are based upon very general observation of nature; even so, they clearly take precedence over the results of this model where any resemblence to nature arises only from logical factors we have built in. But it may be instructive to examine the instances where food supply controlled the herbivores, either in Fig. 8 when predators are almost absent, or in Fig. 5 where they are relatively ineffective. When the herbivores reach high levels, their effect on producers is principally to reduce the winter minima; the effect on the summer maxima is much less frequent and pronounced. Thus, the herbivores in the model exert considerable influence on the producers, but fail to limit them in the strict sense of appearance during the growing season. Hairston *et al.* argued that because herbivores do not reduce their food supply, they are not food limited. We suggest that if herbivores are not limited in some other way they will be food limited. If the growth rate of producers is suffi-

ciently high, plants may then approach the limit of some resource each growing season even though at some other time of the year they may be reduced by herbivores. Thus, a law of minimum food resource operating in time may limit herbivores, even though the producers may not be limited during the growing season.

VI. Conclusions

Construction of an ecosystem model with emphasis on energy exchange, even one as simple as six species and two abiotic factors, has forced attention to a number of neglected phases of population dynamics and suggested questions that must be carried to nature for an answer.

There are important deficiencies in the biological knowledge required to construct such a model on more than very general terms.

The principal weakness of this study is in methods for describing and comparing results when simulating an ecological system.

This work emphasizes that contingency governs population changes; that is, a population will change in the next unit of time contingent upon its status and relationships with the rest of the ecosystem at the present time.

Predator numbers may be controlled by prey density through a threshold effect that constitutes a density-dependent factor in population regulation of the prey.

It seems possible that herbivore numbers are controlled, at least in part, by food availability during some limited season, or in some limited form, and without apparent reduction in general level of the food supply during the growing season.

Appendix A. Glossary of Symbols Used

Text symbol	Definition	Computer program variable name	Subroutine
A	Competition matrix; elements are coefficients of competition for a fixed resource	TERTRY	MAIN
		T	READM
		T	SPACE
a	An element of the competition matrix; also, constant in logistic		
B	Biometric maximum biomass of food intake	BMETM	MAIN
		BM	READM
		B	PRDAT
		B	SATIA
		B	CALOR
b	Physiologically maximal birth rate (instantaneous rate of increase)	BIRTH	MAIN
		B	READM
		B	PRDAT
		BIR	ACTION
b'	Birth rate adjusted for modifying factors	G	MAIN
		G	READM
		G	CALOR
		Y	ACTION
β	Proportionality constant relating birth rate modification to deviation of abiotic factor from optimum	ASLOP	MAIN
		ASL	READM
		B	ABIMOD
C	Predation matrix with elements (predation rates by individual predators) reduced from maximal by satiety		
c	An element in the predation matrix C, reduced from maximal level by satiety		
d	Death rate in logistic equation		
d'	Instantaneous rate of total mortality, sum of separate rates	B	ACTION
d_1	Digestion rate (instantaneous rate)	DIGES	MAIN
		DG	READM
		DIGES	FATLE
d_{11}	Partial digestion rate—carbohydrate		
d_{12}	Partial digestion rate—fat		
d_{13}	Partial digestion rate—protein		
d_2	Proportion of stored fat mobilized daily	FFAMA	MAIN
		FM	READM
		FFAMA	FATLE
Δ	Deviation of abiotic factor from range optimum for species with regard to energy need		

Appendix A (cont.)

Text symbol	Definition	Computer program variable name	Subroutine
δ	Instantaneous rate of death by one of the factors: predation, starvation, abiotic factors, or unspecified factors	D	MAIN
		C	PRDAT
		C	CALOR
		C	ABMORT
		C	ACTION
		D	RECORD
E	An amount of energy	ENERG	MAIN
		ENG	READM
		ENERG	PRDAT
		ENERG	CALOR
		ENERG	FATLE
		Y	CALOR
		E	RECORD
		ETOT	RECORD
E_t	Energy available without use of body protein	DIFF	MAIN
		DIFF	FATLE
		AVCAL	RECORD
exp	The exponential function e^x, where x is the argument, as exp(x)	DEXP	(throughout)
$\mathscr{F}$	Current value of an abiotic factor	FL	MAIN
		FACTR	MAIN
		F	WEATHR
		FL	CALOR
		F	ABIMOD
		F	ABMORT
		FACLEV	RECORD
F	Fat store	FAT	MAIN
		FAT	READM
		FAT	TOTSI
		FAT	PRDAT
		FAT	SATIA
		FAT	CALOR
		FAT	FATLE
		FAT	RECORD
f	Average amount of food ingested during interval	RATIO	MAIN
		RATIO	PRDAT
		FOOD	FATLE
		RATN	RECORD
$\hat{f}$	Average amount of indigested food during interval	FBAR	FATLE

Appendix A (cont.)

Text symbol	Definition	Computer program variable name	Subroutine
φ	Modifying factor for birth rate in population	RSTRC	MAIN
		R	PRDAT
		R	FATLE
		R	SPACE
		R	ABIMOD
		R	ACTION
		R	RECORD
g	Instantaneous rate of change of population size; $b' - d'$	X	MAIN
		X	ACTION
		CHG	RECORD
K	Population maximum biomass; upper asymptote of logistic	A	MAIN
		A	READM
		A	SPACE
k_1	Rate constant relating standardized energy expenditure to satiation level	SK1	SATIA
		S1	READM
k_2	Proportionality constant relating fat stores to satiation level	SK2	SATIA
		S2	READM
L	A constant subtracted from the ratio of energy supply to energy need, for adjusting average value to the population effect		
λ	Proportionality constant relating survival rate to deviation of an abiotic factor from optimum	SLOPE	MAIN
		SL	READM
		S	ABMORT
N	Number of individuals in the population	S	MAIN
		S	READM
		SP	PRDAT
		S	CALOR
		S	FATLE
		S	SPACE
		SP	ACTION
		S	RECORD
O	Optimum value for abiotic factor; bound of optimum zone	OPT	MAIN
		POINT	MAIN
		ALEVE	MAIN
		O	READM
		PT	READM
		ALV	READM
		O	CALOR
		A	ABIMOD
		P	ABMORT
P	Predation matrix; elements are the potential predation	PRED	MAIN
		P	READM
		P	PRDAT
		P	CALOR

Appendix A (cont.)

Text symbol	Definition	Computer program variable name	Subroutine
p	Elements of predation matrix, potential predation rate; also Volterra's coefficients of competition		
Q	Current average energy content of an individual	EIND	CALOR
q	A caloric equivalent of an element of diet, kilocalories per gram	CAL	FATLE
R	Potential ration; biomass a consumer can take at a given prey density	RATION	MAIN
		RATION	PRDAT
		RATIO	CALOR
r	Instantaneous rate of population change in the logistic equation		
S	Satiation requirement; biomass a consumer requires with given fat stores and recent energy expenditure	SATIA	(throughout; function subprogram name)
u	Constant relating some specific energy expense to some factor or activity	E	MAIN
		E	READM
		E	CALOR
v	Constant; exponent in the body–energy relationship		
W	Biomass of an individual organism	SIZE	MAIN
		SZ	READM
		SIZE	TOTSI
		SZ	PRDAT
		SZ	CALOR
		SZ	RECORD

Appendix B. Input Formats

Input data required by computer program. Values given are those used for the simulation in Fig. 7. All cards except numbers 1 and 62–67 with 10-column fields, right-hand justified, input order is card number (not order given below). Card number and species designation not punched in cards.

Appendix B (cont.)

Card number	(Instruction cards)							
1	Print interval (cols 1–3) 15		Instructions (0, 1) to print each of 16 lines (cols 4–19) 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1			Date (cols 20–28) 18 Dec '69	Border (cols 29–52) **********	
2	N Number of species	NF Number of abiotic factors	JS Beginning interval number for printing	JF Ending interval number for printing	SE Argument for sine function for season	F1 Constant to set range for abiotic factor 1	F2 Constant to set range for abiotic factor 2	DG Rate constant for digestion
	6	2	1	10801	.65 + 00	.10 + 03	.55 + 02	−.30 + 01

Card number	Species cards for Species: 1, 2 producers; 3, 4 herbivores; 5, 6 predators (Initial condition cards)					
	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6
3	S = species number of individuals					
	.4101 + 09	.1475 + 08	.325 + 06	.3683 + 06	.3214 + 02	.5212 + 02
4	SZ = beginning weight of individuals of each species					
	.105 + 01	.107 + 02	.1403 + 02	.1403 + 02	.1260 + 03	.1285 + 03
9	FAT = beginning grams of fat per individual					
	.5 − 01	.7 + 00	.403 + 01	.430 + 01	.2599 + 02	.2848 + 02
13	ENG = initial value for energy (kilocalories per individual) expended during previous interval					
	0.0	0.0	.6986 + 01	.7180 + 01	.2009 + 02	.2111 + 02
16	G = initial value for modified birth rate					
	.2389 − 01	.3532 − 01	.1830 − 01	.2593 − 01	.6192 − 02	.7403 − 02
19	EBM = initial value for energy expended in maintenance of body					
	0.0	0.0	.4 + 01	.3456 + 01	.1124 + 02	.1137 + 02

Appendix B (cont.)

Card number	(Variable cards)					
	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6
5	SIZ = nonfat weight of individuals (grams)					
	.01 + 01	.10 + 02	.10 + 02	.10 + 02	.10 + 03	.10 + 03
6	B = maximum birth rate					
	.75 − 01	.70 − 01	.20 − 01	.20 − 01	.90 − 02	.80 − 02
7	A = amount of space available to each species; asymptote for population number (.10 − 01 if logistic is not operating)					
	.80 + 09	.80 + 08	.10 + 01	.10 + 01	.10 + 01	.10 + 01
8	CHO = carbohydrate, body content per individual (grams)					
	.35 + 00	.40 + 01	.10 + 01	.10 + 01	.10 + 02	.10 + 02
10	BM = biometric maximum food intake per individual (grams)					
	0.0	0.0	.104 + 02	.105 + 02	.24 + 02	.25 + 02
11	S1 = rate constant for influence of energy expenditure on satiation level (note negative sign)					
	0.0	0.0	−.10 + 01	−.10 + 01	−.75 + 00	−.70 + 00
12	S2 = proportionality constant for influence of body fat store on satiation level					
	0.0	0.0	.20 + 00	.30 + 00	.15 − 01	.125 − 01
14	STV = rate constant for starvation					
	0.0	0.0	.60 − 02	.55 − 02	.55 − 02	.60 − 02
15	FM = turnover rate for mobilization of fat stores					
	0.0	0.0	.20 + 00	.10 + 00	.20 + 00	.50 − 01
17	PR = protein per individual (grams)					
	.70 − 01	.80 + 00	.15 + 01	.18 + 01	.16 + 02	.15 + 02
18	DTH = basic mortality rate—cause unspecified (note negative sign)					
	−.20 − 02	−.30 − 02	−.18 − 02	−.20 − 02	−.85 − 03	−.80 − 03

Appendix B (cont.)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	P(IJ) = predation matrix 6 × 6; I(row) = predator, J(col) = prey; instantaneous rate of mortality of prey with unit density of predator (note negative sign)						
20	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 1)
21	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 2)
22	−.90 − 07	−.90 − 08	0.0	0.0	0.0	0.0	(Sp 3)
23	−.90 − 08	−.90 − 07	0.0	0.0	0.0	0.0	(Sp 4)
24	0.0	0.0	−.55 − 05	−.525 − 05	0.0	0.0	(Sp 5)
25	0.0	0.0	−.60 − 05	−.525 − 05	0.0	0.0	(Sp 6)
	T(IJ) = competition matrix 6 × 6; I(row) = competitor, J(col) = species being suppressed; competition coefficients: relative amount of space I needs in terms of what J needs (note negative sign)						
26	−.10 + 01	−.50 − 01	0.0	0.0	0.0	0.0	(Sp 1)
27	−.60 + 00	−.10 + 01	0.0	0.0	0.0	0.0	(Sp 2)
28	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 3)
29	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 4)
30	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 5)
31	0.0	0.0	0.0	0.0	0.0	0.0	(Sp 6)

Appendix B (cont.)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	E(IJK) = energy coefficient matrix: energy expenditure for different reasons; I(row) = species; J(successive pairs of cols) = reason for energy expenditure as named; K(1st or 2nd col of 2nd pair) 1st = abiotic factor 1, 2nd = abiotic factor 2, insert zeros in 2nd col for other pairs (10 eight-column fields)						
	Body mass	Abiotic factors	Reproduction	Capturing food	Escaping predators		
62	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0		(Sp 1)
63	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0	0.0 0.0		(Sp 2)
64	.70 + 00 0.0	.10 + 00 .75 − 01	.15 + 01 0.0	.30 + 01 0.0	.80 + 00 0.0		(Sp 3)
65	.60 + 00 0.0	.90 − 01 .65 − 01	.15 + 01 0.0	.267 + 01 0.0	.80 + 00 0.0		(Sp 4)
66	.45 + 00 0.0	.365 + 00 .364 + 00	.15 + 01 0.0	.45 + 01 0.0	0.0 0.0		(Sp 5)
67	.45 + 00 0.0	.365 + 00 .364 + 00	.15 + 01 0.0	.60 + 01 0.0	0.0 0.0		(Sp 6)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	O(IJK) = abiotic factors—optimum range outside of which energy is expended; I(row) = species; J(cols 1, 2 vs 3, 4) factor 1 or 2; K(1st or 2nd col), 1st = lower bound, 2nd = upper bound						
32	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 1)
33	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 2)
34	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 3)
35	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 4)
36	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 5)
37	.75 + 02	.75 + 02	.50 + 02	.50 + 02			(Sp 6)

Appendix B (cont.)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	SL(IJK) = abiotic factors—slope—increase in *proportion dying* of factor per unit deviation from the optimum range stated in PT(IJK) below; I(row) = species; J(cols 1, 2 vs 3, 4) = factor 1 or 2; K(1st or 2nd col) 1st = slope below optimum range, 2nd = slope above optimum range (note negative for 2nd value)						
44	.80 − 04	0.0	.10 − 03	−.10 − 03			(Sp 1)
45	.50 − 04	0.0	.10 − 03	−.10 − 03			(Sp 2)
46	.25 − 04	−.10 − 03	.10 − 03	−.10 − 03			(Sp 3)
47	.20 − 04	−.15 − 03	.10 − 03	−.10 − 03			(Sp 4)
48	.55 − 04	−.12 − 03	.10 − 03	−.10 − 03			(Sp 5)
49	.60 − 04	−.12 − 03	.10 − 03	−.10 − 03			(Sp 6)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	PT(IJK) = abiotic factors—optimum range outside of which *death rate* is increased; I(row) = species, J(cols 1, 2 vs 3, 4) factor 1 or 2; K(1st or 2nd col) 1st = lower bound, 2nd = upper bound						
38	.25 + 02	.106 + 03	.25 + 02	.75 + 02			(Sp 1)
39	.35 + 02	.106 + 03	.25 + 02	.75 + 02			(Sp 2)
40	.35 + 02	.98 + 02	.25 + 02	.75 + 02			(Sp 3)
41	.40 + 02	.101 + 03	.25 + 02	.75 + 02			(Sp 4)
42	.20 + 02	.10 + 03	.25 + 02	.75 + 02			(Sp 5)
43	.25 + 02	.10 + 03	.25 + 02	.75 + 02			(Sp 6)

Appendix B (cont.)

Card number	(Variable cards) Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	
	ASL(IJK) = abiotic factors—slope—constant reducing *birth rate modifier* per unit deviation of factor from optimum range stated in ALV(IJK) below; I(row) = species; J(cols 1, 2 vs 3, 4) = factor 1 or 2; K(1st or 2nd col) 1st = slope below optimum range, 2nd = slope above optimum range (note negative for 2nd value)						
50	.1667 − 01	0.0	.40 − 01	−.40 − 01			(Sp 1)
51	.20 − 01	0.0	.40 − 01	−.40 − 01			(Sp 2)
52	.45 − 01	−.75 − 01	.40 − 01	−.40 − 01			(Sp 3)
53	.47 − 01	−.70 − 01	.40 − 01	−.40 − 01			(Sp 4)
54	.80 − 01	−.50 − 01	.40 − 01	−.40 − 01			(Sp 5)
55	.57 − 01	−.35 − 01	.40 − 01	−.40 − 01			(Sp 6)
	ALV(IJK) = abiotic factors—optimum range outside of which *birth rate* is reduced; I(row) = species; J(cols 1, 2 vs 3, 4) = factor 1 or 2; K(1st or 2nd col) 1st = lower bound, 2nd = upper bound						
56	.105 + 03	.106 + 03	.25 + 02	.75 + 02			(Sp 1)
57	.90 + 02	.106 + 03	.25 + 02	.75 + 02			(Sp 2)
58	.75 + 02	.85 + 02	.25 + 02	.75 + 02			(Sp 3)
59	.78 + 02	.85 + 02	.25 + 02	.75 + 02			(Sp 4)
60	.60 + 02	.80 + 02	.25 + 02	.75 + 02			(Sp 5)
61	.65 + 02	.85 + 02	.25 + 02	.75 + 02			(Sp 6)

Appendix C. Sample Output

```
 ECDSYS MDDEL 2   UPDATED DEC 69

                          ECDSYSTEM INFDRMATIDN FDR INTERVAL NUMBER   541

                  ************************************************************************

INFD FDR SPECIES      1            2            3            4            5            6

                  ************************************************************************

SATIATN LVL (GM)  0.0          0.0          0.4362D 01   0.4943D 01   0.8895D 01   0.9006D 01
RATIDN (GM)       0.0          0.0          0.4362D 01   0.4943D 01   0.8895D 01   0.9006D 01
KCAL EXPENDED
    BDDY MASS     0.0          0.0          0.1594D 07   0.5585D 06   0.1303D 05   0.2484D 05
    ABIDT FACTRS  0.0          0.0          0.2129D 07   0.7507D 06   0.2295D 05   0.4303D 05
    REPRDDUCTIDN  0.0          0.0          0.0          0.0          0.0          0.0
    FEEDING       0.0          0.0          0.2702D 06   0.1278D 06   0.1001D 04   0.2366D 04
    ESCAPING      0.0          0.0          0.2097D 04   0.5962D 03   0.0          0.0
KCAL/INDIVIDUAL   0.0          0.0          0.9098D 01   0.1034D 02   0.3249D 02   0.3291D 02

TDT AVAIL KCAL    0.0          0.0          0.1803D 02   0.1646D 02   0.8359D 02   0.9588D 02
AVAIL KCAL FDDD   0.0          0.0          0.8949D 01   0.1017D 02   0.3090D 02   0.3133D 02

GMS STDRED FAT    0.5000D 01   0.7000D 01   0.4876D 01   0.3750D 01   0.2830D 02   0.3152D 02

BIRTH PRPDRTIDN-
ALITY CDNSTANTS
    WEATHER       0.0          0.0          0.0          0.0          0.0          0.0
    DTHER ABIDT   0.1000D 01   0.10000 01   0.1000D 01   0.1000D 01   0.1000D 01   0.1000D 01
    SPACE         0.1476D 00   0.1525D 00   0.1000D 01   0.1000D 01   0.1000D 01   0.1000D 01
    FOOD LACK     0.1000D 01   0.1000D 01   0.8836D 00   0.8834D 00   0.8510D 00   0.8520D 00

INSTANTANEDUS
DEATH RATES BY
    STARVATION    0.0          0.0          0.0          0.0          0.0          0.0
    WEATHER      -0.2075D-04  -0.5131D-03  -0.2565D-03  -0.3052D-03   0.0         -0.1556D-04
    DTHER ABIDT   0.0          0.0          0.0          0.0          0.0          0.0
    SP  1  PREDN  0.0          0.0          0.0          0.0          0.0          0.0
    SP  2  PREDN  0.0          0.0          0.0          0.0          0.0          0.0
    SP  3  PREDN -0.9092D-03  -0.6566D-03   0.0          0.0          0.0          0.0
    SP  4  PREDN -0.3189D-03  -0.2551D-03   0.0          0.0          0.0          0.0
    SP  5  PREDN  0.0          0.0         -0.1214D-02  -0.1159D-02   0.0          0.0
    SP  6  PREDN  0.0          0.0         -0.2348D-02  -0.2054D-02   0.0          0.0
    DTHER CAUSES -0.2000D-02  -0.3000D-02  -0.1800D-02  -0.2000D-02  -0.8500D-03  -0.8000D-03

PDPN RATE DF CHG -0.3249D-02  -0.4425D-02  -0.5618D-02  -0.5518D-02  -0.8500D-03  -0.8156D-03

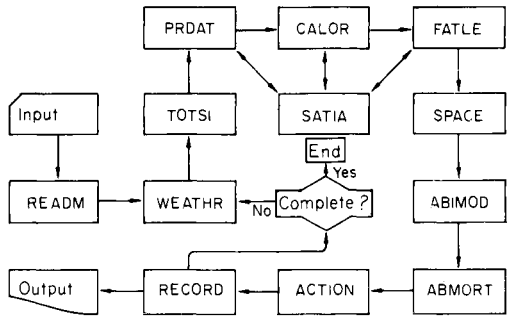
NUMBER DF INDIV   0.1584D 08   0.5693D 07   0.4367D 06   0.1382D 06   0.1137D 04   0.2132D 04
BIDMASS (GM)      0.1664D 10   0.6091D 09   0.6499D 07   0.1901D 07   0.1459D 06   0.2805D 06

                  ************************************************************************

 WEATHER MEASUREMENT:  0.2474D 02    DTHER ABIDTIC FACTDR:  0.5500D 02

                  ************************************************************************
```

Appendix D. The Computer Program

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C ** ECOSYS:  A PROGRAM TO SIMULATE AN ECOSYSTEM WITH SPECIFIABLE
C     INTERRELATIONS AMONG THE MEMBER ORGANISMS, AND WITH SPECIFIABLE
C     PHYSIOLOGICAL CHARACTERISTICS FOR AVERAGE INDIVIDUALS OF EACH
C     MEMBER SPECIES, WITH REGARD TO RESPONSES TO BIOTIC AND ABIOTIC
C     FACTORS.
C
      COMMON CK,DATRUN(9),IPAGE,STARS(3)
      INTEGER CK(16)
      DOUBLE PRECISION S(6),SIZE(6),PRED(6,6),D(6,10),RATIO(6),SUMP(6),
     1PSUM(6),BMETM (6),SKE(6),SKF(6),FAT(6),ENERG (6),CHO(6),STARV (6),
     2FFAMA(6),RSTRC(6,4),OPT(6,2,2),FL(2),G(6),POINT(6,2,2),PRTN(6),
     3SLOPE(6,2,2),ASLOP (6,2,2),ALEVE (6,2,2),TERTR (6,6),A(6),SEASO,
     4BIRTH(6),SIZ(6),E(6,5,2),DIGES,EBM(6),DEATH(6),FACTR,WEATHR,SL(6),
     5RATN(6,6),RATION(6),CSUM(6),EIND(6),Y(6,5),DIFF(6),DIFF1(6),X(6)
      DATA RSTRC /24*0.8D0/,D/60*0.D0/,EIND/2*225.,2*50.,2*325./
    2 FORMAT(I3,16I1,9A1,3A4)
      IPAGE = 1
C ** READ OUTPUT CONTROL VALUES, DATE, AND BORDER FOR HEADING
      READ(5,2)INTRVL,CK,DATRUN,STARS
      ICNT=INTRVL
      CALL READM(NOSPP,NOFAC ,SEASO ,FACTR ,FL, JST, JFIN  ,S,SIZE,PRED,
     1BMETM ,SKE,SKF,CHO,STARV ,DIGES ,FFAMA ,OPT,POINT,SLOPE,ASLOP ,
     2ALEVE ,TERTR ,A,BIRTH,SIZ,FAT,ENERG ,E,G,PRTN,DEATH,EBM)
      DO 1 I=1,NOSPP
      SL(I)=0.D0
      RATIO(I)=0.D0
      DIFF(I)=0.D0
    1 DIFF1(I)=0.D0
      DO 4 IDTH=1,NOSPP
    4 D(IDTH,10)=DEATH(IDTH)
      DO 1000 LENGT=JST,JFIN
      FL(1)=WEATHR(SEASO ,FACTR)
      CALL TOTSI (NOSPP,SIZ,SIZE,FAT)
      CALL PRDAT (NOSPP,NOFAC ,S,SIZE,PRED,D,RATIO ,SUMP,PSUM,BMETM ,
     1SKE,SKF,FAT,ENERG,EBM,BIRTH,RSTRC,RATN,RATION,CSUM,IHETER,SL)
      CALL CALOR (NOSPP,NOFAC ,S,SIZE,PRED,OPT,FL,G,E,BMETM,SKE,SKF,FAT,
     1PSUM,ENERG,SUMP,RATION,EBM,CSUM,D,EIND,Y)
      CALL FATLE(NOSPP,NOFAC,S,D,FAT,CHO,STARV,ENERG,DIGES,FFAMA,RSTRC,
     1PSUM,PRTN,SUMP,EBM,RATN,EIND,DIFF,DIFF1)
      CALL SPACE(NOSPP,NOFAC ,S,TERTR ,A,RSTRC)
      CALL ABIMOD(NOSPP,NOFAC ,ALEVE ,ASLOP ,FL,RSTRC)
      CALL ABMORT(NOSPP,NOFAC ,POINT,SLOPE,FL,D)
      CALL ACTION(NOSPP,NOFAC ,S,RSTRC ,D,BIRTH,G,X)
      IF(S(3).LT.1.D0.OR.S(4).LT.1.D0.OR.S(5).LT.1.D0.OR.S(6).LT.1.D0)
     1CALL RECORD(NOSPP,LENGT,RATIO,ENERG,FAT,RSTRC,D,S,SIZE,FL,Y,DIFF,
     2DIFF1,X,SL)
      IF(ICNT.LT.INTRVL)GO TO 3
      CALL RECORD(NOSPP,LENGT,RATIO,ENERG,FAT,RSTRC,D,S,SIZE,FL,Y,DIFF,
     1DIFF1,X,SL)
      IF(S(3).LT.1.D0.OR.S(4).LT.1.D0.OR.S(5).LT.1.D0.OR.S(6).LT.1.D0)
     1GO TO 1001
```

```
      ICNT=0
      IPAGE=IPAGE+1
    3 SEASO = SEASO + .8726646259971D-02*2.D0
      ICNT=ICNT+1
 1000 CONTINUE
 1001 STOP
      END
      SUBROUTINE READM(N,NF,SE,F1,F,JS,JF,S,SZ,P,BM,S1,S2,CHO,STV,DG,FM,
     1O,PT,SL,ASL,ALV,T,A,B,SIZ,FAT,ENG,E,G,PR,DTH,EBM)
      DOUBLE PRECISION F(2),S(6),SZ(6),P(6,6),BM(6),S1(6),S2(6),CHO(6),
     1FM(6),O(6,2,2),PT(6,2,2),SL(6,2,2),ASL(6,2,2),ALV(6,2,2),T(6,6),
     2A(6),B(6),SIZ(6),FAT(6),ENG(6),E(6,5,2),G(6),PR(6),STV(6),DTH(6),
     3EBM(6),SE,F1,DG
    1 FORMAT(6D10.4)
    2 FORMAT(4I5,4D10.4)
    3 FORMAT(10D8.5)
    4 FORMAT(4D10.4)
    5 FORMAT(' ',6D15.4)
    6 FORMAT('1',4I5,4D15.4)
    7 FORMAT(' ',10D12.3)
    8 FORMAT(' ',4D15.4)
    9 FORMAT('1')
      READ(5,2)N,NF,JS,JF,SE,F1,F(2),DG
      READ(5,1)S,SZ,SIZ,B,A,CHO,FAT,BM,S1,S2,ENG,STV,FM,G,PR,DTH,EBM
      READ(5,1)((P(I,J),J=1,N),I=1,N)
      READ(5,1)((T(I,J),J=1,N),I=1,N)
      READ(5,4)(((O(I,J,K),K=1,2),J=1,NF),I=1,N)
      READ(5,4)(((PT(I,J,K),K=1,2),J=1,NF),I=1,N)
      READ(5,4)(((SL(I,J,K),K=1,2),J=1,NF),I=1,N)
      READ(5,4)(((ASL(I,J,K),K=1,2),J=1,NF),I=1,N)
      READ(5,4)(((ALV(I,J,K),K=1,2),J=1,NF),I=1,N)
      READ(5,3)(((E(I,J,K),K=1,2),J=1,5),I=1,N)
      WRITE(6,6)N,NF,JS,JF,SE,F1,F(2),DG
      WRITE(6,5)S,SZ,SIZ,B,A,CHO,FAT,BM,S1,S2,ENG,STV,FM,G,PR,DTH,EBM
      WRITE(6,5)((P(I,J),J=1,N),I=1,N)
      WRITE(6,5)((T(I,J),J=1,N),I=1,N)
      WRITE(6,8)(((O(I,J,K),K=1,2),J=1,NF),I=1,N)
      WRITE(6,8)(((PT(I,J,K),K=1,2),J=1,NF),I=1,N)
      WRITE(6,8)(((SL(I,J,K),K=1,2),J=1,NF),I=1,N)
      WRITE(6,8)(((ASL(I,J,K),K=1,2),J=1,NF),I=1,N)
      WRITE(6,8)(((ALV(I,J,K),K=1,2),J=1,NF),I=1,N)
      WRITE(6,9)
      WRITE(6,7)(((E(I,J,K),K=1,2),J=1,5),I=1,N)
      RETURN
      END
      DOUBLE PRECISION FUNCTION WEATHR(S,F)
      DOUBLE PRECISION B,S,F
      B=(DSIN(S)+1.D0)/2.D0+.5D-01
      WEATHR=B*F
      RETURN
      END

      SUBROUTINE TOTSI (N,SZ,SIZE,FAT)
C
C ** TOTSI COMPUTES THE CURRENT INDIVIDUAL BIOMASS BY ADDING THE
C    CURRENT AMOUNT OF STORED FAT TO THE BASIC PROTEIN-CHO BODY MASS.
C
      DOUBLE PRECISION SZ(6) ,SIZE(6),FAT(6)
      DO 1 I=1,N
    1 SIZE(I)=SZ(I)+FAT(I)
      RETURN
      END

      SUBROUTINE PRDAT (N,NF,SP,SZ,P,C,RATIO ,SUMP,PSUM,8,SK1,SK2,FAT,
     1ENERG,EBM,BIR,R,RATN,RATION,CSUM,IHETER,SAT)
      DOUBLE PRECISION SP(6),SZ(6),P(6,6),C(6,10),RATIO(6),SUMP(6),
     1PSUM(6),B(6),SK1(6),SK2(6),FAT(6),ENERG (6),EBM(6),SATIA,SAT(6),
```

```
     2ZERO,CSUM(6),F(9),G(6),BIR(6),R(6,4),SDAD(6),SDEAD(6),RATN(6,6),
     3RATION(6)
  11 FORMAT(15X,'INPUT ERROR - POSITIVE SUM OF PRED RATES BY SP ',I3)
     ZERO=0.D0
     ITERAT = ZERO
     IHETER = 1
     M = N+NF+2
     L = NF+2
     DO 10 I=1,N
     SUMP(I)=ZERO
     RATIO(I)=ZERO
     SAT(I) = ZERO
     CSUM(I) = ZERO
     G(I) = BIR(I)
  10 PSUM(I)=ZERO
     DO 2 I=1,N
     DO 5 I1=1,L
   5 G(I)=G(I)*R(I,I1)
     K=I+NF+1
     DO 2 J=1,N
     C(J,K)=P(I,J)*SP(I)
     SUMP(J)=SUMP(J)+C(J,K)
   2 PSUM(I)=PSUM(I)+P(I,J)
     DO 1 J=1,N
     IF(PSUM(J))1,3,12
C
C ** IHETER IMPOSES A RESTRICTION ON INPUT TO THE ECOSYSTEM MODE
C    THOSE SPECIES WHICH ARE AUTOTROPHIC MUST BE GIVEN THE LOW ORDER
C    SUBSCRIPTS, WITHOUT ANY HETEROTROPHIC SPECIES HAVING SUBSCRIPTS
C    LOWER THAN ANY AUTOTROPHIC SPECIES. IHETER IS NO. AUTOTROPHS +1.
C
   3 IHETER = IHETER + 1
     GO TO 1
  12 WRITE(6,11)J
     STOP
   1 CONTINUE
     DO 4 I=IHETER,N
C
C ** SATIATION LEVEL REMAINS CONSTANT.
C
   4 SAT(I)=SATIA(FAT,ENERG,B,SK1,SK2,I,EBM)
     DO 14 I=1,N
     DO 14 J=1,M
C
C ** DEATH RATES FOR THE INITIAL COMPUTATIONS ARE SET AT THEIR MAXIMUM.
C
  14 CSUM(I)=CSUM(I)+C(I,J)
     DO 8 I=1,N
C
C ** SDEAD IS THE TOTAL DEATHS DURING THE INTERVAL.
C
     IF(DABS(G(I)+CSUM(I))-0.1D-10)25,26,26
  25 SDEAD(I)=(-1.D0*CSUM(I)*SP(I))
     GO TO 8
  26 SDEAD(I)=(-1.D0*CSUM(I)/(G(I)+CSUM(I)))*SP(I)*(DEXP(G(I)+CSUM(I))-
    11.D0)
   8 CONTINUE
     DO 6 I=IHETER,N
     DO 6 J=1,N
C
C ** THE MAXIMUM RATION, THAT WHICH WOULD OCCUR IF PREDATORS HUNTED TO
C    THEIR MAXIMUM CAPABILITY FULL TIME, IS USED IN THE INITIAL COMPUTA-
C    TION.  THE NAME"RATIO" IS RETAINED, EVEN THOUGH IT IS REDUCED.
C    THE UNIT OF MEASURE FOR "RATIO" IS BIOMASS.
C
   6 RATIO(I)=RATIO(I)+P(I,J)/CSUM(J)*SDEAD(J)*SZ(J)
     DO 30 I=IHETER,N
  30 RATION(I)=RATIO(I)
  20 ITERAT=ITERAT+1
C
C ** TEST TO PREVENT REMAINING IN LOOP IF THE COMPUTATIONS SHOULD NOT
```

```
C     CONVERGE.  THERE WILL BE A MAXIMUM OF 50 COMPUTATIONS.
C
      IF(ITERAT.GE.50)RETURN
      DO 9 I=IHETER,N
      K=I+NF+1
C
C ** F(K) IS THE PROPORTIONAL REDUCTION IN THE MAXIMUM DEATH RATE DUE
C     TO PREDATION.  THE REDUCTION IS BECAUSE OF ABUNDANT FOOD.  THE
C     PREDATOR IS SPECIES I.
C
      IF (RATIO(I).EQ.0.D0) RATIO(I)=.1D-9
      F(K)=SAT(I)/RATIO(I)
      IF(F(K).GT.1.D0)F(K)=1.D0
      DO 9 J=1,N
      C(J,K)=F(K)*C(J,K)
      RATN(I,J)=ZERO
    9 CONTINUE
      DO 13 J=1,N
      CSUM(J)=ZERO
   13 RATIO(J)=ZERO
      DO 15 K=1,M
      DO 15 J=1,N
   15 CSUM(J)=CSUM(J)+C(J,K)
      DO 40 I=1,N
      IF(DABS(G(I)+CSUM(I))-0.1D-10)41,41,42
C
C ** RECOMPUTATION OF SDEAD(I) USING THE ADJUSTED PREDATION RATES.
C
   41 SDEAD(I)=(-1.D0*CSUM(I)*SP(I))
      GO TO 40
   42 SDEAD(I)=(-1.D0*CSUM(I)/(G(I)+CSUM(I)))*SP(I)*(DEXP(G(I)+CSUM(I))-
     1 1.D0)
   40 CONTINUE
      DO 18 I=IHETER,N
      K=I+NF+1
      DO 18 J=1,N
C
C ** RATN(I,J) IS THE NUMBER OF INDIVIDUALS ONE INDIVIDUAL OF THE I TH
C     POPULATION TAKES FROM THE J TH BY PREDATION.
C
      RATN(I,J)=C(J,K)/(SP(I)*CSUM(J))*SDEAD(J)
C
C ** RECOMPUTATION OF RATIO AFTER FINDING THAT THE PREVIOUS RATIO WAS
C     TOO LARGE.
C
      RATIO(I)=RATIO(I)+C(J,K)/(SP(I)*CSUM(J))*SDEAD(J)*SZ(J)
   18 CONTINUE
      DO 19 I=IHETER,N
      K=I+NF+1
C
C ** IF THE NEWLY COMPUTED RATION APPROXIMATES THE SATIATION LEVEL FOR
C     ALL PREDATORS, THEN THE ITERATION IS COMPLETE AND THE PREDATION
C     MATRIX IS CORRECT IN ALL ENTRIES TO <=.01% IN THE ADJUSTMENT FACTOR
C     (DENSITY DEPENDENCY ADJUSTMENT) UNLESS THE FOOD SPECIES POPULATION
C     LEVELS ARE TOO LOW FOR THE PREDATOR'S MAXIMUM PREDATION RATES TO BE
C     EFFECTIVE.
C
      IF(F(K).GT..9999D0)GO TO 19
      GO TO 20
   19 CONTINUE
      RETURN
      END

      DOUBLE PRECISION FUNCTION SATIA(FAT,ENERG,B,SK1,SK2,I,EBM)
      DOUBLE PRECISION FAT(6),ENERG(6),SK1(6),SK2(6),B(6),EBM(6),E,F
      IF(ENERG(I))1,1,2
    2 F=FAT(I)
      E=ENERG(I)
      SATIA=(B(I)-SK2(I)*F**2)*(1.D0-DEXP(SK1(I)*(E-EBM(I))/EBM(I)))
      IF(SATIA)1,3,3
    3 RETURN
```

```
    1 SATIA = 0.D0
      RETURN
      END

       SUBROUTINE CALOR(N,NF,S,SZ,P,O,FL,G,E,B,SK1,SK2,FAT,PSUM,ENERG,
      1SUMP,RATIO,Y1,CSUM,C,EIND,Y)
C
C ** CALOR IS A SUBROUTINE TO COMPUTE THE ENERGY EXPENSE OF THE
C    ORGANISMS DUE TO BODY MASS, ABIOTIC FACTORS, REPRODUCTION, FEEDING,
C    AND ESCAPING THEIR PREDATORS.
C
       DOUBLE PRECISION E(6,5,2),S(6),SZ(6),O(6,2,2),FL(2),G(6),RATIO(6),
      1B(6),SK1(6),SK2(6),ENERG(6),FAT(6),PSUM(6),Y(6,5),SUMP(6),EIND(6),
      2P(6,6),Y1(6),SATIA,SATLV,X,OPTMU,CSUM(6),C(6,10),FOOD(6),SBAR(6)
       IHETER = 1
       DO 98 I=1,N
       DO 99 J=1,5
   99 Y(I,J)=0.D0
   98 FOOD(I)=0.D0
       DO 11 I=1,N
       IF(PSUM(I))4,3,3
    4 SATLV=SATIA (FAT,ENERG ,B,SK1,SK2,I,Y1)
C
C ** ENERGY EXPENSE DUE TO BODY MASS
C
       X=E(I,1,1)*SZ(I)**(2.D0/3.00)*S(I)
       Y(I,1)=X
       Y1(I)=Y(I,1)/S(I)
C
C ** ENERGY EXPENSE DUE TO ABIOTIC FACTORS
C
       DO 2 J=1,NF
       OPTMU =.5D0*(O(I,J,1)+O(I,J,2))
    2 X=X+E(I,2,J)*(DABS(FL(J)-OPTMU ))*S(I)
       Y(I,2)=X-Y(I,1)
C
C ** ENERGY EXPENSE DUE TO REPRODUCING, NURSING, REARING YOUNG, ETC.,
C    ASSUMED PROPORTIONAL TO PRODUCTION OF BIOMASS; AN AMT OF ENERGY IS
C    SPENT EQUAL TO 1.5 TIMES THE BIOMASS PRODUCED, BUT THAT IS NOT ALL
C    LOST, SINCE THE ENERGY OF NEW BIOMASS IS AN ENERGY GAIN.
C
       X=X+E(I,3,1)*G(I)*S(I)*EIND(I)
       Y(I,3)=X-Y(I,2)-Y(I,1)

C
C ** ENERGY EXPENSE DUE TO CAPTURING FOOD, PROPORTIONAL TO SATIATION
C    LEVEL AND INVERSELY PROPORTIONAL TO FOOD RATIDN POTENTIAL
C
       IF (RATIO(I).EQ.0.D0) RATIO(I)=.1D-9
       Y(I,4)=E(I,4,1)*SATLV*S(I)/RATIO(I)
       IF(Y(I,4)/S(I).GT.2.D0*Y1(I))Y(I,4)=Y1(I)*S(I)*2.D0
       X=X+Y(I,4)
       GO TO 11
    3 X=0.D0
       IHETER=IHETER+1
   11 ENERG(I)=X
C
C ** ENERGY EXPENSE DUE TO ESCAPING PREDATORS, PROPORTIUNAL TO THE
C    AMOUNT OF ENERGY ALL PREDATORS EXPEND IN CAPTURING MEMBERS OF THIS
C    SPECIES
C
       X=0.D0
       DO 28 I=1,N
       IF(DABS(G(I)+CSUM(I))-.1D-10)26,27,27
   26 SBAR(I)=S(I)
       GO TO 28
   27 SBAR(I)=S(I)*(DEXP(G(I)+CSUM(I))-1.D0)/(G(I)+CSUM(I))
   28 CONTINUE
       DO 21 I=1,N
       IF(SUMP(I))8,9,9
```

```
    8 DO 29 JP=IHETER,N
      JPRED=JP+NF+1
      DO 6 JPREY=1,N
    6 FOOD(JP)=FOOD(JP)+C(JPREY,JPRED)*SBAR(JPREY)
      IF(FOOD(JP).NE.0.D0)Y(I,5)=Y(I,5)+C(I,JPRED)*SBAR(I)/FOOD(JP)*
     1Y(JP,4)
   29 FOOD(JP)=0.D0
      Y(I,5)=E(I,5,1)*Y(I,5)
      IF(Y(I,5)/S(I).GT.2.D0*Y1(I))Y(I,5)=Y1(I)*S(I)*2.D0
      GO TO 7
    9 Y(I,5)=0.D0
    7 X=Y(I,5)
   21 ENERG(I)=ENERG(I)+X
      DO 30 I=IHETER,N
   30 ENERG(I)=ENERG(I)/S(I)
      RETURN
      END

      SUBROUTINE FATLE(N,NF,S,D,FAT,CHO,STV,ENERG,DIGES,FFAMA,R,PSUM,PR,
     1SUMP,EBM,RATN,EIND,DIFF,DIFF1)
      DOUBLE PRECISION S(6),D(6,10),FAT(6),CHD(6),STV(6),ENERG(6),
     1FFAMA(6),R(6,4),PSUM(6),SUMP(6),SUMPD(6),PR(6),CAL(2),RATN(6,6),
     2EBM(6),DIGES,C,F,FOOD,UNTKN,E,FCL,FBAR,CCHO,CFAT,ENGDI,FENMA,ZERO,
     3EIND(6),DIFF1(6),DIFF(6),STRV
      ZERO=0.D0
      M=NF+2
      MN=N+NF+2
      CAL(1)=4.1D0
      CAL(2)=9.3D0
      DO 14 I=1,N
      R(I,4)=1.D0
      D(I,1)=0.D0
   14 SUMPD(I)=ZERO
C
C ** COMPUTATION OF THE NO. OF CALORIES IN AN INDIVIDUAL OF EACH SPECIES
C    (THIS INFO PASSED TO CALOR).
C
      DO 30 I=1,N
   30 EIND(I)=CAL(1)*CHD(I)+CAL(2)*FAT(I)+CAL(1)+PR(I)
      DO 1 I=1,N
      IF(PSUM(I))6,1,1
    6 C=ZERO
      F=ZERO
      FOOD=ZERO
      NG=NF+1+I
      DO 7 J=1,N
      DO 13 K=1,MN
   13 SUMPD(J)=SUMPD(J)+D(J,K)
      UNTKN=0.D0
      IF(SUMPD(J))15,7,7
C
C ** UNTKN = NUMBER OF PREY TAKEN BY ONE INDIVIDUAL PREDATOR.  AMOUNT OF
C    FAT, CHO, PR, OR SZ TIMES UNTKN IS AMOUNT OF FAT, CARBOHYDRATE,
C    PROTEIN, OR BIOMASS (WET WEIGHT) TAKEN, RESPECTIVELY, BY THAT
C    INDIVIDUAL PREDATOR.
C
   15 UNTKN=RATN(I,J)
C
C ** F, C, AND FOOD ARE THE AMOUNTS OF FAT, CHO, AND FOOD EATEN BY
C    SPECIES I, J IS PREY SPECIES, AND NG INDEXES THE APPLICABLE DEATH
C    RATE DUE TO PREDATION.
C
      F=F+FAT(J)*UNTKN
    7 C=C+(CHD(J)+PR(J))*UNTKN
      FOOD=F+C
      E=ENERG (I)
C
C ** FCL IS AMOUNT OF UNDIGESTED FOOD MATERIAL.
C
      FCL=FOOD*DEXP(DIGES)
```

```
C
C ** FBAR IS MEAN FOOD AVAILABLE DURING THE CURRENT INTERVAL.
C
      FBAR=(FCL-FOOD)/DIGES
C
C ** CCHO IS PROPORTION OF DIGES WHICH MULTIPLIES FBAR TO GIVE AMOUNT
C    OF CHO DIGESTED IN THE INTERVAL.
C
      IF((C+F).EQ.0.D0) F=.1D-9
      CCHO=-DIGES*C/(C+F)
C
C ** CFAT IS PROPORTION OF DIGES WHICH MULTIPLIES FBAR TO GIVE AMOUNT
C    OF FAT DIGESTED IN THE INTERVAL.
C
      CFAT=-DIGES*F/(C+F)
C
C ** ENGDI IS ENERGY EXPENDED MINUS FOOD CHO ENERGY.
C
      ENGDI =E-CAL(1)*CCHO*FBAR
C
C ** FENMA IS ENERGY FROM TOTAL FAT AVAILABLE DURING THE INTERVAL AS
C    FREE FATTY ACIDS.
C
      FENMA = CAL(2)*(CFAT*FBAR + FFAMA(I)*FAT(I))
      DIFF(I)=ENGDI-FENMA
      DIFF(I)=E-DIFF(I)
      DIFF1(I)=CAL(1)*CCHO*FBAR+CAL(2)*CFAT*FBAR
      IF(ENGDI)8,8,9
    8 FAT(I)=FAT(I)+F-ENGDI/CAL(2)
      GO TO 10
    9 IF(FENMA-ENGDI)11,12,12
   11 FAT(I)=FAT(I)+F-FENMA/CAL(2)
      GO TO 10
   12 FAT(I) = FAT(I)+F-ENGDI/CAL(2)
   10 IF(FAT(I))4,5,5
    4 FAT(I)=ZERO
    5 R(I,M)=DIFF1(I)/E-.1D0
      IF(R(I,M).GT.1.D0)R(I,M)=1.D0
      IF(R(I,M).LT.0.D0)R(I,M)=0.D0
      STRV=DIFF(I)/E-.25D0
      IF (STRV.GT.1.D0)STRV=1.D0
      IF(STRV.LT..1D-02)STRV=.1D-02
      D(I,1)=STV(I)*DLOG(STRV)
    1 CONTINUE
      RETURN
      END

      SUBROUTINE SPACE(N,NF,S,T,A,R)
      DOUBLE PRECISION S(6),T(6,6),A(6),R(6,4),SUM(6)
      M=NF+1
      DO 1 I=1,N
      SUM(I)=0.D0
    1 R(I,M)=SUM(I)
      DO 3 I=1,N
      DO 2 J=1,N
    2 SUM(I)=SUM(I)+T(J,I)*S(J)
      IF (SUM(I).GT.0.D0) SUM(I)=0.D0
    3 R(I,M)=(A(I)+SUM(I))/A(I)
      RETURN
      END

      SUBROUTINE ABIMOD(N,NF,A,B,F,R)
      DOUBLE PRECISION A(6,2,2),B(6,2,2),F(2),R(6,4),X
      DO 1 I=1,N
      DO 1 J=1,NF
      IF(F(J)-A(I,J,1))2,3,4
    4 IF(F(J)-A(I,J,2))3,3,5
    2 X=B(I,J,1)*(F(J)-A(I,J,1))+1.D0
      GO TO 6
    5 X=B(I,J,2)*(F(J)-A(I,J,2))+1.D0
    6 IF(X)7,7,8
    7 R(I,J)=0.D0
      GO TO 1
```

```
 8 IF(X-1.D0)9,9,3
 9 R(I,J)=X
   GO TO 1
 3 R(I,J)=1.D0
 1 CONTINUE
   RETURN
   END

   SUBROUTINE ABMDRT(N,NF,P,S,F,C)
   DOUBLE PRECISION P(6,2,2),S(6,2,2),C(6,10),F(2),B,X
   DO 11 I=1,N
   DO 11 J=1,NF
   IF(F(J)-P(I,J,1))2,3,4
 4 IF(F(J)-P(I,J,2))3,3,5
 2 B=S(I,J,1)
   X=F(J)-P(I,J,1)
   GO TO 6
 5 B=S(I,J,2)
   X=F(J)-P(I,J,2)
   GO TO 6
 3 C(I,J+1)=0.D0
   GO TO 11
 6 IF((1.D0+B*X).LT.0.85D-02) GO TO 3
   C(I,J+1)=DLOG(1.D0+B*X)
11 CONTINUE
   RETURN
   END

   SUBROUTINE ACTION(N,NF,SP,R,C,BIR,Y,X)
   DOUBLE PRECISION SP(6),R(6,4),C(6,10),BIR(6),X(6),Y(6),A,B
   K=NF+2
   L=N+NF+2
   DO 1 I=1,N
   A=1.D0
   B=0.D0
   DO 2 J=1,K
 2 A=A*R(I,J)
   DO 3 J=1,L
 3 B=B+C(I,J)
   X(I)=BIR(I)*A+B
   Y(I)=X(I)-B
   SP(I) = SP(I)*DEXP(X(I))
 1 IF(SP(I).LT.1.D0) SP(I)=1.D0
   RETURN
   END

   SUBROUTINE RECORD(N,LENGT,RATN,ETDT,FAT,R,D,S,SZ,FACLEV,E,AVCAL,
  1KCALFD,CHG,SL)
   COMMON CK,DATRUN(9),IPAGE,STARS(3)
   DOUBLE PRECISION RATN(6),ETOT(6),FAT(6),R(6,4),D(6,10),S(6),SZ(6),
  1BIOMAS(6),FACLEV(2),E(6,5),AVCAL(6),CHG(6),SL(6)
   DOUBLE PRECISION KCALFD(6)
   INTEGER CK(16)
 1 FORMAT('0    SATIATN LVL (GM)'8D12.4)
 2 FORMAT('     RATION (GM)     '8D12.4/)
 3 FORMAT('     KCAL EXPENDED'/8X' BODY MASS'3X,8D12.4)
 4 FORMAT('         ABIDT FACTRS'8D12.4)
 5 FORMAT('         REPRDDUCTION'8D12.4)
 6 FORMAT('         FEEDING     '8D12.4)
 7 FORMAT('         ESCAPING    '8D12.4)
 8 FORMAT  ('     KCAL/INDIVIDUAL '8D12.4)
 9 FORMAT('0    TOT AVAIL KCAL  '8D12.4)
10 FORMAT('     AVAIL KCAL FOOD '8D12.4)
11 FORMAT('0    GMS STORED FAT  '8D12.4)
12 FORMAT('0    BIRTH PRPORTION-'/4X' ALITY CONSTANTS'/9X'WEATHER'5X,
  18D12.4)
13 FORMAT('         OTHER ABIOT '8D12.4)
14 FORMAT('         SPACE       '8D12.4)
15 FORMAT('         FOOD LACK   '8D12.4)
```

```
 16 FORMAT('0    INSTANTANEOUS'/4X' DEATH RATES BY  '/9X'STARVATION',
   12X,8D12.4)
 17 FORMAT('         WEATHER      '8D12.4)
 18 FORMAT('         SP'I3,'  PREDN'6D12.4)
 19 FORMAT('0    POPN RATE OF CHG' 8D12.4)
 20 FORMAT('0    NUMBER OF INDIV ' 8D12.4)
 21 FORMAT('     BIOMASS (GM)    '8D12.4)
 22 FORMAT('         OTHER CAUSES' 8D12.4)
 23 FORMAT('1     ECOSYS MODEL 2   UPDATED DEC 69'53X,9A1,4X,'PAGE'I4)
 24 FORMAT('0'35X,'ECOSYSTEM INFORMATION FOR INTERVAL NUMBER'I6)
 25 FORMAT('0'21X,24A4)
 26 FORMAT('0    INFO FOR SPECIES'I7,7I12)
 27 FORMAT('0'5X,'WEATHER MEASUREMENT:'D12.4,4X,'OTHER ABIOTIC FACTOR:
   1'D12.4)
 28 FORMAT(I5,6D11.4)
    DO 100 I=1,N
100 BIOMAS(I)=S(I)*SZ(I)
    WRITE(6,23)DATRUN,IPAGE
    WRITE(6,24)LENGT
    WRITE(6,25)(STARS,I=1,N)
    WRITE(6,26)(I,I=1,N)
    WRITE(6,25)(STARS,I=1,N)
    IF(CK( 1).EQ.1)WRITE(6, 1)SL
    IF(CK( 2).EQ.1)WRITE(6, 2)RATN
    IF(CK( 3).EQ.1)WRITE(6, 3)(E(I,1),I=1,N)
    IF(CK( 4).EQ.1)WRITE(6, 4)(E(I,2),I=1,N)
    IF(CK( 5).EQ.1)WRITE(6, 5)(E(I,3),I=1,N)
    IF(CK( 6).EQ.1)WRITE(6, 6)(E(I,4),I=1,N)
    IF(CK( 7).EQ.1)WRITE(6, 7)(E(I,5),I=1,N)
    IF(CK( 8).EQ.1)WRITE(6, 8)ETOT
    IF(CK( 9).EQ.1)WRITE(6, 9)AVCAL
    IF(CK(10).EQ.1)WRITE(6,10)KCALFD
    IF(CK(11).EQ.1)WRITE(6,11)FAT
    IF(CK(12).EQ.1)WRITE(6,12)(R(I,1),I=1,N)
    IF(CK(12).EQ.1)WRITE(6,13)(R(I,2),I=1,N)
    IF(CK(12).EQ.1)WRITE(6,14)(R(I,3),I=1,N)
    IF(CK(12).EQ.1)WRITE(6,15)(R(I,4),I=1,N)
    IF(CK(13).EQ.1)WRITE(6,16)(D(I,1),I=1,N)
    IF(CK(13).EQ.1)WRITE(6,17)(D(I,2),I=1,N)
    IF(CK(13).EQ.1)WRITE(6,13)(D(I,3),I=1,N)
    DO 88 K=1,N
    J=K+3
    IF(CK(13).EQ.1)WRITE(6,18)K,(D(I,J),I=1,N)
 88 CONTINUE
    IF(CK(13).EQ.1)WRITE(6,22)(D(I,10),I=1,N)
    IF(CK(14).EQ.1)WRITE(6,19)CHG
    IF(CK(15).EQ.1)WRITE(6,20)S
    IF(CK(16).EQ.1)WRITE(6,21)BIOMAS
    IF(CK(4).EQ.0.AND.CK(12).EQ.0.AND.CK(13).EQ.0)GO TO 99
    WRITE(6,25)(STARS,I=1,N)
    WRITE(6,27)FACLEV
 99 WRITE(6,25)(STARS,I=1,N)
    RETURN
    END
```

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7

Systems Approaches to the Study of Forest Floor Arthropods

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I. Introduction

The assemblage of organisms living on the deciduous forest floor plays an important role in the decomposition and recycling of organic matter and nutrients (e.g., Van der Drift, 1951). Because of this function, an understanding of the dynamics of this subcommunity can make a major contribution to knowledge of the forest ecosystem as a whole. Bray (1961) has calculated that as much as 94% of forest primary production may

cycle directly through the decomposers. Additionally, large decomposer components have been found in a number of other natural ecosystems (e.g., Odum, 1957).

Describing the dynamics of cryptozoa has been a difficult task because they constitute a complex system with hundreds of populations and intricate trophic interactions (Burges and Raw, 1967). With the introduction of high-speed computers and techniques of systems analysis, mathematical methods are becoming available to treat such systems. However, there remains a gap between theoretical development of the techniques and their application in simulating real situations. This problem is being solved, nevertheless, by simplifying the quantification of these systems and simulating behavior which deviates significantly from a simple equilibrium.

The cryptozoa present several problems of particular interest. First, these organisms exhibit large seasonal fluctuations in numbers and energy flow. Such behavior is not described adequately by constant coefficient linear equations. Second, assigning values for material transfers within such a complex system is difficult and calls for development of simplifying techniques. Third, the logic of compromising available modeling techniques and the usual paucity of available information to produce a reasonable simulation never has been defined well. Approaches to these problems are being developed, and a sampling will be presented in this chapter. Extensive examples are used to demonstrate how the methods can be used to solve real problems. An attempt also will be made to follow in some detail the logical steps needed to construct a preliminary working model of an entire cryptozoan system. The discussion will emphasize the balance which must be achieved between elegance of mathematical tools and limited empirical knowledge.

II. Techniques for Simulating Large-Scale Fluctuations

A. Seasonal Dynamics

Energy flow studies have recognized the importance of soil invertebrate dynamics. Attempts to estimate annual energy flow have been made in a number of natural populations such as mites (Engelmann, 1961), millipedes (Bocock *et al.*, 1967), isopods (Saito, 1965), and collembola (Healey, 1967). In these studies total energy entering the population through feeding was measured together with excretion and respiration losses. These studies represent a considerable advancement in knowledge of cryptozoa and also a significant development of methods for measuring energy flux dynamics. However, they largely ignored an important

aspect of temporal dynamics, the fluctuations which occur during the year. Such seasonal changes are often dramatic among soil populations and must be understood before the total system dynamics can be.

This section will outline one method by which temporal dynamics can be modeled. The method involves treating energy transfer as a variable coefficient linear system. The variable coefficients are expressed as functions of a set of environmental variables, and the equations are represented economically in matrix notation. The method is then applied is an illustration to a study of seasonal energy fluctuations in a millipede population (O'Neill, 1968a).

1. *The Variable Coefficient Method*

Consider the simple system shown in Fig. 1, where X represents standing crop of the population (calories per unit area), I is input flux or ingested energy, E is output flux in excretions, and R is output flux as respiration. All three fluxes are in units of calories per unit area per unit time. Changes in standing crop are then defined by the difference

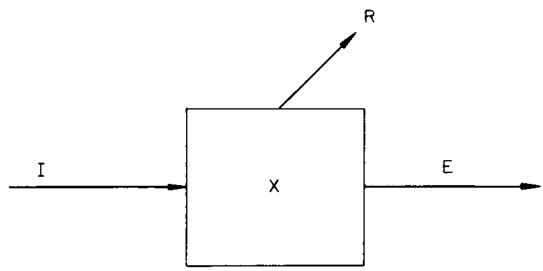

FIG. 1. Simplified representation of energy flow through an animal population, where I represents energy ingested, E and R represent energy losses to excretion and respiration, respectively, and X represents standing crop of the population.

between input and output fluxes. For simplicity, let us consider only one of the three fluxes, the respiratory output R, and assume that it can be represented as a simple linear function

$$R = aX, \tag{1}$$

where a is a coefficient expressing the fraction of the energy pool lost per unit time (calories per calories-time). Assume for the moment that the other fluxes in Fig. 1 can be described by a similar function. (Further discussion of this point will be covered in the analysis of the millipede example below.)

If the transfer coefficient in Eq. (1) is expressed as a constant, the magnitude of the flux depends only on the standing crop of the population and the type of system employed will be similar to conventional studies of energy flow. That is, the model will be unable to account for seasonal changes in respiration rates. To account for such changes, the coefficient must be expressed as a function of a set of environmental variables

$$a = f(\{y_i\}), \tag{2}$$

where $\{y_i\}$ is a set of such variables as rainfall, temperature, etc. The task then becomes one of discovering the appropriate variables and devising an expression for the function in Eq. (2). A variety of approaches is available but multiple regression recommends itself for several reasons. Multiple regression analyses have become familiar tools in ecological research, and discussions are available in a wide number of excellent statistical texts. As a result, the method is perhaps the most universally understood. In addition, the implementation known as stepwise multiple regeression permits determination of the appropriate variables as well as an expression for the function in Eq. (2).

In general, this technique involves a factorial experiment or extensive field sampling in which a dependent variable a such as the transfer coefficient, is measured with a number, $n - 1$, of independent variables y_i. The data are fitted to a linear model of the form

$$a = c_0 + \sum_{i=1}^{n-1} c_i y_i + \epsilon, \tag{3}$$

where c_0 is the additive constant, c_i is the ith coefficient, y_i is the ith variable, and ϵ is an error term. In effect, the technique for a vector of coefficients minimizes the error of estimate. In stepwise multiple regression, independent variables enter the equation in the order of significance, i.e., the first variable to enter will account for the greatest variance in the dependent variable. Other variables enter the equation until further additions no longer reduce the error significantly.

This method enables us to produce a workable expression for the function in Eq. (2). If the error term is assumed to be zero, we can express Eq. (3) more simply by matrix notation and definition of the dot product

$$a = \mathbf{cy}, \tag{4}$$

where $\mathbf{c}$ is a vector of coefficients and $\mathbf{y}$ is the vector of independent variables with unity as its first element (inclusion of the number one

corresponds to the inclusion of c_0 as the first element of the coefficient vector). Both vectors are of dimension n ($\mathbf{c}$ is a row vector, $\mathbf{y}$ a column vector), where n is the number of independent variables plus one.

If we assume that the population is at equilibrium, i.e., that the standing crop is constant, Eq. (4) can be substituted into Eq. (1) to yield

$$R_j = \mathbf{c}\mathbf{y}_j X, \tag{5}$$

where R_j is the respiratory flux at time j and $\mathbf{y}_j$ is the vector of environmental variables measured at time j. If a more empirical expression is desired which does not assume equilibrium, then the constant X in Eq. (5) can be replaced by X_j, the standing crop measured at time j. The respiratory energy flux at time j would then be expressed as

$$R_j = \mathbf{c}\mathbf{y}_j X_j \tag{6}$$

and the total energy flux for the year R_T as

$$R_T = \mathbf{c}Y\mathbf{x}\,\Delta t, \tag{7}$$

where Y is an $n \times m$ matrix of $n - 1$ independent variables measured at m successive intervals, $\mathbf{x}$ is an $m \times 1$ vector of standing crop determinations made at m successive intervals, and Δt is the length of time between samplings. Equation (7) expresses the total respiratory flux in a manner that explicitly accounts for fluctuations in the respiration transfer coefficient during the year. In addition, Eq. (6) can evaluate the flux at various times during the year and produce a vector $\mathbf{r}$ of fluxes for m successive periods.

This method is a discrete time approximation. The changes that occur in nature are continuous, implying that Δt in Eq. (7) approaches zero and m, the number of evaluated points in time, approaches infinity. The above formulation has the advantage, however, of being adapted to the digital computer which employs discrete time calculations, and is adequate to describe the typically discontinuous collection of data in the field.

2. *Application to a Study of Millipede Energetics*

In the millipede study mentioned above (O'Neill, 1968), measurements of feeding and excretion coefficients (calories per calories-day) were made with adult *Narceus americanus*. Temperature, relative humidity, and moisture content of the food were found to be primary variables determining these coefficients. Equation (1) provided a satisfactory model for the excretory flux since excretion depended only on the

standing crop of millipedes. The model was also an adequate description of ingestion flux, since the millipedes neither were limited by food nor displayed density-dependent limitations at the population levels studied. Therefore, the input flux depended only on the millipede population and not on size of the food supply or any powers of the millipede standing crop.

The multiple regression techniques used in this study deviated from the procedure recommended in Section II.A.1 and it is perhaps worthwhile to examine this alternative method for choosing the appropriate environmental variables. In the millipede study, the appropriate variables had been determined in preliminary trials. The problem then was to include sufficient power terms and cross-products to reach a predetermined level of prediction and still set a practical upper limit on the total number of variables used. A prediction goal was set at a multiple correlation coefficient of 0.85. To achieve this, logical criteria were chosen for limiting variables.

Experimental results revealed that the regression on temperature could be described as a cubic function. Therefore, temperature variables to the third power were included. Inclusion of the fourth power did not seem justified when an adequate description could be made with a cubic function. Only two humidities were used in the experiment and a linear function was sufficient to describe this relation. Three levels of food moisture were involved and a quadratic function sufficed. This was the basis used to determine the power to which each of the variables would be raised. These were included as independent variables along with the possible cross-products. In this way it was possible to include sufficient variables to achieve the degree of prediction desired. Inclusion of further terms might continue to improve the prediction slightly but would make the formula too cumbersome; furthermore, their inclusion could not be justified by the criteria just outlined. Table I summarizes the coefficients and variable vectors appropriate for use in Eqs. (6) and (7).

By applying the variable coefficient method to these data, it was possible to determine the feeding and excretion fluxes at weekly intervals and compare the prediction with major features of the animals' life cycle. The original paper should be consulted for details of this analysis. It will suffice for our purposes to examine Fig. 2 and note that energy peaks occur in the spring during the mating season and in the fall when energy reserves are being deposited for hibernation. The predicted drop in mid-August corresponds to the period of annual molt. Of greater interest at present is the comparison between predicted excretory coefficients and actual coefficients measured in the field on a confined population. Figure 3 compares these values and indicates that the model

TABLE I

VECTOR OF ENVIRONMENTAL VARIABLES AND COEFFICIENT VARIABLES FOR COMPUTATION OF INGESTION AND ELIMINATION PARAMETERS[a]

Variable vector	Coefficient vector for ingestion	Coefficient vector for excretion
T[b]	−120.4	−73.8
H[c]	−697.4	−369.4
M[d]	+4347.9	+4266.8
T^2	+16.2	+12.4
T^3	−0.4	−0.4
TH	+363.4	+253.9
T^2H	−38.6	−29.2
T^3H	+1.0	+0.8
TM	+148.6	+93.7
T^2M	−94.1	−84.8
T^3M	+3.6	+3.4
T^2M^2	+232.2	+211.2
T^3M^2	−9.8	−9.2
THM	−3721.2	−3147.0
T^2HM	+433.3	+369.4
T^3HM	−11.5	−9.9
THM^2	+9198.4	+7657.4
T^2HM^2	−110.5	−926.2
T^3HM^2	+30.1	+25.6
M^2	−12947.1	−12056.4
HM	+5680.7	+4392.4
HM^2	−21954.6	−9611.0
1	+7.9	−131.6

[a] Data from O'Neill (1968).
[b] T is temperature in degrees Centigrade.
[c] H is relative humidity in fraction (99% = 0.99).
[d] M is food moisture in fraction (dry weight per wet weight).

was able to give a reasonable estimate of this parameter's fluctuation under field conditions.

This method has been utilized implicitly in a limited number of energy studies (e.g., Healey, 1967; Berthet, 1967; White, 1968) and also in a study of nitrogen cycling by earthworms (Satchell, 1963). In these papers the form of the expression in Eq. (2) was determined by regression against temperature alone and was therefore a less complete representation of the natural systems. Equations (6) and (7) constitute a realistic and practical method for expressing temporal fluctuations of energy flow through natural populations. Figure 2 should provide some impression of the loss of information in regarding the transfer coefficient of Eq. (1)

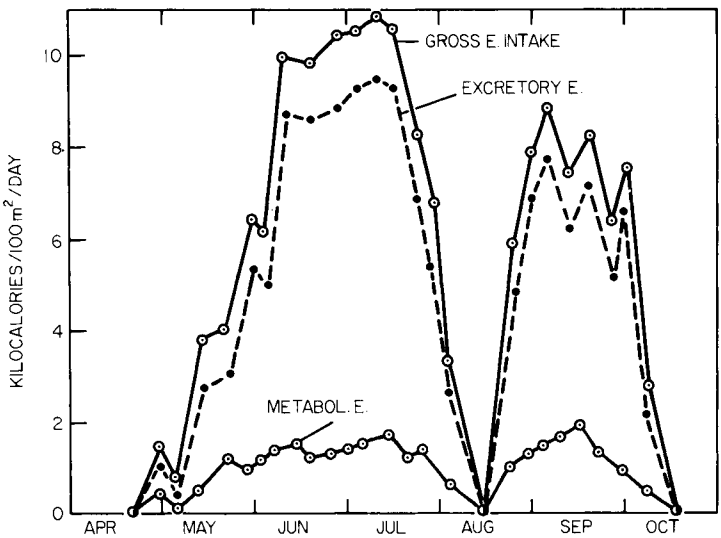

FIG. 2. Values for energy intake, energy loss, and available metabolizable energy for a population of millipedes, *Narceus americanus*, in an Illinois woodland.

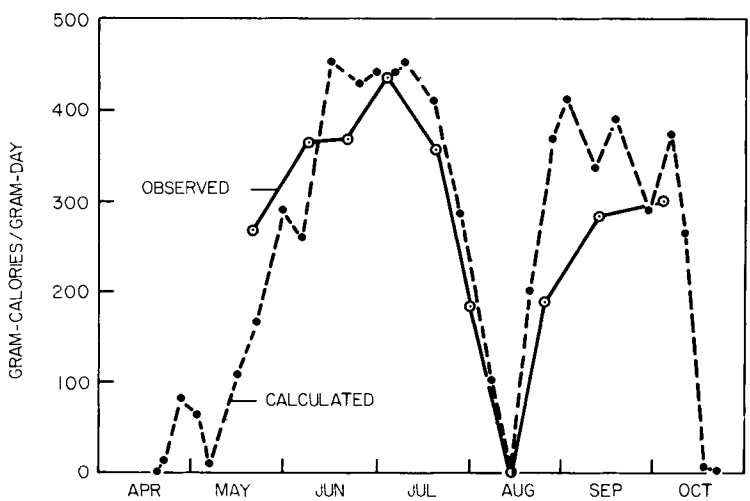

FIG. 3. Comparison of observed and predicted values for caloric excretory loss coefficient in a population of millipedes, *Narceus americanus* (from O'Neill, 1968).

as a constant. Use of the multiple regression technique to determine the function in Eq. (2) makes the method flexible and readily available to the researcher. In other studies, where seasonal changes in fluxes constitute an important component of the total system, this method could provide a useful tool.

B. Population Dynamics

As mentioned in the Introduction, challenging problems of the forest floor ecosystem include understanding and predicting large fluctuations in population size. The techniques of simulation modeling are readily applicable to these problems. This section will elaborate on a method for simulating population fluctuations on the digital computer. We will make use of nonlinearities and the technique of variable transfer coefficients developed in the previous section to simulate system behavior under natural conditions. To illustrate the method, we will model a hypothetical collembola population and attempt to predict effects of ionizing radiation as a demonstration of applying the theory to the preliminary solution of a real problem.

1. *Basic Population Simulation Methods*

In order to model population fluctuations, it is necessary to divide the total population N_t into discrete age groups N_i so that

$$N_t = \sum_{i=1}^{n} N_i , \tag{8}$$

where n is the number of age groups. Each of the n age groups is then considered as a separate compartment whose changes with time are defined by

$$dN_i/dt = \mu_{i-1} N_{i-1} - \lambda_i N_i - \mu_i N_i , \tag{9}$$

where N_{i-1} is the previous age group, μ_{i-1} is the transfer coefficient which expresses the proportion of animals of age $i - 1$ that will develop into the next age group during an interval of time, and λ_i is the mortality coefficient of animals dying per animal of age i during the time interval. The population can then be represented as a compartment model (Fig. 4).

Once the problem has been placed into this context, a number of different analytical approaches can be used. Differential equations such as Eq. (9) could be constructed for each compartment and the equations

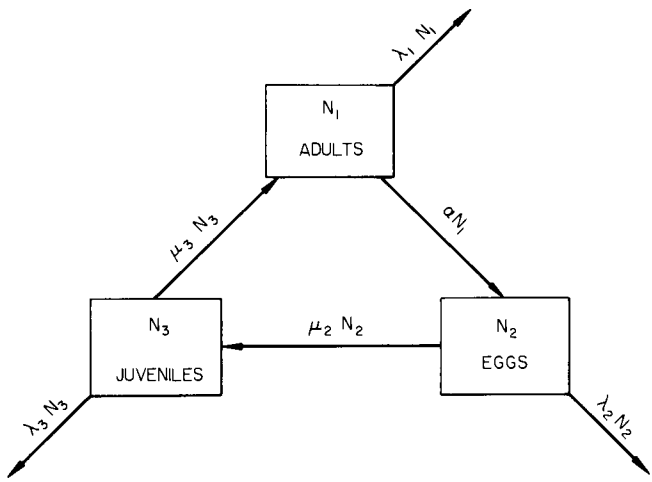

FIG. 4. Simplified compartment model of a cryptozoan population. Each compartment is represented as containing individuals of a particular age group and arrows represent maturation of individuals or mortality. The parameters of the system are explained in the text.

solved for $N_i(t)$ by analytical methods, by the use of an analog computer or by systems analytical techniques of matric calculus. We could also proceed by noting that Eq. (9) is analogous to a Poisson birth–death process and the transfer coefficients express the probability of an animal dying or maturing to the next age group. It is now possible to construct a stochastic model of the population. All of these methods require that the transfer coefficients remain constant. To make use of variable coefficients, we will proceed by developing an iterative simulation model appropriate for the digital computer. To implement this approach, Eq. (9) can be reformulated by the Euler method to obtain a difference equation to be solved at short intervals of time,

$$N_i(t) = N_i(t-1) - \mu_i N_i(t-1) - \lambda_i N_i(t-1) + \mu_{i-1} N_{i-1}(t-1) \qquad (i = 1, 2, \ldots, n). \tag{10}$$

The implementation makes it possible to express μ and λ as functions of environmental variables such that they are evaluated in the computer program before the set of equations is solved.

Making use of the difference equation formulation, the system (Fig. 4) can be simulated. In this representation, the maturation coefficients can be expressed as reciprocals of the average development times. This might

be adequate for some purposes but is seriously lacking in one important respect. An examination of the figure will show that a fraction of eggs layed at time t will pass to the juvenile state at time $t + 1$ and, at time $t + 2$, a fraction of these will become adults. If the interval of calculation is one day, the model would cause eggs laid on Monday to become adults on Wednesday even if development time were months in length. The problem is basically one of queueing, or allowing delays in the various developmental stages. This is circumvented by the simple device of defining age groups on the basis of the interval of calculation. If the model is iterated at intervals of one day, then the n of Eq. (8) is defined as one plus the average number of days required for an egg to become an adult. Considering a population that required three days for the egg to hatch and three more days for the juvenile to develop into an adult, we can redefine our system to contain seven compartments. In this representation, it is not until the seventh day that an egg can enter the adult compartment. This device also has simplified the calculations since, during the interval of one day, all the contents of an immature compartment are lost to maturation or mortality and the new members are simply the surviving members of the previous age group. This is equivalent to making the maturation rate equal to $1 - \lambda_i$. The equation defining an immature compartment then reduces to

$$N_i(t) = N_{i-1}(t - 1)[1 - \lambda_{i-1}]. \tag{11}$$

The adult population in this scheme must be handled somewhat differently since it contains individuals of different ages which are not maturing into another age group. The adult compartment N_a can be described as

$$N_a(t) = N_a(t - 1)[1 + \lambda_a] + N_n(t - 1)[1 - \lambda_n], \tag{12}$$

where N_n is the oldest group of juveniles. The equation which describes the first day egg compartment N_1 also must be modified to

$$N_1 = \alpha N_a(t - 1), \tag{13}$$

where α is the fecundity rate in eggs per adult per day.

Models of this general form have been used successfully to simulate laboratory populations of rotifers (King and Paulik, 1967) and Collembola (O'Neill and Styron, 1968). The real advantage of the method is its capacity to simulate natural populations under variable environmental conditions. The model uses estimates of fecundity, mortality, and maturation measured in the laboratory and representing growth under

optimal conditions. Populations under natural conditions are prevented from reaching this ideal growth by environmental stresses. It should be possible, therefore, to fabricate limiting functions which serve to limit the laboratory model and simulate field conditions. This type of simulation was performed on the Collembola population mentioned above. We will examine this study in detail to see how this conversion to the field model was accomplished and to illustrate the type of information that can be obtained from the model.

2. *Applications to a Study of Collembola Populations*

There are three types of limiting functions that can be applied to the basic model; each was used to simulate the hypothetical population and to study effects of ionizing radiation on this group of animals.

The first type of limiting function describes intraspecific competition due to lack of space, accumulation of excrements, etc. To model this competition adequately it is necessary to introduce nonlinearities. The nonlinear term in this case is of the simplest type, i.e., one of the transfers is described by a cross-product term. A quantity K which represents the maximum population size of adults is defined and Eq. (12) is modified to

$$N_a(t) = (1 - \lambda_a)(N_a(t-1)) + [(1 - \lambda_n)(N_n(t-1))][K - N_a(t-1)/K]. \tag{14}$$

This formulation contains the product $N_n N_a$ and produces the desired effect, since the increment to the adult compartment approaches zero as the number of adults approaches K.

Interspecific competition is the second type of limitation and involves another nonlinearity. Here, also, we can employ a simple cross-product term, introduced by generating a predatory mite population M. This added mortality factor m can be introduced by evaluating the following function at each iteration of the model:

$$m(t) = \beta M(t), \tag{15}$$

where β is the proportion of the Collembola compartment consumed per individual mite per day. The value for $m(t)$ is added to the mortality constant λ_i in each equation of the model.

The third type of limitation involves the imposition of environmental stresses. The transfer coefficient parameters of the model are not constants but functions of environmental variables. Realism can, therefore, be introduced by the method of variable coefficients discussed above. In the present model, fecundity is regarded as a function of

temperature. A sine wave temperature function is generated and a Q_{10} value measured in the laboratory provides the information needed. At each iteration a temperature value is generated and used to calculate the appropriate fecundity.

The third type of limitation can be exemplified by the effect of ionizing radiation on the various model parameters. Quantitative effects of acute gamma radiation on the various transfer coefficients in the model had been measured in the laboratory (Styron and Dodson, 1968). In addition, recovery from irradiation insult occurred at low doses and could be quantified. Using the basic model and the three limiting functions discussed above, it was possible to generate a "control" population. The behavior of this population could then be compared to populations in which the adults had received various doses of acute gamma radiation.

The control curve in Fig. 5 shows how the hypothetical population

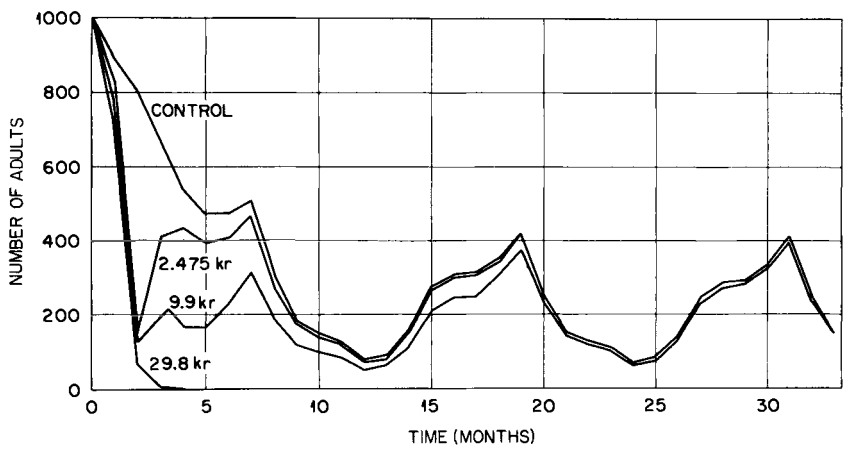

FIG. 5. Simulated behavior of Collembola populations released to natural conditions after being subjected to various doses of acute gamma radiation.

behaves under simulated field conditions at moderate predation pressure for a period of several years. The population showed peaks during the summer months and lows during the winter. The population reached a fluctuating equilibrium with its environment after an initial delay of several months. Other curves in the figure show the predicted behavior of similar populations which had received various doses of radiation. It can be seen that at low doses, where recovery occurred rapidly, the population was capable of reaching control levels quite quickly. At higher doses, no significant recovery occurred and the population went to extinction.

Although this is a hypothetical population, it is apparent that the simulation technique could be applied to real field problems involving the prediction of population response to other forms of environmental stress. It would be necessary to formulate the basic model, measure the parameters of the model in the laboratory, and then construct realistic limiting functions to simulate field conditions. These limiting functions can be modified by field data until the investigator is confident that he has accounted for the major environmental limitations. It is then possible to introduce the treatment of interest and produce preliminary predictions of system behavior.

III. Techniques for Estimating Parameter Values in Large Systems

We have seen something of models which can be applied to animal populations and their energy dynamics. The next major challenge proposed in the Introduction remains to be discussed. It is useless to devise complex models of ecosystems if, practically, it is impossible to quantify them because of the number of parameters. If the modeling approach with its many advantages is to make an impact on the study of ecology, it is important to devise, within the context of systems ecology, methods and simplifications which will allow the ecologist to quantify the system with which he is concerned. A major difficulty lies in attempting to estimate fluxes between compartments. Conventional methods for measuring input flux, for example, would involve gravimetric measurements of food available and food remaining after some period of time (e.g., Gere, 1956; Bocock *et al.*, 1967). These measurements are time consuming and place complex systems beyond the reach of the experimenter. Let us examine two methods which have been developed to deal with this problem.

A. Quantifying Complex Predator–Prey Relationships

The problem of estimating parameters is particularly difficult in a system containing complex food webs. In such a system one predator population may feed on a number of different species, and the task of evaluating the contribution from each prey is formidable.

1. *The Conditional Probability Method*

Let us consider a predator population x_j feeding on members of several potential prey species. What is the probability that x_j will feed on an individual of one prey population x_i rather than another? This prob-

ability is directly proportional to the standing crop x_i of the prey population (O'Neill, 1969). The more prey available, the more likely they are to be encountered and eaten. Once prey are encountered, palatability and defense mechanisms must be considered since a given prey may be encountered frequently but not always consumed. All the possible factors that could affect the probability of successful predation can be combined into a single weighting factor w_{ij}. Since we have accounted for differences in availability, this factor actually expresses the relative frequency or the ratio in which various prey would be eaten if they were present in equal standing crops. If species 2 is eaten twice as often as species 1 when both are equally available, we can assign the following values to w_{ij}: $w_{1j} = 1.0$ and $w_{2j} = 2.0$.

Using this discussion as a basis, we can express the probability P_{ij} that predator j will feed on prey i as

$$P_{ij} = x_i w_{ij} \Big/ \sum_{i=1}^{n} x_i w_{ij} . \tag{16}$$

This parameter satisfies the criteria for a probability measure since

$$0 \leqslant P_{ij} \leqslant 1 \tag{17}$$

and

$$\sum_{i=1}^{n} P_{ij} = 1 \qquad (i = 1, 2, \ldots, n). \tag{18}$$

This formulation is analogous to a theorem of conditional probability known as Bayes' theorem. If we let $x_i / \sum_{i=1}^{n} x_i$ equal $P(x_i)$, the probability that species i will be encountered, and $w_{ij} / \sum_{i=1}^{n} w_{ij}$ equal the conditional probability $P(y \mid x_i)$ that feeding will occur given that species i is encountered, then the probability, $P(x_i \mid y)$, that it is species i that has been eaten given that something has been eaten, can be expressed as

$$P(x_i \mid y) = P(y \mid x_i)\, P(x_i) \Big/ \sum_{i=1}^{n} P(y \mid x_i)\, P(x_i), \tag{19}$$

which can be seen as analogous to the expression in Eq. (16).

We can now ask what proportion of the total diet of predator j is composed of members of species i and we can see that the expected value approaches P_{ij}. We can then proceed to define the total diet from feeding experiments or more simply assume a steady state. Under the latter assumption, input to the predator population equals the output in

energy respired and excreted. This energy output is represented as R_j and the flux from population i would be $P_{ij}R_j$.

An interesting by-product of the technique is an index of the predation pressure on the various prey species. This estimate Z_i can be calculated as

$$Z_i = P_{ij}R_j/x_i. \tag{20}$$

The result of this analysis is a technique for the indirect estimation of fluxes into a predator compartment. We have achieved this result by introducing a new parameter w_{ij}. A basic limitation on use of the technique is the accuracy with which w_{ij} can be estimated. The problem is relatively simple for cryptozoan organisms, since it is possible to construct reasonably realistic microcosms in the laboratory and present the predator with equal standing crops of prey populations. From the analogy between $w_{ij}/\sum_{i=1}^{n} w_{ij}$ and the conditional probability $P(y \mid x_i)$, it is also possible to estimate w_{ij} as the proportion of i actually consumed from a number of observed encounters in the field or laboratory microcosms. Where an adequate estimation of w_{ij} can be achieved, the technique is applicable to the problem of quantifying complex predator relations.

2. *Applications to Predator Problems*

In a series of microcosm experiments, individual centipedes of the species *Otocryptops sexspinosus* were presented with equal biomasses of eight prey species (O'Neill, 1968). The prey were tagged with cesium-137 so that it was possible to determine the number of prey consumed during the week-long trials. The percentage of available prey consumed is indicated in the third column of Table II. Even though prey species

TABLE II

INDIRECT ESTIMATES OF ENERGY FLOW TO A CENTIPEDE POPULATION[a]

Prey	x_i	w_{ij}	P_{ij}	$P_{ij}R_{ij}$
Beetle larvae	796.0	15.5	0.287	15.56
Spiders	956.0	8.5	0.189	10.24
Centipedes	961.0	7.0	0.156	8.46
Crickets	272.5	18.4	0.117	6.34
Caterpillars	262.0	16.8	0.102	5.53
Isopods	375.0	8.6	0.075	4.06
Roaches	199.5	8.5	0.039	2.11
Fly larvae	127.0	12.0	0.035	1.91

[a] Methods of calculation are explained in the text. $R_{ij} = 54.21$ cal/m^2.

were presented in independent trials, these precentages represent estimates of the weighting factor w_{ij}. The centipede has rather simple behavioral patterns and, therefore, the weighting factor is determined only by ability of the centipede to subdue the prey and is not affected by presence or absence of other species. The average annual standing crop (calories per 10 square meters) was determined from 0.25 m^2-quadrat samples and is shown in the second column of the table. The fourth column contains the precentage of the total centipede diet composed of each prey. The total energy requirement of the centipede population was estimated to be 54.21 cal from data on respiration rates. Knowing this total energy requirement, it was possible to calculate the annual fluxes from each prey species as shown in the last column.

Another way of utilizing the technique can be illustrated by data on feeding relations of web spiders (Kajak, 1965). In this study, measurements were made of the prey available to spiders by the use of sticky traps. These data represent x_i of the model and are shown in the second column of Table III. In addition, measurements were made of the

TABLE III

CALCULATIONS OF PREDATOR–PREY DYNAMICS FOR A WEB SPIDER[a]

Prey	x_i	$P_{ij}R_j$	P_{ij}	w_{ij}
Diptera	155.9	60.7	0.817	0.524
Homoptera	30.2	0.1	0.001	0.003
Aphididae	23.2	11.1	0.150	0.646
Hymenoptera	3.5	1.6	0.022	0.629
Coleoptera	8.0	0.4	0.005	0.062
Thysanoptera	0.8	0.4	0.005	0.625

[a] Calculations are explained in the text (from Kajak, 1965).

numbers of individuals of several insect orders actually captured and eaten by spiders. These data represent the fluxes from prey to predator which were defined above as $P_{ij}R_j$. The total energy intake can then be calculated since, from Eq. (18),

$$\sum_{i=1}^{6} P_{ij}R_j = R_j \sum_{i=1}^{6} P_{ij} = R_j . \tag{21}$$

The sum of the values in column three of Table III can, therefore, be divided into each value in the column to produce the estimates of P_{ij}

shown in the fourth column. Making use of Eq. (16), it is possible to set up six equations for w_{ij} containing six unknowns

$$w_{ij} = P_{ij} \sum_{i=1}^{6} x_i w_{ij} / x_i \qquad (i = 1, 2,..., 6). \tag{22}$$

Placing this system of homogeneous equations into echelon form reveals, however, that there are more unknowns than nonzero equations, which implies that there are an infinite number of sets of w_{ij} satisfying the equalities. This reflects the fact that the absolute values given to w_{ij} can be arbitrary so long as the ratio between them remains constant. A unique solution to the set of equations can be obtained only by imposing further restrictions, i.e., introducing another equation into the system. The method used here was to set the quantity $\sum_{i=1}^{6} x_i w_{ij}$ equal to an arbitrary number, 100. Column five in Table III shows the values of w_{ij} calculated in this way.

It is possible to use the technique to calculate values of w_{ij} which express the relative susceptibility to capture of the prey species. In the present example, it is clear that homopterans must possess some mechanism which enables them to avoid capture in the spider webs.

It will become more clear in later sections how valuable this simple model is for calculating energy fluxes through complex food webs with polyphagous predators. Because of its ability to simplify complex food web relationships, this technique has great potential for quantifying ecosystem processes.

B. Theoretical Developments in Radioisotope Tracer Methods

Another set of techniques under extensive development during the last decade is the use of radioisotopes for measuring nutrient, trace element and energy transfers in ecosystems. These methods result in considerable economy in research time, and it is appropriate to discuss the most relevant developments at this point. Since our concern is methods for quantifying complex ecosystems, we will not describe the details of labeling and measurement, but will consider only developments of the theory which permit quantification of a flux with little information other than a series of whole-body counts on an animal.

If an animal is labeled with a radioactive isotope and body burden is measured during subsequent time periods, radioactivity Q after some time interval t is given by

$$Q_t = Q_0 e^{-kt}, \tag{23}$$

where Q_0 is the initial radioactivity (dpm per animal) and k is the biological elimination constant (dpm per dpm · unit time = time^{-1}). We will assume throughout discussion that the isotope has a long half-life and physical decay can therefore be ignored. The biological elimination rate is related to the more commonly used biological half-life T_b by the expression

$$T_b = 0.693/k. \tag{24}$$

It was pointed out by Davis and Foster (1958) that if an animal is at equilibrium, i.e., if it has been feeding on a labeled medium for a sufficient time, its body burden has become a constant. Then, the rate r at which the animal ingests the label is related to the equilibrium body burden Q_e and the biological elimination rate as

$$r = kQ_e/a, \tag{25}$$

where a is the fraction of ingested label that is assimilated and eliminated at rate k. Equation (25) states that at equilibrium, the rate at which an animal ingests the element must equal the rate at which it loses the element.

Equation (25) can be used to estimate the rate of ingestion of a radioisotope if Q_e and k are known. The biological elimination rate can be measured by feeding labeled food to an animal for some period and measuring the decreasing body burden when it is placed on normal food. If percentage retention is graphed against time on semilog paper, a straight line is produced since Eq. (23) can be written as

$$\ln Q_t = \ln Q_0 - kt, \tag{26}$$

which is the equation for a straight line. Equation (26) shows that the biological elimination rate can then be measured as the slope and estimated by linear regression.

If body burden is measured after a single ingestion of radioisotope, it is common to find a two-component curve such as that shown in Fig. 6. It is possible to resolve this curve into two lines by extending the straight-line portion of the curve back to $t = 0$, and subtracting this line from the original curve to yield a second straight line. A single net elimination constant is then calculated as (Reichle and Crossley, 1965)

$$k = 0.693/(P_1T_{b1} + P_2T_{b2}), \tag{27}$$

where the subscripts refer to the first or second curve and P is the y-intercept.

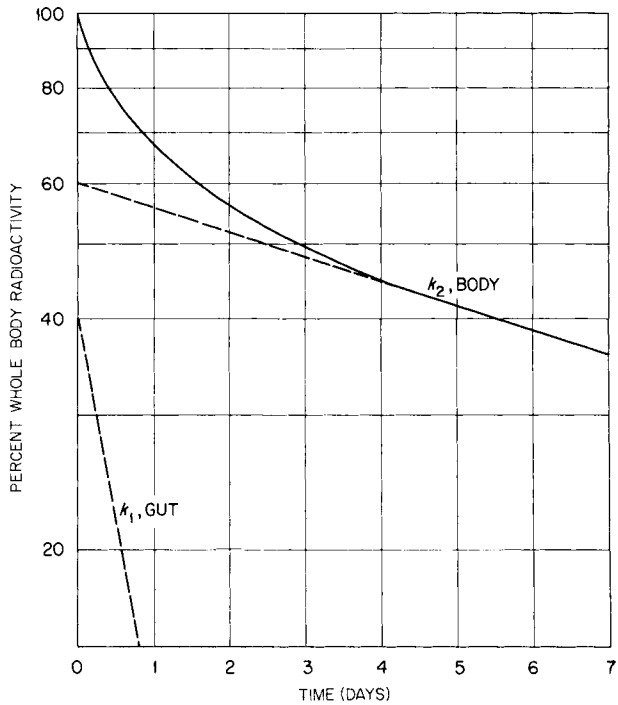

FIG. 6. Typical two-component curve for percent retention of a radioisotope following a single ingestion. The initial rapid loss at rate k_1 represents gut elimination. The slower loss at rate k_2 represents elimination of the isotope which has been assimilated into the tissues.

The equilibrium body burden can be measured by feeding the animal on labeled food for an extended period of time. About 97% of equilibrium is reached in a period of time equal to five times the half-life. Since this period may be quite long, the equilibrium level can be calculated after a shorter interval, t, by the relationship (Crossley and Howden, 1961)

$$Q_e = Q_t/(1 - e^{-kt}). \tag{28}$$

It is possible to estimate both Q_e and k, and calculate the rate of ingestion far more simply than by standard gravimetric techniques. This concept can be extended to measure the rate of food consumption R. If concentration of the label in food, d, is known, then R can be estimated as

$$R = Q_e k/ad. \tag{29}$$

This concept has been extended by Kevern (1966) to include animals feeding on a variety of foods of different concentrations, each food making up a fraction f_i of the total diet

$$R = Q_e k \Big/ \sum_{i=1}^{n} a_i d_i f_i . \tag{30}$$

Having established these simple relationships, we are in a position to discuss additional techniques in terms appropriate to compartment modeling. If we consider the animal as a compartment with a constant input r, then we can describe the changes in body burden as

$$dQ/dt = ra - kQ. \tag{31}$$

Solving this equation for Q_e gives Eq. (25). If the equation is solved for Q_t we arrive at

$$Q_t = (ra/k)(1 - e^{-kt}) + Q_0 e^{-kt}. \tag{32}$$

Assuming an initial radioactivity of zero, the second term on the right is eliminated, giving the expression presented by Crossley (1963). For the case of two or more components to the elimination rate, we can express the body burden as

$$Q_t = \sum_{i=1}^{n} (rP_i/k_i)(1 - e^{-k_i t}). \tag{33}$$

Equations (32) and (33) carry the analysis a step further since they make it possible to calculate intake without knowing the equilibrium level and the measurements can be made in a single experiment in which the labeled food is offered for a period of perhaps 24–48 hr to arrive at a value of Q_t. Measurements are then made of the elimination from this body burden to estimate k and P by the graphic method outlined above.

An additional technique has been outlined by Crossley and Reichle (1969) for a variable food supply losing radioactivity exponentially. The radioactivity of an animal feeding on this food will rise to a peak and then fall. The time to this peak, t_{max}, is related to the elimination constants of the two compartments

$$t_{max} = \frac{1}{k_2 - k_1} \ln \frac{k_2}{k_1}, \qquad Q_0 \equiv 0. \tag{34}$$

Knowing the rate of loss of the first compartment, k_1, it is possible to calculate the second loss rate. Since $Q_{t_{max}}$ is measured, and assuming

$n = P = 1.0$, we can calculate ingestion from Eq. (33). The authors point out how this method can be used on field data when a radionuclide is introduced into the trophic base of an ecosystem.

It can now be appreciated that radioisotope techniques can reduce quantifying a flux to consecutive measurements of body burden. Since this measurement is easily accomplished with modern counting equipment and techniques, it is possible to measure fluxes in a number of animal populations with great economy of effort. The availability of radioisotopes and the accompanying mathematical theory represent a potential breakthrough in measuring the dynamics of complex ecosystems.

IV. A Model for Radiocesium Movement on the Forest Floor

As mentioned in the Introduction, our aim has been to develop methods for applying compartment models to the cryptozoan fauna. These methods, along with techniques of systems ecology discussed throughout this book, are presently being used to develop a generalized model of the cryptozoa.

It will be helpful to consider in detail the logic underlying this effort since our emphasis has been on ways of actually applying models. We are not so much concerned with elegance of the mathematics, as with an appropriate balance between elegance and practicality as necessitated by limitations in available data. We consider how a model of radiocesium kinetics on the forest floor is formed and implemented on the digital computer, how the model's parameters are quantified, how the model can be used to perform simulations, and how such a model is capable of incorporating future developments. This exercise is intended to give the reader a better background for bridging the gap between theoretical developments and practical applications. The focus will be on principles involved in compromising, first, the model to reality (by accepting less than the best mathematical formulation), and second, reality to the model (by making assumptions that hamper one's ability to describe the real system).

A. Choosing Compartments for the Model

The first problem is deciding how to divide a cryptozoan community into reasonable compartments. The compartments must be distinct from each other and few in number so that realistic measurement of parameters is possible. Four alternatives are available.

1. *Division by Species*

Probably, an optimum model would have each species of the system depicted as a separate compartment. Such a model can be constructed to yield good predictions as shown by the millipede study discussed above. It is possible to obtain excellent measurements of the relevant parameters and devise formulae for transfer which will mimic the real system realistically and account for a wide range of population densities and environment variables.

Where this type of model is possible, there is little question of compartment division. In the case of the cryptozoa, however, this approach is out of the question. Here we encounter our first practicality barrier. The species involved in the cryptozoan community typical of a deciduous forest number in the hundreds; even lumping species that are ecologically similar would make the task of quantifying such a model formidable. In addition, although such a model might produce a fair degree of precision in simulating some particular configuration of species, it could not be applied directly to other configurations. This method of compartment division must be rejected therefore, since implementation would be prohibitive and applications would be limited. It is obvious, then, that the model has to be an approximation and species must be grouped into larger compartments.

2. *Division by Trophic Levels*

The concept of trophic levels has had a long and fruitful development since its introduction by Lindeman (1942). A division on this basis would reduce our model to a trophic base or producer compartment, an herbivore compartment and one or more levels of predator compartments. Static models of this type have been formulated by Macfadeyen (1963) for comparing soil ecosystems from different habitats. The data needed to quantify such a model are limited but the information which the model yields is correspondingly limited. Much more information is available than would be required for this simple model. Since we wish to make most efficient use of the available information, a trophic level division would not be best. The aim is to create as close an analogy to the real system as possible within limitations imposed by lack of information. The choice of trophic levels as the dividing line would compromise the degree of reality beyond that dictated by this basic limitation.

A far more serious objection to the use of trophic levels is the weak applicability of the concept to cryptozoa. This community is a decomposer system, i.e., it is entirely within one of the major divisions of the trophic level scheme, and the real situation deviates significantly from

the original concept in several important respects. First there is a large and important feedback or cycling parameter, since excrements and dead bodies reenter the detritus pool and again become available to the system. Secondly, it would be extremely difficult to assign some of the component populations to a particular trophic level, since many populations will feed freely on detritus as well as capture and feed on other animal life. Thirdly, one of the most interesting aspects of the cryptozoan community is the interaction between populations. Such interactions would be disregarded if the populations were designated as belonging to the same trophic level. The stabilities which characterize the cryptozoan community would be lost. We must decide, then, on the basis of available data and the desire to approximate reality, that such a division is unrealistic.

3. *Division by Trophic Characteristics*

A more logical basis for lumping populations is by their trophic characteristics, i.e., placing all detritus-feeders into one compartment, moss-feeders into a second, and wood-feeders into a third. This produces a system with 15 or 20 compartments (Edward *et al.*, 1969), but several problems still remain in application. Many compartments would contain several taxonomically distinct populations, unique in their responses to factors such as temperature and population density. In addition, there may be extensive interactions between these populations which would be disregarded by this analysis. Even more serious is that it would be quite difficult to assign populations to this classification. Many species would have to be divided among several compartments since they feed both on detritus and living material. Indeed, any individual animal might have to be assigned to different compartments during different intervals of its life history. It must be concluded, therefore, that this classification is not optimal.

4. *Division by Taxonomic Groups*

It would be possible to lump populations of similar taxonomic affinities: all millipedes, all molluscs, etc. This schema has several practical advantages. Biomass data are traditionally lumped in this manner and a large body of data would be applicable for use in the model. It is reasonable to assume that parameters of transfer which have been measured for one species would be good estimators for the parameters of similar species, and for responses to environmental variables such as temperature. At least this assumption would be more valid than a classification based on trophic characteristics. It is also possible to

account for most, though certainly not all, trophic interactions between species. Such a model, based on the major groups of animals, would have far wider application since the major groups are ubiquitous even though species compositions change. Because this seemed to be the most reasonable approach, compartments were devised as shown in Table IV.

TABLE IV

LIST OF COMPARTMENTS FOR PRELIMINARY MODEL OF FOREST FLOOR ARTHROPODS

0. External source (litter) and external sink (soil)	8. Isopoda
1. Detritus	9. Annelida
2. Formicidae	10. Collembola
3. Diplopoda	11. Coleoptera
4. Mollusca	12. Araneida
5. Orthoptera	13. Chilopoda
6. Lepidoptera	14. Acarina
7. Diptera	15. Predators external to system

Readers familiar with the cryptozoa will be struck by the arbitrary nature of the divisions. Other choices could have been made and other taxonomic groups included. Therefore, we must regard this model as a first approximation and await further changes and improvements.

B. CHOOSING FLUXES FOR THE MODEL

It is necessary to account for interactions between compartments so that radionuclide routes can be traced through the system. This constiutes a major difficulty for two reasons. First, in the present state of knowledge, trophic interactions are quite unknown for many species and only general statements can be made about the diet and predators of any particular group. Secondly, many more interactions can be conceived in this complex ecosystem than can be quantified. It is necessary to limit the number of interactions based on some criterion such as "major" sources of food. This criterion is subjective and the interactions which may be chosen are subject to further improvements as knowledge increases. Meanwhile, a preliminary matrix of transfers can be constructed such as that shown in Table V.

C. BUILDING THE MATHEMATICAL MODEL

The next task is to formulate a mathematical representation of the system: the type of model and the form of expressions describing

TABLE V

MATRIX OF TROPHIC TRANSFERS IN FOREST FLOOR ARTHROPODS[a]

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0		+														
1	+		+	+	+	+	+	+	+	+	+	+		−	+	
2		+										−	−	−		
3		+										−				−
4		+										+				+
5		+										−	+	+		+
6		+	−		−							+	+	+		+
7		+	−		−							+	+	+		+
8		+										−	−	+		−
9		+										−	−	+		+
10		+										+	+	+	+	
11		+											+	+		+
12		+												+		
13		+											−			
14		+											−			
15																

[a] Numbers refer to compartments listed in Table IV. A + indicates a positive transfer from the compartment at the end of the row to the compartment at the head of the column. A − indicates a transfer of less importance which has been ignored in the preliminary model.

transfers and environmental interactions. In this step, as before, we will attempt to build the most realistic model that is consistent with our knowledge and data limitations. This step will be performed by adding refinements to a simple formulation.

1. *Constant Coefficient, Linear Model*

We will begin by noting that change in a compartment with time can be characterized by the equation

$$dX_j/dt = \sum_{i=1}^{n} a_{ij}X_i - X_j \sum_{k=1}^{n} a_{jk}, \tag{35}$$

where X_j is the compartment of interest, X_i is one of several (n) donor compartments, a_{ij} is the transfer coefficient expressing the fractional transfer from the donor compartment to the compartment of interest, and a_{jk} is the transfer coefficient from the compartment of interest to other compartments. This model represents a logical (e.g., Chapter 1) starting place.

2. *Variable Coefficient, Linear Model*

In this step we will change the constants in Eq. (35) into variables dependent on the environment. Due to limitation in present knowledge, this relationship is limited to a simple Q_{10} relationship with temperature, where Q_{10} is taken as equal to 2 (Reichle, 1968). This predicts that biological processes will double in rate with a temperature increase of 10 C; it is sufficiently well established to be assumed for all parameters in the model. It also imposes significant limitations, however, which will be discussed in a later section.

3. *Nonlinear Model*

It was noted in the Collembola population study that faithful representation of a natural system requires the introduction of nonlinearity. This is obvious since feeding fluxes must depend on the amount of food available and the number of animals available to feed. Here is one of the severest restrictions on our ability to produce a realistic model. The simple cross-product term used to introduce nonlinearity into the Collembola model is unsatisfactory, and adequate formulations of nonlinear functions are largely unexplored. High and low density populations tend to reach asymptotes, and rates are not described adequately by the cross-product formulations, which do not account for these asymptotes. Watt (1968) has discussed this question in regard to population modeling and presents a large number of possible representations for the nonlinear terms. A smaller hierarchy appears in Chapter 1, Section III.G.

Lack of knowledge about the exact form of these functions restricts our model to the variable coefficient, linear form. We shall soon see what limitations this decision places on applying the model to simulate experiments.

4. *Difference Equation Formulation*

The only further refinement needed is formulation of the discrete-time-interval expression (Euler method)

$$X_j(t) = X_j(t-1) + \sum_{i=1}^{n} a_{ij}X_i(t-1) - X_j(t-1)\sum_{k=1}^{n} a_{jk}\,. \qquad (36)$$

This formulation is appropriate for each system equation when the digital computer is used for calculation. Since the formulae will be iterated over short time intervals, the cumulative truncation errors

associated with the Euler approximation method (cf. Chapter 1, Section VII.C for discussion) should not represent a significant problem.

5. *Temperature Generator*

It was mentioned in Section IV.C.2 that advantage would be taken of the Q_{10} relationship to introduce seasonal fluctuations into the model. To introduce this aspect of the model, it is necessary to produce a function which simulates annual temperature fluctuations. A sine wave will be used for this purpose of the form

$$T(t) = 12.5 \sin(2\pi t/365) + 12.5, \tag{37}$$

where T is temperature and t is the day of the year (1–365). Equation (37) generates a sine curve with a period of 365 days and a range from 0 to 25 C. This represents a reasonable approximation of the annual temperature fluctuation in southeastern deciduous forests where the model will first be applied.

6. *Stochastic Elements*

Realism can be improved further by recognizing randomness as a common phenomenon in nature. It is possible to introduce such stochastic elements into several aspects of the model. In the present development, a random temperature function is introduced, i.e., annual temperature is best represented as a normal distribution of temperatures about a sine-wave model. When the entire model is recalculated under several different random temperature schemes, the effects of this random temperature can be evaluated and differences in the system due to changes in annual temperature regime can be investigated. In the simulations which follow, temperature has been varied from the sine-wave model by adding a random variable with a normal distribution generated by the computer with a mean of zero and a variance of one.

7. *Computer Code*

We are now in a position to construct a computer program to perform simulations of the forest floor system. Mechanics of the model are illustrated by the flow chart seen in Fig. 7. Simulation is produced by generating a temperature for time t, evaluating the dependent variables at this temperature, and then using this value to evaluate fluxes in the system. These fluxes are then used to alter the state variable values (concentrations of radionuclide in the compartments), and the program proceeds to the next time period. After a number of years have been calculated, the computer prints the compartment values, plots them,

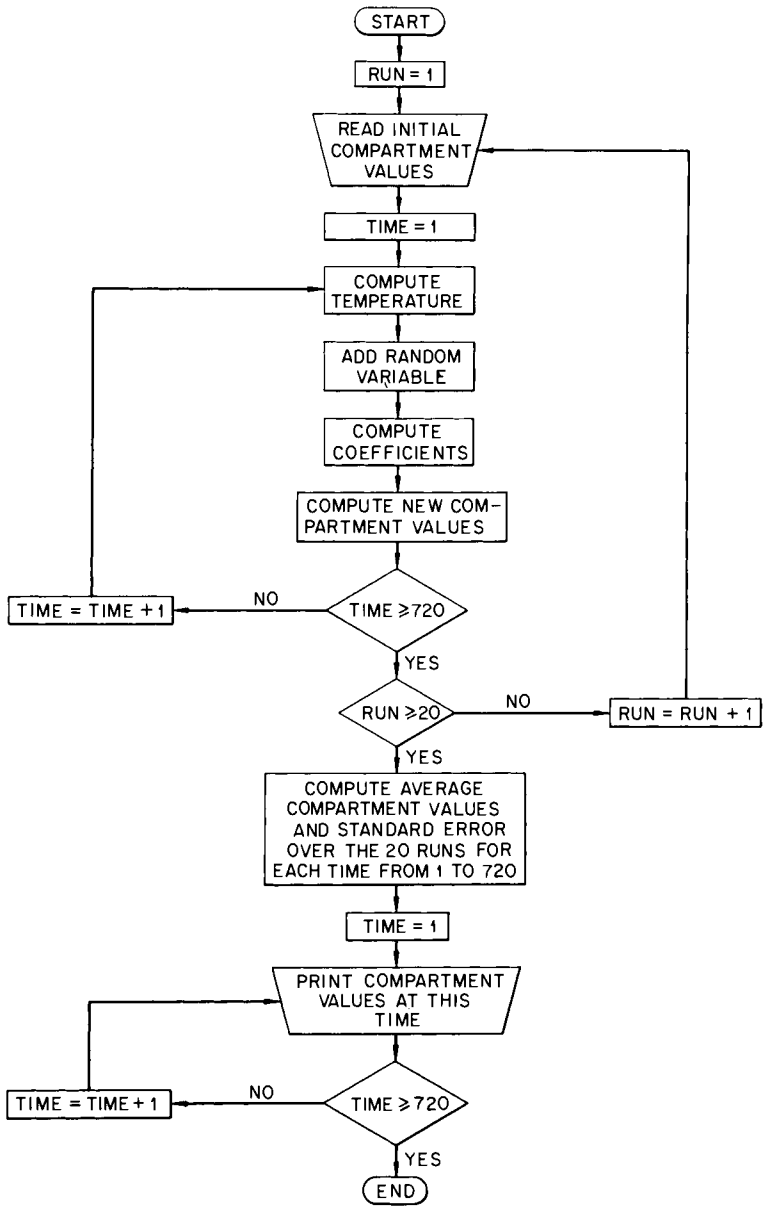

FIG. 7. Flow chart of a digital computer program to perform repeated simulations of radiocesium movement in forest floor arthropods under different random temperature regimes.

and proceeds to a new calculation which differs only in the set of random variables used to fluctuate temperature. A listing of essential features of the program appears in Table VI.

TABLE VI

SIMPLIFIED FORTRAN PROGRAM FOR CRYPTOZOAN MODEL[a]

```
      DIMENSION X(15,1000), A(15,15), FI(15), FO(15)
      DO 10, L = 1,20
C     READ INITIAL CONDITIONS
      READ 100, (X(I, 1), I = 1,15)
C     READ COEFFICIENT ARRAY
      DO 11, I = 1,15
      READ 100, (A(I, J), J = 1,15)
   11 CONTINUE
      X = 13
      DO 12, K = 2,1000
C     GENERATE TEMPERATURE AND RANDOM VARIABLE
      T = FLOATF(I)
      TEMP = SINF(0.01745329252 * T) * 12.5 + 12.5
      Y = RNORM(X)
      TEMP = TEMP + Y
      X = Y
C     CALCULATE VARIABLE COEFFICIENT (Q10 = 2)
      DO 13, M = 1,15
      DO 13, N = 1,15
   13 A(M, N) = A(M, N) * EXPF(TEMP * 0.693)
C     CALCULATE NEW COMPARTMENT VALUES
      DO 14, M = 1,15
      FI(M) = 0.0
   14 FO(M) = 0.0
      DO 15, M = 1,15
      DO 15, N = 1,15
      FI(M) = FI(M) + X(N, K - 1) * A(N, M)
   15 FO(M) = FO(M) + X(M, K - 1) * A(M, N)
      DO 16, M = 1,15
   16 X(M, K) = X(M, K - 1) + FI(M) - FO(M)
   12 CONTINUE
C     PRINT RESULTS
      DO 17, K = 1,1000
      PRINT 101, (X(I, K), I = 1,15)
   17 CONTINUE
  100 FORMAT(15F5.0)
  101 FORMAT(1H0, 15F5.2)
   10 CONTINUE
      END
```

[a] Function RNORM used to generate random variable with normal distribution is not included and format statements are greatly simplified.

We are not yet ready to perform simulations. It will be necessary first to examine the limitations placed on our ability to make predictions.

D. Limitations of the Model

It should be clear at this point that the model is merely a mathematical analog of the real system, a partial representation. We must be aware, therefore, of its limitations. Only a narrow range of situations can be predicted with any degree of accuracy. These limits are dictated by the nature of the model itself and by the assumptions used in its construction. It is imperative that the constraints be clearly outlined so that the degree of confidence in any particular class of simulations is well defined.

1. *Equilibrium Constraint*

Flows between compartments have been assumed to be describable by simple linear functions, but we have pointed out that there is good reason to believe that these expressions should be nonlinear. The basic limitation which this assumption places on the model is that it only can describe situations within a narrow range of equilibrium. Within this range the behavior of nonlinear systems can be adequately represented as linear. This means that we must limit ourselves to the description of undisturbed situations in which an ecological equilibrium can be reasonably assumed.

2. *Environmental Constraint*

We have assumed that all seasonal fluctuations are functions of temperature and temperature alone. In mesic forests this is reasonable since rainfall is abundant and factors such as desiccation do not play a major role (Witkamp, 1966). This limits our simulations to areas where this assumption is reasonable. It would not be valid, for example, to simulate behavior of the millipede system in which seasonal drying of the leaf litter is common.

3. *Constraints from Choice of Compartments and Fluxes*

The choice of a method to lump compartments and the choice of fluxes is limited by practical restraints of available information and represents another major limitation. It is a well-established hypothesis that stability of a system and its sensitivity to fluctuations are a function of the number of interactions in the system (MacArthur, 1955). Our lumping procedure has severely limited the number of interactions represented, compared to a division by species. The model can only claim, therefore, the most meager ability to predict reactions to disturbances. Again we must limit ourselves to simulations of an equilibrium state.

A discussion of these principal limitations of the model does not constitute a complete analysis of the assumptions implied in the model. It is hoped, however, that their brief discussion will give the reader an appreciation of the types of limitation which can be expected, and of the value of this kind of exercise.

E. Quantification of the Model

The model is presently being applied to the community on the floor of a *Liriodendron* forest in East Tennessee. A section of this forest was labeled with cesium-137 in 1962 and a general description of the radionuclide dynamics is available (Olson, 1965). In these first stages the model is being designed to simulate only general characteristics of radiocesium transfer through the forest floor arthropods.

Since we have emphasized methods which can be used to assign values to parameters of a complex model, it is appropriate to describe the methods used to arrive at values for the state variables X, the X_j of the system equations, and the transfer coefficients. The labeled forest provided a situation in which the state variables, Q_e of Eq. (25), could be obtained from field data. Some of these results have been reported by Reichle and Crossley (1965) and Reichle (1968). Using these data and our assumption of an equilibrium state, it is possible to calculate values for the parameters of the system. Several possible cases arise which will be described briefly.

1. *Single Input and Output*

In this case the compartment has a single food source and a single loss function in excretion. The loss coefficient is equal to the biological elimination coefficient in this and all cases of excretion as demonstrated in Eq. (25). In the single input case, the input flux is set equal to the output and division by the appropriate donor compartment yields the desired value for a_{ij}

$$\text{input:} \qquad a_{ij} = Q_{ej}k_j/Q_{ei} \tag{38}$$

$$\text{output:} \qquad a_{jk} = Q_{ej}k_j/Q_{ej} = k_j\,, \tag{39}$$

where j is the compartment of interest, feeding on comparment i and eliminating at a rate k_j.

2. *Multiple Input or Output*

In other cases which involve multiple sources of food or predation it is necessary to follow one of two paths:

(a) If the entire population is feeding on a number of potential prey (e.g., the centipede compartment), we can use the technique described in Section III.A provided we have measured values for w_{ij}. For the centipede population the R_j of the model is the excretory flux. The input from species i at equilibrium is then

$$a_{ij} = P_{ij}Q_{ej}k_j/Q_{ei}\,. \tag{40}$$

(b) When a compartment has more than one output, that is, both excretion and predation, the population ingests sufficient amounts of the radionuclide for both losses and therefore

$$R_j = Q_{ej}\left(k_j + \sum_{k=1}^{m} a_{jk}\right). \tag{41}$$

Substituting into Eq. (40) we arrive at the expression for the transfer coefficient

$$a_{ij} = P_{ij}Q_{ej}\left(k_j + \sum_{k=1}^{n} a_{jk}\right)\Big/Q_{ei}\,. \tag{42}$$

By proceeding from the top predator of the system, Eqs. (38)–(42) can be used to calculate all transfer coefficients in the system, knowing the equilibrium body burdens, the biological elimination coefficients and the appropriate w_{ij}'s.

F. Simulation Experiments

With the fully quantified system, it is possible to simulate situations of interest. To illustrate the type of information that can be obtained from the model we will simulate two such situations. In both cases we will be assuming an undisturbed condition in which the populations and the interactions remain constant or within a narrow range of fluctuations about this constant. This condition is consistent with the steady state assumption of the model.

1. *Pulse Input*

First we wish to predict the behavior of radiocesium in the forest floor community following a pulse input of the isotope to the litter. This mimics the situation in which a forested area is contaminated by a single event, such as a reactor accident. The information which the model must provide is the peak concentrations reached in the various compartments and the rates at which each loses radioactivity. Figure 8 shows the graphic response of three compartments of the ecosystem to the introduction of 1000 units of radiocesium into the detritus compartment. It is

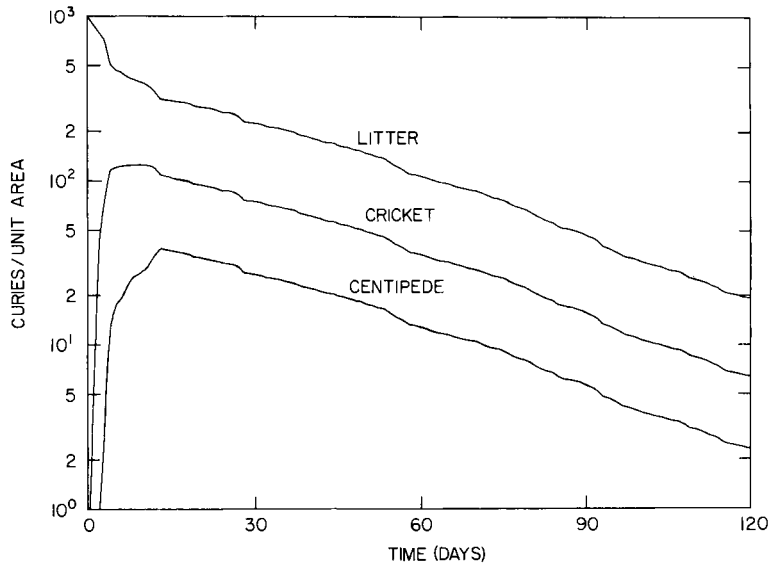

FIG. 8. Patterns of radionuclide movement through three components of a hypothetical forest floor community. This behavior is predicted from the compartment model explained in the text following a pulse input of 1000 Ci to an extensive area of forest litter.

easily seen that the desired information can be obtained from values generated by the model.

2. *Constant Input*

If the input to the system were constant, as might be expected from fallout contamination, the system would be expected to reach an equilibrium as shown in Fig. 9 with only seaonal fluctuations. Equilibrium time, maximal and minimal seasonal concentrations, and similar predictions can then be obtained from the model. A large number of other cases can be simulated based on different modes of introduction of the radionuclide to the system, elimination of certain components of the fauna, etc. The model is extremely versatile and represents the best possible prediction of radiocesium behavior in this portion of the ecosystem.

G. Further Developments of the Model

It is important to realize that construction of the model and its initial use in making predictions represents only part of the potential it possesses. As discussed elsewhere in this book, equilibrium sensitivity analysis (Kaye and Ball, 1969) and various stability indices

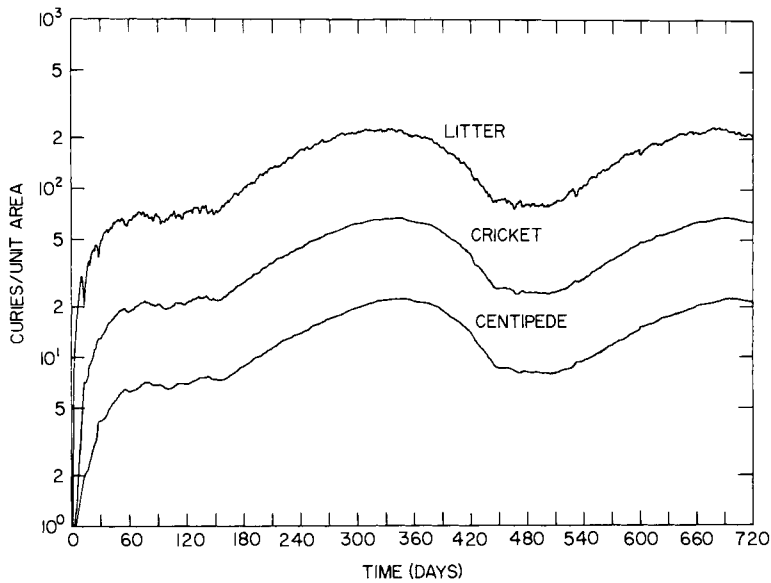

FIG. 9. Patterns of radionuclide concentration in three components of a hypothetical forest floor community. This behavior is predicted from the compartment model explained in the text when a constant input is applied to an extensive area of the litter compartment.

(e.g., Patten and Witkamp, 1967) can yield additional information. Comparison of predictions generated by the model with data from real systems provides a positive feedback which can be used to correct and improve the model. In particular, it is possible to account for deviations from a steady state condition due to seasonal fluctuations in system parameters. The model can be developed in other directions if the caloric equivalent of the radiocesium concentrations can be determined (e.g., Reichle and Crossley, 1967). The radiocesium can then be used as a tracer to simulate energy flow through the system.

The model should be regarded, therefore, not as an end product but as a tool to guide and orient future research. At any stage of a research program, a model represents a useable summary of all understanding gained up to that point in time, but it should always retain the potential to incorporate further information.

V. Conclusions

The emphasis of this chapter has been on practicality. An attempt has been made to apply techniques of mathematics and systems analysis

to actual prediction of ecological phenomena related to forest floor arthropods. The examples have been presented to demonstrate that these methods are successful in providing first approximations. It is felt that this approach is essential when ecologically related problems, such as population and pollution, demand a capability to produce approximations of ecosystem dynamics long before traditional ecological approaches can provide more detailed conclusions.

At the present time, techniques of systems ecology can provide seemingly reasonable predictions based on limited available information. They are capable of drawing from available data implications, conclusions and insights which are otherwise obscured in the complexity of the system. In addition, modeling techniques provide a framework to which additional information can be added as it becomes available, and provide clues concerning the most important information to gather.

Unfortunately, the mathematical tools used in this type of approach are often beyond the grasp of the working ecologist. It is hoped that our attempt to keep mathematical presentations as simple as possible and to present the methods needed to apply the modeling technique to actual problems involving field data will contribute toward bridging the gap between the theoretical developments of systems ecology and the applications of these techniques to important ecological problems of our day.

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8

A Compartment Model Simulation of Secondary Succession

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I. Introduction

The current trend in environmental biology toward the use of mathematics, statistics, and computer languages for description of experimental data raises the question of whether or not these methods are at variance with the traditional methods and concepts of ecology. Is it possible to place early classical ecological studies in a quantitative framework and preserve the values therein? If so, are there advantages to be gained by a fresh look at classic data through the viewpoint of a mathematical treatment?

In an attempt to answer these questions, as well as to provide a starting point for modeling studies in an important phase of ecology, two classical studies of succession in abandoned cultivated fields (Billings, 1938; Smith, 1940) have been used to develop systems of equations which reflect the observations and conclusions of the original authors. The data which were gathered in the two studies are primarily semiquantitative in form and not of a type which readily lends itself to objective measures of "goodness-of-fit," such as minimum squared error. Nevertheless, much of the progress in modern ecology and the understanding of mechanisms of environmental biology is based upon observations and data of this type. If the techniques of systems ecology are to supplement previous findings of ecologists, they must build upon traditional techniques rather than seek to supplant them. The main objective of this chapter is to show that quantitative methods can be made to intermesh in a workable manner with qualitative statements of hypotheses. The important aspect of a quantitative model is translation of the verbally stated mechanism into mathematical form; use of empirical numerical data to test the model statistically is only one of several ways of gaining confidence in its efficacy. We hope to demonstrate that the techniques of modeling and simulation are equally applicable to situations involving nonnumerical or semiquantitative data.

A compartment model or system of ordinary, first-order differential equations has been chosen for the form of the simulation. Differential equations were used because the variables in question are basically continuous and many techniques are available for treating such systems. The equations are first order since the fundamental relations are between the time rates of change of the system variables and the state of the system. Time lag effects are considered too complex for the degree of development desired, so the use of difference equations can be avoided. The current development is without consideration of spatial variation in the dependent variables, hence the use of ordinary (nonpartial) differential equations in a "lumped parameter" system.

Intuitively, a compartment model is an abstraction of a system whose dependent variables can be thought of as describing the contents of various blocks or compartments between which a flow of material or energy, represented by interconnecting arrows, takes place. This concept is generalized to the point that we might consider using the block diagram to describe what happens when, in succession, the biomass of species A declines as that of species B increases. We are aware that no flow of organic material actually is taking place, however, the analogy is still useful in an abstract sense. The same mathematical form can be employed whether the flow is real or abstract.

II. Mathematical Framework of the Model

In order to present the mathematical framework into which the ecological model has been set, we will consider a series of forms of first-order ordinary differential equations. Readers who do not wish to concern themselves with mathematical details of the model may go on to Section III. The forms will be presented in order of increasing complexity and generality.

A. Linear Constant-Coefficient Equations

The general form of a linear, constant-coefficient model for a system of n compartments is defined to be

$$\dot{x}_i(t) = \sum_{j=1}^{n} a_{ij}x_j(t), \qquad i, j = 1,..., n, \tag{1}$$

where $x_i(t)$ is the content of the ith compartment as a function of time t, $\dot{x}_i(t)$ is the time derivative of the ith compartment with respect to time, and a_{ij} is one of n^2 constant coefficients which are parameters of the system. In matrix notation,

$$\dot{\mathbf{x}} = A\mathbf{x}, \tag{2}$$

where $\mathbf{x}$ is a column vector of functions of time

$$\begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{bmatrix},$$

$\dot{\mathbf{x}}$ is a column vector

$$\begin{bmatrix} \dot{x}_1(t) \\ \dot{x}_2(t) \\ \vdots \\ \dot{x}_n(t) \end{bmatrix},$$

and A is an $n \times n$ square matrix,

$$\begin{bmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{bmatrix}.$$

Two forms of linear constant-coefficient compartment models will be distinguished.

1. *Closed System*

By a "closed, linear, constant-coefficient, compartment model" is meant that the sum of all the compartment contents is constant in time, i.e.,

$$\sum_{i=1}^{n} x_i(t) = \text{positive constant} \qquad \text{for} \quad t \geqslant 0. \tag{3}$$

As a consequence, some restrictions are placed on A. Equation (3) implies

$$\mathbf{u}^{\mathrm{T}}\dot{\mathbf{x}} = 0 \tag{4}$$

where $\mathbf{u}$ is the $n \times 1$ unit vector,

$$\begin{bmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{bmatrix}.$$

We obtain, combining (2) and (4)

$$\mathbf{u}^{\mathrm{T}}A\mathbf{x} = 0. \tag{5}$$

Since $\mathbf{x}$ varies with time in n-dimensional space, Eq. (5) can be true only if

$$\mathbf{u}^{\mathrm{T}}A = \mathbf{0}, \tag{6}$$

or the columns of A must each sum to zero. In analogy to the use of compartment models in tracer kinetics experiments, it is desirable to be

able to interpret the off-diagonal elements of A, a_{ij} for $i \neq j$, as flow rates from compartment j to compartment i. Therefore, we must have

$$a_{ij} \geqslant 0 \qquad \text{for} \quad i \neq j, \qquad i, j = 1, \ldots, n. \tag{7}$$

Combining Eqs. (6) and (7), the following constraints on A are required for a closed system:

$$\begin{aligned} a_{ij} &\geqslant 0 \qquad \text{if} \quad i \neq j, \\ a_{ii} &= \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ji} \, . \end{aligned} \tag{8}$$

Thus, diagonal elements are nonpositive and nondiagonal elements are nonnegative and less than or equal to the absolute value of the diagonal element in their column.

2. *Open System*

For an "open, linear, constant-coefficient, compartment model" (referred to hereafter as an open system) we can relax the restriction of Eq. (3). Intuitively, we think of an open system as one in which a substance can enter or leave that part of the system being modeled. If the diagonal terms of A, a_{ii}, are thought of as the negative of the total flow rate from compartment i, then this must be greater than the sum of the individual flows from i to other compartments explicitly contained in the model. Thus we have as restrictions on A for an open system

$$\begin{aligned} a_{ij} &\geqslant 0 \qquad \text{if} \quad i \neq j, \\ a_{ii} &\geqslant \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ji} \, . \end{aligned} \tag{9}$$

3. *Significance of A Matrix*

Notice that A can be interpreted as describing the directional arrows in a diagram such as Fig. 1. The 5×5 matrix corresponding to Fig. 1 has the form

$$A = \begin{bmatrix} a_{11} & 0 & 0 & 0 & a_{15} \\ a_{21} & a_{22} & a_{23} & 0 & a_{25} \\ 0 & a_{32} & a_{33} & 0 & a_{35} \\ 0 & 0 & a_{43} & 0 & a_{45} \\ a_{51} & a_{52} & a_{53} & 0 & a_{55} \end{bmatrix}. \tag{10}$$

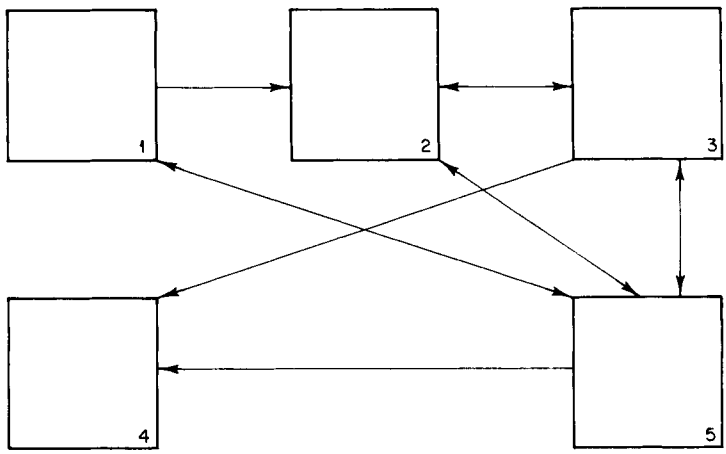

FIG. 1. Block diagram for a matrix whose zero components occur in the same positions as those in the matrix of Eq. (10).

The zeroes correspond to those a_{ij} for which there is no arrow from compartment j to i. Compartment 4 is a "dead-end" or "sink," i.e., it has no arrows leaving it. Correspondingly, column 4 of A contains all zeroes. Intuitively, compartment 4 must eventually contain all the material in the closed system. If there were two "sink" compartments, eventually all of the material of the system would be divided (not necessarily equally) between them.

When the dependent variables of the system do not allow use of a conservation law we will want to require that

$$\begin{aligned} a_{ii} &\leqslant 0, \qquad i,j = 1,\ldots,n, \\ a_{ij} &\geqslant 0, \qquad i \neq j, \end{aligned} \tag{11}$$

with no restrictions on the relative sizes of the on- and off-diagonal elements.

B. EQUATIONS WITH VARIABLE COEFFICIENTS

In a more general case, A in Eq. (2) can be replaced by $A^* = [a_{ij}^*]$, $i,j = 1,\ldots, n$, where

$$a_{ij}^* = a_{ij}\, g_j(\mathbf{x}, t, \mathbf{d}), \tag{12}$$

where a_{ij} is a constant, $\mathbf{d}$ is an $m \times 1$ vector of constants which are parameters of the system being modeled, $\mathbf{x}$ is as previously defined, and

g_j is a real function which assumes the value one for some combination of values of its arguments. Thus a_{ij} can be considered the "normal" value of a_{ij}^* corresponding to the simpler constant-coefficient model.

An important case is where g_j is related to the unit step function $u(t)$, defined by

$$u(t) = \begin{cases} 1 & \text{if } t > 0 \\ 0 & \text{if } t \leqslant 0. \end{cases}$$

We might have

$$a_{ij}^* = a_{ij} u[\pm(t - t_0)] \tag{13}$$

to allow for the occurrence of threshold processes in time described by Holling (1966) as being important in biological models. A still more versatile form of the step function is given by

$$g_j(\mathbf{x}, t, \mathbf{d}) = u[\pm(t - t_0)] \cdot u[\pm(x_i - d_k)], \tag{14}$$

where d_k is a constant value which the function $x_i(t)$ takes on at some time t_k; $d_k = x_i(t_k)$. In this case the step is a function of both time and some state variable (x_i) of the system. This form is useful when a lack of detailed knowledge about the system enables one to say "a flow occurs under some conditions and not under others," but no information is available about the manner in which the transition occurs.

If more information about the system is available, but still detail is lacking, the following piecewise-linear form (Fig. 2) may be useful

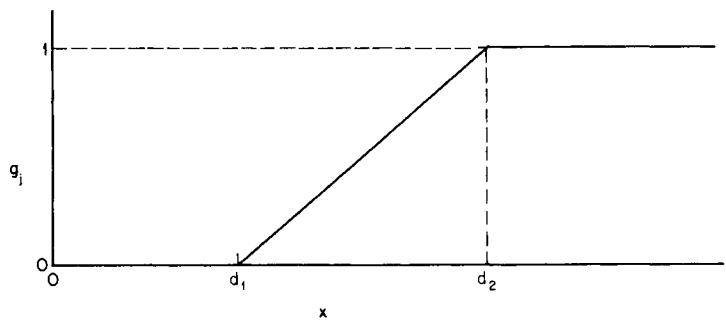

FIG. 2. Graphical appearance of a piecewise-linear coefficient as defined by Eq. (15).

$$g_j = \begin{cases} 1 & \text{if } x_k \geqslant d_2 \\ \dfrac{x_k - d_1}{d_2 - d_1} & \text{if } d_1 \leqslant x_k < d_2 \\ 0 & \text{if } x_k < d_1 . \end{cases} \tag{15}$$

C. Other Useful Equation Forms

Variables which approach an asymptote for large values of time and have derivatives close to zero for time near zero are fairly common in ecology. This is an example of an approach to a limiting value, as described by Holling (1966). Provision for this type of variable is made by the following differential equation for the ith compartment.

$$\dot{x}_i = a_{ii}x_i - b_{ii}x_i^2, \tag{16}$$

where $a_{ii} \geqslant 0$ and $b_{ii} \geqslant 0$. The solution to this equation has the s-shaped form known variously to biologists as the "Verhulst–Pearl" law of population growth (Lotka, 1924) or a "logistic" or "sigmoid" growth curve (Slobodkin, 1964).

In general, and for purposes of this study, the compartmental differential equations may take any form which is first order and ordinary. If other differential equation forms are used, the compartment analogy loses much of its meaning. The forms presented above are those which seem most useful from an historical point of view and which have proved useful in the examples of later sections.

D. Properties of Linear Compartment Models

A treatment of the mathematical properties of Eq. (2) with the constraints of Eq. (9) is given by Hearon (1963). Bledsoe (1968) has reviewed and discussed these properties from the standpoints of ecological applications. The general solution to Eq. (2) is

$$x_i(t) = \sum_{j=1}^{k} P_{ij}(t) \cdot e^{\lambda_j t}, \tag{17}$$

where λ_j is the jth distinct (complex) root of A having multiplicity m_j, $P_{ij}(t)$ is a polynomial in t of maximum order $m_j - 1$, and k is the number of distinct roots of A. This general solution can take a number of different forms depending upon the characteristics of A. These forms have been categorized by Brown (1968).

Some of the properties of Eq. (17) can be summarized as follows: (1) the solution is bounded and approaches a constant nonnegative vector; (2) the solution is nonnegative if the initial condition vector, $\mathbf{x}(0)$, is nonnegative (Hearon, 1963); (3) if the relation in Eq. (9) is an equality the steady state vector is nonzero; (4) damped sinusoidal oscillations

will occur in the solution if A has complex roots. The frequency of the oscillations will be no greater than

$$\max_{i=1,n} \frac{1}{2\pi} \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ij}$$

(from Brauer, 1946); and (5) the solution will be a sum of exponential terms for all compartments if and only if both of the following are true: (a) all roots are real and (b) multiple roots have independent eigenvectors equal in number to their respective multiplicities.

III. Old-Field Succession in Central Oklahoma

Smith (1940) studied succession of plants and animals and accompanying soil changes on abandoned farmland in central Oklahoma. Succession was studied on 30 sites which were categorized as being in one of six successional stages (termed A, B, C, D, E, and F) ranging from two to four years since abandonment to 20 to 30 years in subclimax *Andropogon-Bouteloua* grassland (bluestem-grama). The point was made by Smith that the term "successional stages" does not imply that succession is a discrete process, rather that this is merely a way of viewing a continuous phenomenon. One advantage of the proposed mathematical model is that it enables succession to be conveniently viewed as a continuous process for those ecologists who object to the "stage" point of view.

Of 140 plant species recorded in the study, 36 were cataloged as most important and classified in an ascending scale of abundance from zero to five (only integers used) for each successional stage. These 36 species were arranged in order from those species most abundant in early stages to those most abundant in climax vegetation. Abundance, as used by Smith, is a subjective estimate of the relative percent cover of the vegetation type. By studying his tabulated data it is possible to visualize the transition in flora as succession progresses. From Smith's text certain dominant and subdominant species can be identified at the various stages and used to construct an initial model.

A. Choice of Units

The problem of proper units for dependent variables of the model is a difficult one. The study on which the simulation is based does not involve quantitative vegetation estimates. It is not possible to determine

or even estimate the standing crop of a species in objective units such as grams of dry matter per square meter from the data given. It is also not possible to estimate the relative peak standing crop values of any two species. The data does indicate relative rates of increase and decline of standing crop and the time or range of times in which peak standing crop occurred for each species. For this reason the abcissas of the graphs which give simulation results are marked "arbitrary units." If estimates of the peak standing crop (grams per square meter) for each compartment could be made, experimentally or otherwise, then each curve could be multiplied by a unique factor allowing the graph to be labeled in objective physical units.

It may be desirable to have the model results in other units such as percent cover. The same procedure can be used without implying that percent cover in an area must be proportional to standing crop. This is because the model results reflect a central tendency and can be expected to have a large amount of random error. Nevertheless, the error is not so large as to prohibit a clear view of the successional trend in Oklahoma, as Smith saw it. While standing crop may not be proportional to percent cover, the two variables are closely related for a given species in a given environment.

B. Identification of Seral Stages

The first stage, A, "mixed weed," is characterized by weeds present on the land at the time of abandonment, chiefly *Helianthus annuus* (sunflower) and *Digitaria sanguinalis* (crabgrass). These two species will compose the first compartment. Stages B and C are dominated by *Aristida oligantha* (three-awn grass) and *A. oligantha-A. basiramea* (together), respectively. It is not necessary that the compartments correspond directly to the stages identified by Smith; however, the stages must be identifiable in the equation solutions if the model is to be an accurate reflection of the ecological conclusions drawn. Since compartments 2 and 3 correspond to approximately the same time period, flow from compartment 1 will be to both 2 and 3, with a smaller coefficient for transfer from 1 to 3.

Stage D is dominated by a combination of *Eragrostis secundiflora* (lovegrass) and the two *Aristida* species, with *A. oligantha* declining and *A. basiramea* reaching a peak. The fourth compartment will be identified with *E. secundiflora* and has a transfer only from compartment 3. Stage E, the subclimax, has no true dominants but is marked by decline of stage D dominants, and establishment of species which will dominate the climax grassland, i.e., *Andropogon scoparius* (little bluestem) and

Bouteloua curtipendula (sideoats grama). Compartment 5 will be identified with these two species and the final climax stage, F, will be marked in the simulation by the approach to constant size by this compartment.

C. Construction of the Initial Model

The model at this point is shown in Fig. 3 and a first approximation to

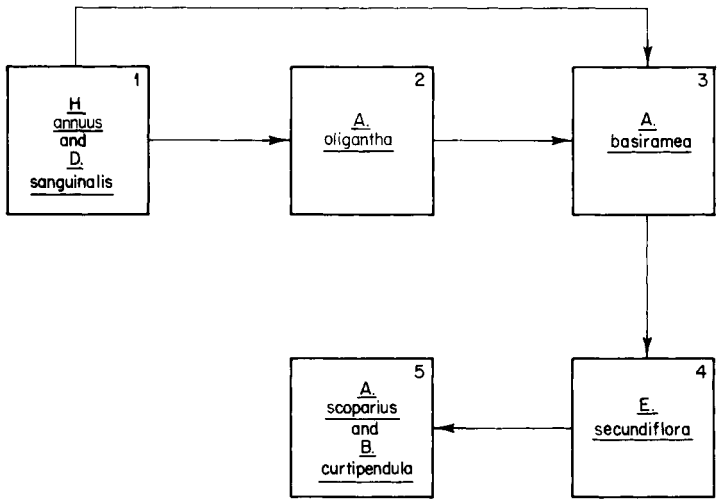

FIG. 3. Form of the initial five-compartment model for succession of dominant species on abandoned cropland in central Oklahoma.

the matrix of transfer coefficients, A, is given in Table I. Bledsoe and Van Dyne (1969) give a method for determining these initial coefficients.

TABLE I

INITIAL MATRIX OF COEFFICIENTS FOR COMPARTMENTAL TRANSFER FOR ANALOG COMPUTER MODEL OF SUCCESSION IN CENTRAL OKLAHOMA[a]

	From: 1	2	3	4	5
To: 1	−1.0	0.0	0.0	0.0	0.0
2	0.8	−1.0	0.0	0.0	0.0
3	0.2	1.0	−1.0	0.0	0.0
4	0.0	0.0	1.0	−1.0	0.0
5	0.0	0.0	0.0	1.0	0.0

[a] A depiction is presented in Fig. 3.

Table I does not attempt to account for differences in the lengths of time each stage is present. Table II gives A in a first attempt to allow for the

TABLE II

A MODIFIED MATRIX OF TRANSFER COEFFICIENTS FOR AN ANALOG COMPUTER MODEL OF CENTRAL OKLAHOMA SUCCESSION[a]

	From: 1	2	3	4	5
To: 1	−1.0	0.0	0.0	0.0	0.0
2	0.8	−1.0	0.0	0.0	0.0
3	0.2	1.0	−0.7	0.0	0.0
4	0.0	0.0	0.7	−0.8	0.0
5	0.0	0.0	0.0	0.8	0.0

[a] A depiction is shown in Fig. 3 incorporating a first attempt to introduce variable time delays between compartments. Figure 4 gives the system solution corresponding to this matrix.

fact that floral changes in later periods of succession are slower than those in the earlier stages (as shown by Smith's data). The average age since abandonment for the study sites in each successional stage can be used as an index to times of maxima for the various species and the compartments representing them (Table 29 of Smith, 1940). In constructing such an approximation, the approach to use is that the ith diagonal element will determine the rate at which the contents of the ith compartment decay into the connecting compartments. Thus, the last compartment has a zero diagonal since it does not decline at all. The remaining elements in each column are then adjusted by an appropriate factor so that the columns sum to zero.

At this point the equations were solved on an analog computer and the coefficients adjusted to provide the best approximation of the qualitative description provided by Smith. Analysis by analog computer is very convenient at this stage when the equations are relatively simple and small in number.

A digital computer program such as COMSYS 2 (Bledsoe and Van Dyne, 1969) could be used in an alternative approach. A graph approximating the desired appearance of the equation solution would be prepared. Then the graph would be sampled for each compartment at an interval sufficiently fine to reflect the structure of the system. The sampled points would be used as input data for the optimization program which should predict appropriate coefficients on a minimum squared-error basis.

The analog results for the Smith study (based on the Table II coefficient matrix) are shown in Fig. 4. Figure 5 is the solution with

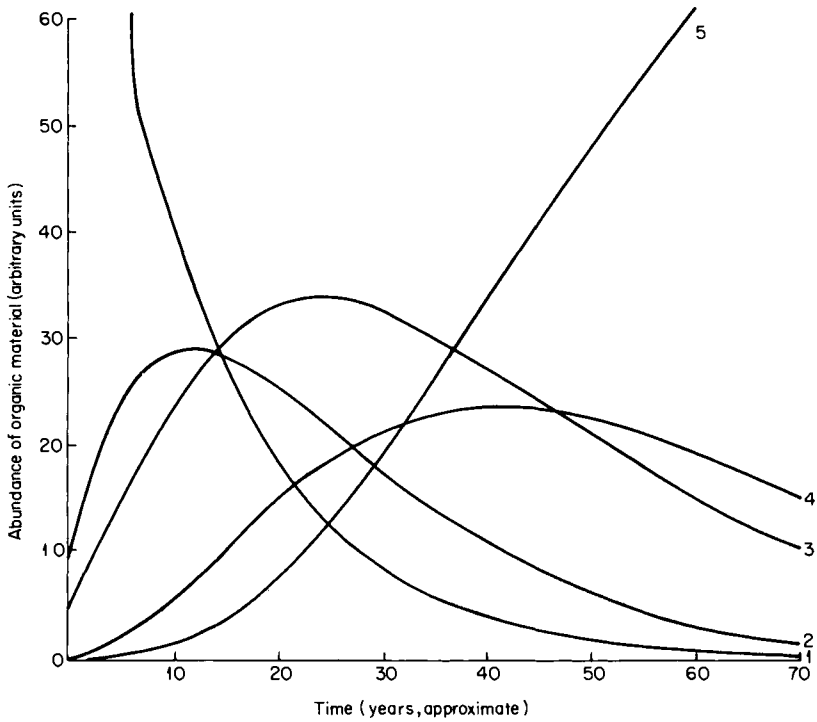

FIG. 4. Initial analog computer simulation of succession in central Oklahoma. Labels corresponding to compartment numbers are as given in Fig. 3.

coefficients as given in Table III. Figure 5 contains two lines labeled compartment 5, one produced by the five-compartment system shown in Fig. 3 (labeled "5a") and a second produced by the insertion of an extra compartment between numbers 4 and 5 (labeled "5b"). The contents of this extra compartment do not correspond to a physical variable, but merely represent a device to introduce extra time delay into the model as suggested by Berman *et al.* (1962). This modified model is still an example of the linear constant-coefficient form as defined by Eq. (2).

Because the data used are qualitative, because times and abundances are approximate in Smith's report, and because the object of the model is to depict general trends rather than exact relations, the scales of time and abundance are left as arbitrary units. Abundance could be interpreted as biomass density, energy, cover, or some qualitative measure of the

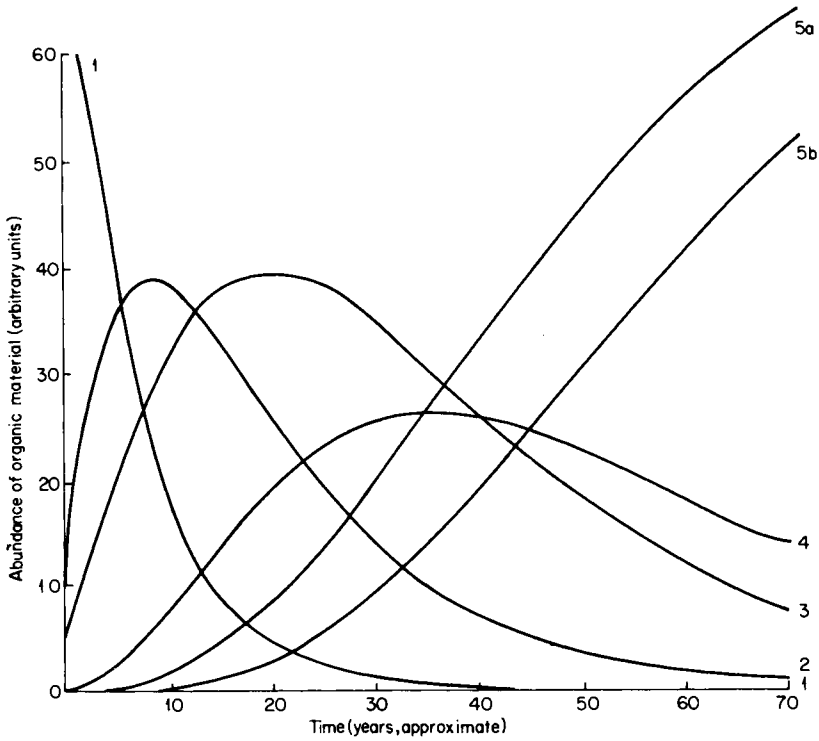

FIG. 5. Final analog computer simulation of succession in central Oklahoma. Labels corresponding to compartment numbers are as given in Fig. 3. The curve labeled "5b" is produced by inserting a time delay between compartments 4 and 5. Curve "5a" is compartment 5 without the delay.

vegetation, as discussed above. The times at which peaks occur agree approximately with the results given by Smith. It is evident from the data that there is wide variation in these times. However, a general trend for the peaks to occur at more widely separated times during the latter stages can be seen. This trend is reflected in the model.

D. INCLUSION OF MECHANISTIC EFFECTS

At this point the model is simply a convenient way of empirically summarizing secondary succession in central Oklahoma. Improvement dictates addition of some mechanistic effects. A mechanistic model is one which reflects the observed phenomena and, to some degree, the underlying causal processes as well. A mechanistic model is the opposite of a "nude" model, in the sense used by Nooney (1965).

TABLE III

FINAL MATRIX FOR ANALOG COMPUTER MODEL OF CENTRAL OKLAHOMA SUCCESSION

		From: 1	2	3	4	5	
To:[a]	1	−2.0	0.0	0.0	0.0	0.0	
	2	1.6	−1.0	0.0	0.0	0.0	
	3	0.4	1.0	−0.7	0.0	0.0	
	4	0.0	0.0	0.7	−0.8	0.0	
	5	0.0	0.0	0.0	0.6	0.0	
		From: 1	2	3	4	5	6
To:[b]	1	−2.0	0.0	0.0	0.0	0.0	0.0
	2	1.6	−1.0	0.0	0.0	0.0	0.0
	3	0.4	1.0	−0.7	0.0	0.0	0.0
	4	0.0	0.0	0.7	−0.8	0.0	0.0
	5	0.0	0.0	0.0	0.0	0.0	1.0
	6	0.0	0.0	0.0	0.6	0.0	−1.0

[a] Five-compartment form.

[b] Six-compartment form. Extra compartment inserted to produce additional time delay. Figure 5 gives the system solution corresponding to this matrix.

Smith emphasizes throughout his study the importance of the depth of the humus layer (i.e., litter) or the percentage of organic material in the soil as a factor in determining the time of invasion of the various species. Percent organic material in the soil can be identified as a compartment whose rate of increase is roughly proportional to time since abandonment, assuming that normal succession has been occurring. If data were available on the differential contributions of the various species to humus accumulation this could be incorporated. The effect of the increasing humus layer on the vegetation compartments can be incorporated by allowing the positive terms in each row of the coefficient matrix to be step functions of the humus compartment. There will be, for the ith vegetative compartment, a value, c_i, of the sixth (humus) compartment when the off-diagonal elements of the transfer coefficient matrix become nonzero and assume the value given in Table IV. We have

$$a_{ij}^{*} = \begin{cases} 0 & \text{if } x_6 \leqslant c_i \\ a_{ij} & \text{if } x_6 > c_i \end{cases} \qquad i, j = 1, 2, \ldots, 5, \tag{18}$$

where a_{ij} is the ith row, jth column entry in the matrix of Table IV and c_i is the value of x_6 at some time, t_i, when growth in the ith compartment

TABLE IV

FINAL PARAMETERS FOR THE DIGITAL COMPUTER MODEL OF SUCCESSION IN CENTRAL OKLAHOMA[a]

	From:	1	2	3	4	5	6
To:[b]	1	−0.1739	0.0	0.0	0.0	0.0	0.0
	2	0.4347	−0.8695	0.0	0.0	0.0	0.0
	3	0.1739	0.8695	−0.0609	0.0	0.0	0.0
	4	0.0	0.0	0.1304	−0.8695	0.0	0.0
	5	0.0	0.0	0.0	0.0522	0.0	0.0
	6	0.0148	0.0870	0.0870	0.0870	0.0870	−0.2609

c_i:	c_1	c_2	c_3	c_4	c_5
	0.0	2.7	3.0	6.5	8.2

[a] The sixth compartment corresponds to the humus compartment; others are as labeled in Fig. 3.

[b] Values of a_{ij}.

should start. The values of c_i must be chosen to force the equation solutions to reflect the real situation. If more precise quantitative data were available, this would be done in a least-squares sense.

It may be more realistic to make the a_{ij}^* some other function of x_6 such as a piecewise-linear form like that shown in Fig. 2. It is doubtful whether the data available are sufficiently detailed to warrant such a refinement, making its inclusion merely speculation.

Some limitations of the model of Table III can be avoided by the step function additions. Variation of the a_{ij} values together with the c_i values allows the experimenter a much greater control over the peak and duration times for the various seral dominants. In addition, the model is no longer completely nonmechanicstic, but reflects the knowledge of the ecologist concerning some of the causal relationships in the ecosystem. Notice that the relationships reflected involve a feedback mechanism: vegetation is responsible for the buildup of humus; amount of humus, through its modification of soil porosity, water holding capacity, etc. is responsible for the establishment of other species of vegetation.

Figure 6 shows the results of computer experimentation with the modified equation system. The seral stages are clearly visible and marked. Table IV gives the values of the constants c_i in the bottom part; in the top part, is the matrix of a_{ij} values subsequently decided upon to give the most realistic results. It was no longer necessary to use the extra compartment to provide the time delay for compartment 5. The

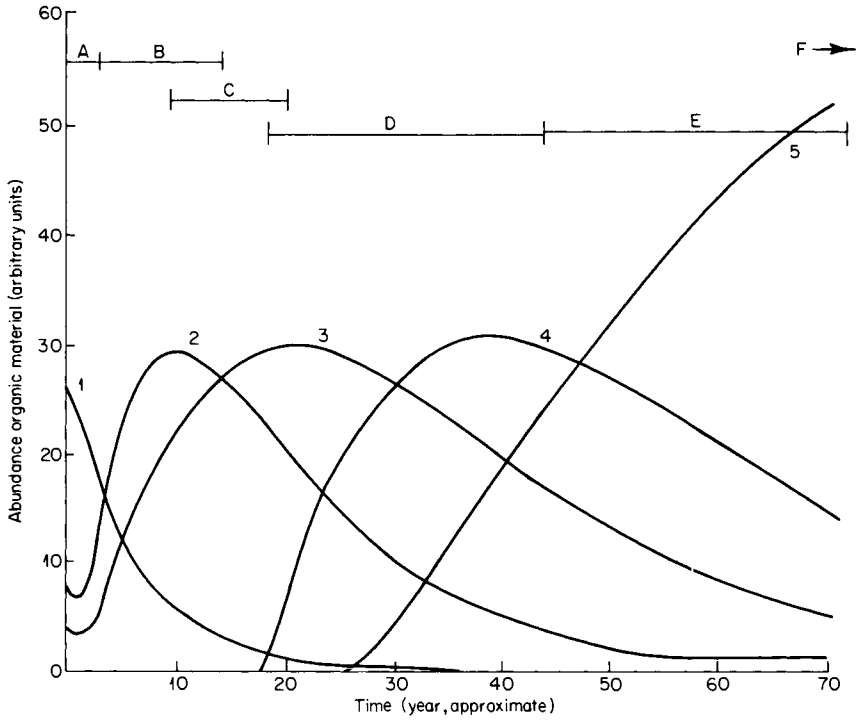

FIG. 6. Results of digital computer simulation of succession on abandoned cropland in central Oklahoma. Labels corresponding to compartment numbers are as given in Fig. 3. Lettered line segments correspond to seral stages as described in the text.

values were arrived at by the trial and error manipulation on the digital computer using the COMSYS 1 (Bledsoe and Olson, 1969) simulation program. It would be possible to modify COMSYS 2 or some other optimization algorithm to do the manipulation automatically and systematically. For the data in question, the trial-and-error method gave a satisfactory result.

E. DIRECTIONS FOR FURTHER WORK

Smith emphasizes that the dominant plants play the major role in central Oklahoma secondary succession as they interact with the soil. Animals play a secondary role and the nondominant plants do not exert a major effect on the dominants. Nevertheless it may be desirable to include some of the other plant and animal species in a more mechanistic model. Smith also emphasizes the importance of amount of rainfall in

influencing the rate of accumulation of the humus layer. Though no data are provided on rainfall, such an effect could be introduced by allowing the entries in rows 1 through 5 of column 6 of the coefficient matrix to become increasing linear functions of an annual rainfall parameter.

Considerable data on arthropod populations are available for the area; their ecology is complex. Phytophagous species are present at times when their particular plant food is available. Parasitic or predaceous species are present when their food species are present. Some species are predaceous during part of their life cycle and phytophagous at other times. The presence of any insect species depends ultimately upon presence of specific plants and virtually every species would have to be given a separate compartment with its individual flow functions and feedback mechanisms. This would necessitate considerable extension of the plant part of the model. For example, the Colorado potato beetle, *Leptinotarsa decimlineata*, feeds on certain species in the Solanaceae which occur during the early forb stages. A compartment of these species, *Solanum carolinense* and *Physallis heterophylla*, would have to be formed and linked to compartment 1 as an associate of *Helianthus annuus*. An increase in this compartment would then trigger growth in the potato beetle compartment. Other Coleopterans are characteristic of different seral stages; sometimes two species in the same genus occur at quite different successional stages.

Some 293 insect species were found by Smith (1940). A model which reflected each of their ecological habits might involve well over 300 compartments if the interactions of each species were unique. If sufficient autoecological information were available for the species involved, such enormous models could be constructed and are within the simulation capabilities of present-day high-speed computers, although existing simulation programs would require considerable modification and streamlining. It should be apparent from the foregoing that construction of such a model would be tedious, but possible and straightforward, given sufficient data.

IV. Old-Field Succession in the North Carolina Piedmont

Billings (1938) explains the mechanisms of change in an old-field system of the North Carolina Piedmont from a grass-forb stage to a shortleaf pine stage and finally to a deciduous forest. A general compartment model and possible transfer equations for some of the compartments are developed herein with explanations of how to experiment with the equations as a prelude to further empirical analysis.

A. Grass, Forb, and Shrub Compartments

Upon abandonment, and after annual and perennial weed stages, old fields in this area are invaded primarily by broomsedge (*Andropogon virginicus*). It is at this point in time where the present model will commence. The live vegetation component of the broomsedge community we shall term x_1, and an s-shaped logistic curve with respect to time would be expected for the biomass of broomsedge. This suggests a differential equation for the change of biomass in the first compartment as a function of time as given by Eq. (19),

$$\dot{x}_1 = a_{11}x_1 - b_{11}x_1^2. \tag{19}$$

Constants a_{11} and b_{11} in the above equation are positive constants to be determined experimentally. This equation will produce the desired s-shaped growth curve with the initial condition for compartment 1 set to some small positive quantity. The limiting value of this curve will be a_{11}/b_{11}, and the rate of increase will be determined by a_{11} alone. Solution to Eq. (19) is

$$x_1 = \frac{a_{11}}{b_{11}}[1 + e^{-a_{11}(t-t_0)}]^{-1}. \tag{20}$$

Here

$$t_0 = \frac{1}{a_{11}} \ln\left(\frac{a_{11}}{b_{11}x_1(0)} - 1\right) \tag{21}$$

gives the initial conditions. Growth of subdominant forbs and woody shrubs (e.g., *Viburnum*, *Aster*, *Plantago*) accompanies the broomsedge community and can be modeled approximately by the equation for compartment 2,

$$\dot{x}_2 = a_{21}x_1 + a_{22}x_2 . \tag{22}$$

Billings' data shows a gradual increase in organic matter in the soil as a result of dead and decaying vegetation in these first two compartments. This can be shown as a gradual buildup in compartment 3, soil organic matter. Humus, per se, according to Billings, is not present in any quantity until at least 20 years after abandonment.

$$\dot{x}_3 = a_{31}x_1 + a_{32}x_2 + a_{33}x_3 . \tag{23}$$

B. "Shade" Compartment

The taller forbs and shrubs have a shading effect upon the species of a lower growth form. Compartment 4 will represent this effect and might

be called "amount of shading in lower synusia" or simply the "shade" compartment. Equation (24) will govern compartment 4

$$\dot{x}_4 = a_{42}x_2 + a_{44}x_4 . \tag{24}$$

This compartment will be quite useful later. The equation for compartment 1 can be modified to include this "shading" effect by replacing a_{11} with a_{11}^*, where

$$a_{11}^* = a_{11}(d_1 - x_4)/d_1 \tag{25}$$

for d_1 equal to some positive constant. This will force the value of x_1 down as x_4 increases; when x_1 is near zero with a_{11}^* negative, the quadratic term in Eq. (19) can be ignored and x_1 will go asymptotically to zero as desired. This agrees with Billings' data which shows that many woody shrubs persist much longer than broomsedge.

At this point the system is summarized in Fig. 7. The solid lines indicate a direct transfer of the compartment contents via a nonzero entry in the coefficient matrix A. The dotted lines indicate that one compartment affects the growth rate of another by modification of some parameter in the equation which governs the affected compartment.

C. Pine Compartment

Billings and others (e.g., McQuilkin, 1940) indicate that seed source is the major factor in invasion by *Pinus echinata* of old fields in this area, though organic matter accumulation has some effect. Accordingly we shall allow x_5, the pine compartment, to commence growth when time t reaches a threshold value corresponding to a time when natural seeding occurs. The parameters of the x_5 equation can be varied to simulate the effect of seed sources varying in quantity and quality if it is desirable. Equation (26) gives the form for $\dot{x}_5$.

$$\dot{x}_5 = a_{55}^* x_5 - b_{55}x_5^2. \tag{26}$$

Since the demise of pine is due to failure to reproduce under its own cover as a result of seedling mortality, the growth of x_5 can be controlled by letting a_{55}^* be a step function of two variables, one to initiate growth and one which causes growth to cease. Billings' data indicates that pine seedling mortality might be caused by insufficient root development to

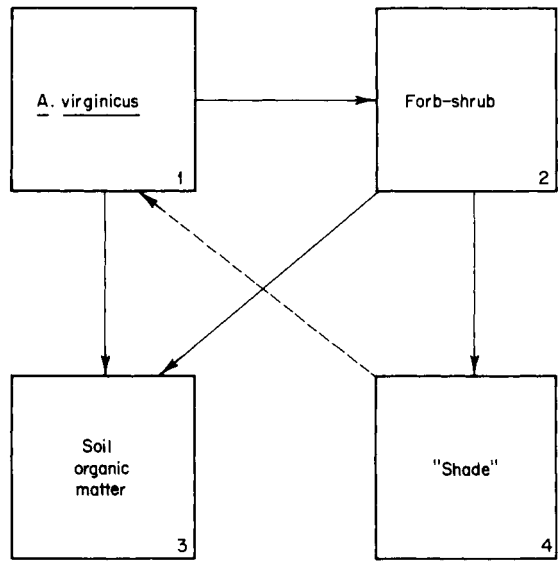

FIG. 7. Initial compartment model for early stages of succession in the North Carolina Piedmont. Solid lines indicate compartmental transfers achieved through nonzero entries in a transfer coefficient matrix. Dotted lines indicate that one compartment affects the contents of another by modification of one of its growth parameters, as in Eq. (25), where x_4 affects the a_{11}^* value for compartment 1.

compete successfully with the roots of mature pines in the top 6-in. layer of soil. Thus we formulate a_{55}^*

$$a_{55}^* = \begin{cases} a_{55} & \text{if } t > t_1 \text{ and } x_3 < d_2 \\ 0 & \text{otherwise.} \end{cases} \tag{27}$$

As in the previous model, it might be more realistic to allow a_{55}^* to be a smoother function, such as piecewise-linear, to avoid unnaturally sudden changes in the model predictions. Again, because of lack of data to indicate the exact form such a function should take and because this is an initial model reflecting only the gross mechanisms involved, the step function will be adequate.

At the same time that the growing pine stand is failing to reproduce due to intraspecific competition, it is also having a very important effect upon the litter of the forest floor. Compartment 5 should be contributing

greatly to the litter accumulation in compartment 3 and can be taken into account by a modification of Eq. (23) for $\dot{x}_3$:

$$\dot{x}_3 = a_{31}x_1 + a_{32}x_2 + a_{33}x_3 + a_{35}x_5 . \tag{28}$$

By the mechanisms of Eqs. (27) and (28) the pines will effect their own demise through litter buildup and its effect on seedling mortality. Actually, Billings attributes the mortality to soil factors which act on the root morphology of the pine seedlings. However, each of these soil changes is brought about by the action of the pine litter-fall. Thus, the parent factor is the litter accumulation which acts through other soil changes not explicitly represented in the model.

D. Feedback Effects

Compartment 3 should also have a reducing effect on the shrub–forb compartment due to inability of the light seeds to reach mineral soil and germinate. This can be effected by modifying a_{21} in inverse proportion to x_3 . Let a_{21} in Eq. (22) be replaced by a_{21}^* :

$$a_{21}^* = a_{21}(d_3 - x_3)/d_3 . \tag{29}$$

This is analogous to the method of modification of a_{11} in Eq. (25). The constant d_3 is to be determined by computer experimentation.

Two other compartments, deciduous, climax-dominant overstory trees (oak–hickory) and deciduous trees such as *Cornus florida* and *Acer rubrum* which make up an understory in the hardwood climax forest, will be considered in this model.

E. Oak–Hickory Compartment

The oak seedlings become established as soon as sufficient litter has developed to prevent dehydration of the acorns and the soil compaction has been reduced by accumulation of organic matter. The root morphology of the oaks is such that the seedlings are able to extract water from beneath the zone of intense pine root competition, i.e., the top 6-in. soil layer. Thus oaks do not suffer, through moisture stress, the adverse mortality effects reflected in the pine through Eq. (24). On the contrary, the attainment of a threshold in the x_4 compartment initiates oak growth, rather then retarding it.

Let x_6 be the oak–hickory variable. The following two equations summarize mathematically the statement of the preceeding paragraph.

$$\dot{x}_6 = a_{66}x_6 - b^*_{66}x_6^2, \tag{30}$$

where

$$b^*_{66} = \begin{cases} 1/(d_5 \cdot x_4) & \text{if } x_3 > d_4 \text{ and } \max(x_2, x_5, x_6, x_7) \neq x_6 \\ b_{66} & \text{if } \max(x_2, x_5, x_6, x_7) = x_6 \\ 0 & \text{otherwise.} \end{cases} \tag{31}$$

The max function in the above equations assures that the largest of the several compartments, x_2, x_5, x_6, or x_7, produces the controlling shade effect on compartment six. If x_6 is largest then the oaks cause no shading of themselves. Equation (24) must be modified to allow for shading by the pine compartment (x_4)

$$\dot{x}_4 = a_{42}x_2 + a_{44}x_4 + a_{45}x_5 . \tag{32}$$

F. Understory Species

These species invade at about the same time as do the oak seedlings. Their growth is faster than the oaks but they too are suppressed by the pine canopy. According to Billings, mature oaks are larger than the mature maples. Since the pines do not die off significantly until both oaks and maples have formed a well-developed understory (with other species), the oaks, through shading, prevent dominance by maples. Alternatively, Billings raises the question of whether the maples might assume a temporary dominance if the pine were cut at a stage before the slowly growing oaks had reached a temporary equilibrium in the understory. With this in mind, compartment 7 can be formulated as

$$\dot{x}_7 = a_{77}x_7 - b^*_{77}x_7^2, \tag{33}$$

where

$$b^*_{77} = \begin{cases} 1/(d_6 \cdot x_4) & \text{if } x_3 > d_4 \text{ and } \max(x_2, x_5, x_6, x_7) \neq x_7 \\ b_{77} & \text{if } \max(x_2, x_5, x_6, x_7) = x_7 \\ 0 & \text{otherwise.} \end{cases} \tag{34}$$

Notice that d_4 is the same threshold used to initiate growth in x_6, the oak compartment. Since the maples grow more rapidly than oaks we have

$$a_{77} > a_{66} . \tag{35}$$

Adjustments must be made in b_{77} and b_{66} to provide for a higher steady state in x_6 than x_7. Since the steady state is inversely proportional to the coefficient of the quadratic term,

$$b_{66} < b_{77} \tag{36}$$

is the desired relation. Constants d_6 and d_7 are chosen to produce appropriate intermediate threshold levels. Figure 8 summarizes the model at this point.

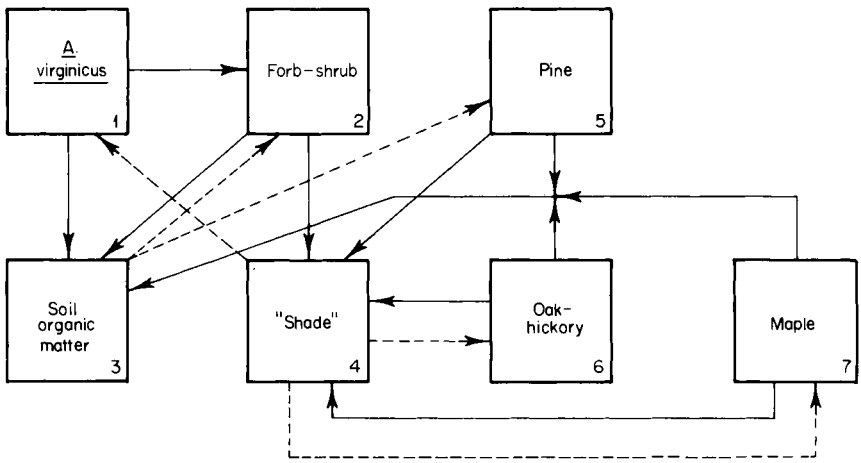

FIG. 8. Final compartment model for succession in the North Carolina Piedmont. Solid and dotted line conventions are the same as for Fig. 7.

G. DETERMINATION OF COEFFICIENTS AND SIMULATION

Determination of the proper coefficient values involves making rough initial guesses at constants related to the earlier stages, solving the model numerically, adjusting the coefficients, accordingly, and resolving the system of equations. The model already is too extensive for a small analog computer, but a large or medium size analog system could solve the problem easily without the difficulties and delay associated with a batch-processing digital machine. Alternatively, a time-shared remote computer terminal, as used by Parker (1969), would be useful at this stage.

The equation governing the "shade" compartment has been modified to take account of the shading phenomenon throughout the successional period. A better name for this compartment might be "shade in the

secondary synusium." The principal cause of shading during the period when a particular compartment is dominant is that compartment itself. When that compartment ceases to be dominant, the principal source of shade in the understory must come from a new species association. This agrees with Cain (1934) and Billings (1938) that synusia are dependent upon an overstory but independent of its floristic composition. Shading has the same effect on the second story regardless of the source of the transfer into compartment 3. This mechanism is reflected in the equation for compartment 4. The equation governing x_4 becomes

$$\dot{x}_4 = a_{44}x_4 + a_{4i}x_i\,, \tag{37}$$

where i is 2, 5, 6, or 7 depending upon which of these compartments is largest (i.e., i is a function of time).

Figure 9a, b, and c gives the results of a straightforward simulation, using the COMSYS 1 program, of Eqs. (19), (22), (23), (26), (27), (30)–(34), and (37) which summarize the succession model described in the preceding section. Constants of the system, together with their values as determined by computer experimentation are listed in Table V.

TABLE V

CONSTANTS USED IN THE SIMULATION OF SUCCESSION ON THE NORTH CAROLINA PIEDMONT[a]

A

0.4595	0.0	0.0	0.0	0.0	0.0	0.0
1.0	−1.0	0.0	0.0	0.0	0.0	0.0
0.1	0.1	−0.05	0.0	0.1	0.1	0.1
0.0	1.0	0.0	−1.0	1.0	1.0	1.0
0.0	0.0	0.0	0.0	0.8700	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.7546	0.0
0.0	0.0	0.0	0.0	0.0	0.0	1.2667

c_{11}	c_{22}	c_{33}	c_{44}	c_{55}	c_{66}	c_{77}
−4.5951	0.0	0.0	0.0	−0.0145	−0.0084	−0.0181

d_1	d_2	d_3	d_4	d_5	d_6
60.0	125.0	30.0	3.0	1.1044	0.4605

$t_1 = 2.0$

[a] The graph of Fig. 9 was generated with this data.

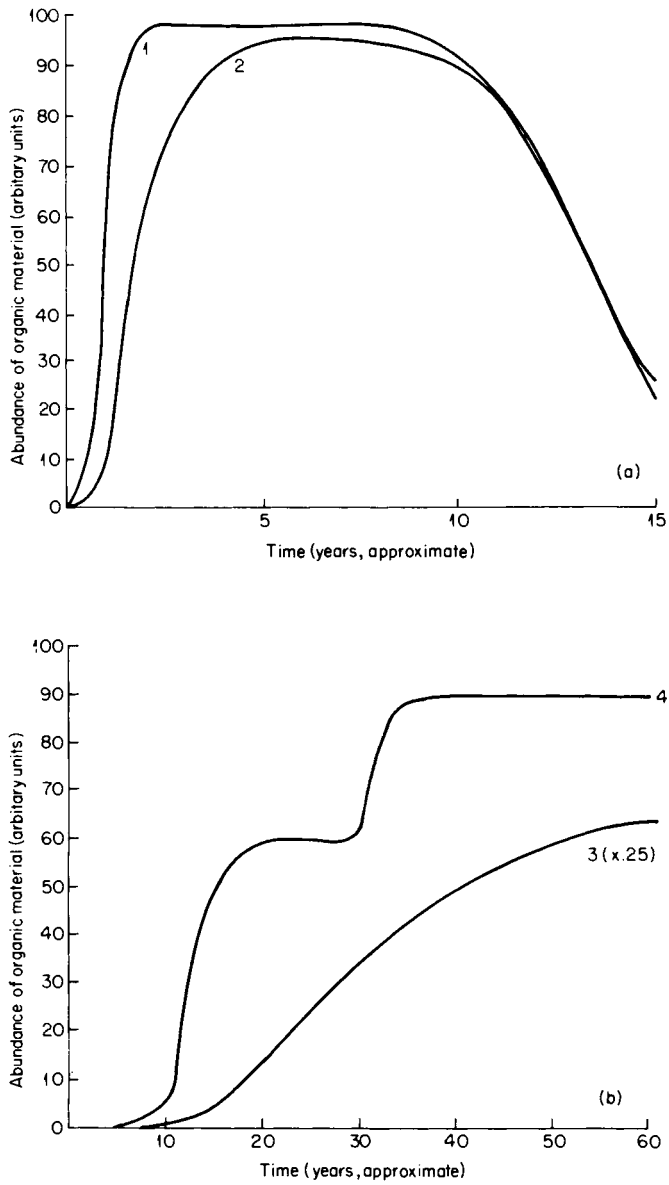

FIG. 9. Results of digital computer simulation of succession in the North Carolina Piedmont. (a) *A. virginicus* (1) and forb–shrub (2) compartments. (b) Soil organic matter (3) and "shade" (4) compartments.

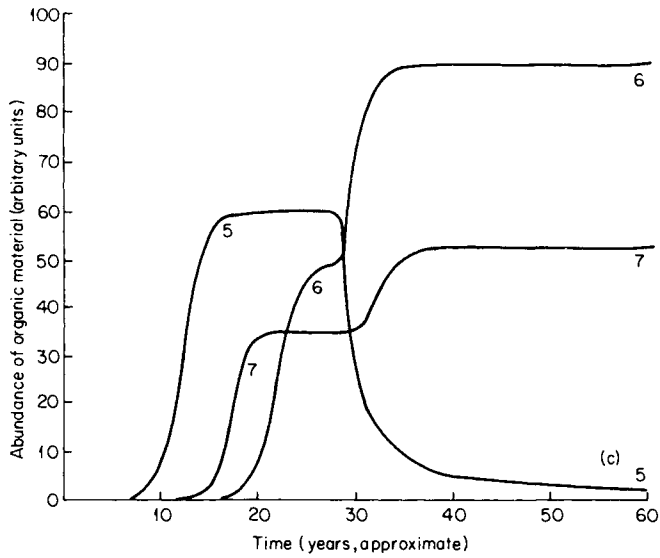

FIG. 9 (c) Pine (5), oak–hickory (6), and maple (7) compartments.

H. EXPERIMENTATION WITH THE MODEL

Billings suggests that if the pine stand were cut at any early time in its development, the fast-growing maples would assume temporary dominance. The oaks, however, would eventually overtop the maples to produce the normal oak–hickory climax. By modifying optional subroutines in COMSYS 1 we can investigate effects of cutting the pine. The results, as shown in Fig. 10, predict this early maple dominance.

The model coefficients need not be modified to predict the early dominance of maple; however, increase of the oak under the maple shading would require a more precise adjustment of coefficient values. This is not surprising, nor does it obviate the usefulness of the model for experimentation purposes, since data on which the solution curves are based are initially qualitative. The fact that maple increase could be predicted by the model purely on the basis of the qualitative conjecture that red maple grows faster than oak in the open is rather more surprising. The resurgent pine peak at $t = 32$ is due to the delay in oak and maple litter build-up.

A mathematical experiment relative to the forb–humus interaction can be performed. It is asserted that die-off under a forest canopy of many herbaceous species (compartment 2) is due to failure of their light

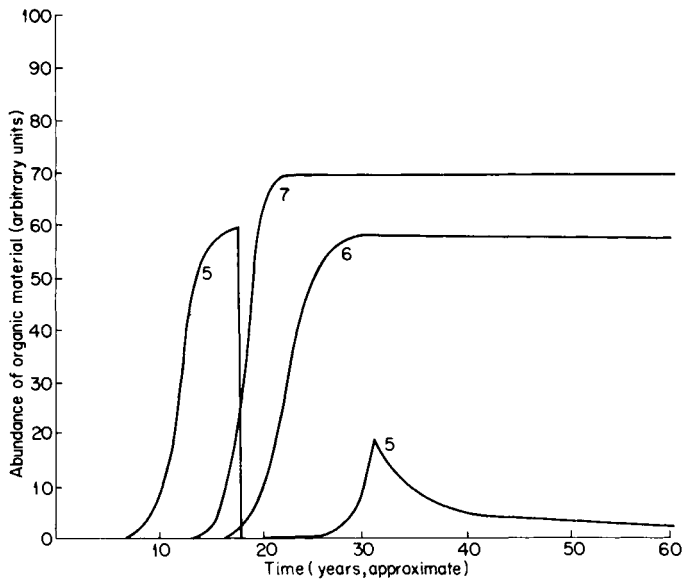

FIG. 10. Effect of pine removal at 18 yr on the oak–hickory and maple compartments of a model for succession in the North Carolina Piedmont. Labels corresponding to compartment numbers are as given in Fig. 8. The resurgent pine peak at 32 yr is due to delay in litter build-up from the deciduous compartments.

seeds to reach mineral soil and proper germination conditions in the dense litter mat of the pine stand. Billings reports a high inverse correlation ($r = -0.97$) between depth of litter and presence of old-field species and cites the work of Reed (1934) and Kawada (1931) in support of this argument. It is reasonable to suppose, and is suggested by the work of Kawada (1931), that artificial removal of litter from the forest floor during the pine stage would result in a resurgence of the herbaceous flora. This experiment was tried on the model by appropriate modifications to the subroutines of COMSYS 1; results are given in Fig. 11(a) and (b).

In addition to the expected result, two other effects can be seen. The pine forest in Fig. 11(b) does not begin to die off until a later time (compare with Fig. 9). Also, the oak and maple compartments are delayed in their succession. The former effect can be expected since it is the litter compartment which controls lack of reproduction in the model. This is contrary to a later suggestion of Oosting and Kramer (1946) that it is the shading effect controlling the root morphology of pine seedlings which is responsible for their lack of production. Such a mechanism could be included but would be contrary to the aim of

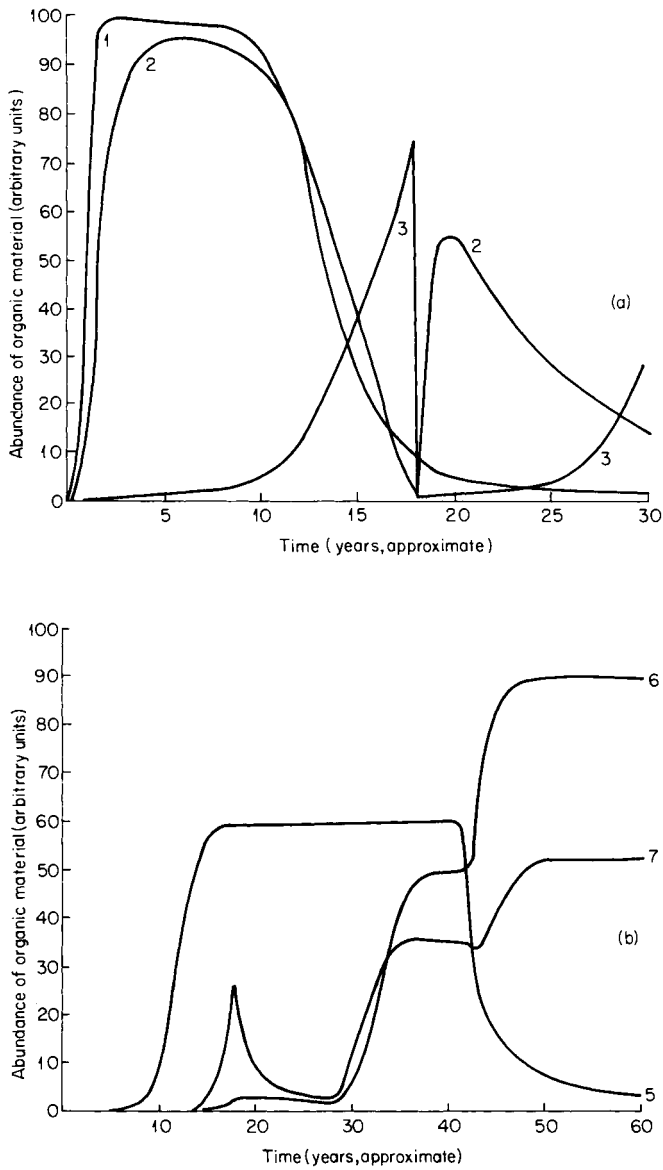

FIG. 11. Effect of litter removal at 18 yr on the compartments of a model for succession in the North Carolina Piedmont. Labels corresponding to compartment numbers are as given in Fig. 8. (a) Grass, forb–shrub, and litter compartments. (b) Pine, oak–hickory, and maple compartments.

reflecting Billings' conclusions. The latter effect is a consequence of the former. Whether pine litter removal would actually prolong succession of the oak and maple flora is a question for experimental work and a much more complex model.

I. Discussion of the Piedmont Succession Model

A number of logical extensions of the model could be made. Since failure to reproduce in the pine compartment is such an important effect, this could be shown more specifically by subdivision of compartment 5 into age cohorts with linear transfers between each cohort. Similarly, root competition plays a large role in this study and provision of a "root density" compartment for the top 6-in. soil layer would provide far more explicit control of root interactions. The primary contributor to such a compartment would be the pines, since oaks and hickories are more deeply rooted species. A compartment whose variable was soil moisture in the top 6-in. layer might be profitably used. It would be contributed to by the litter, root density, and shading compartment and would provide more realistic and explicit mechanisms for the initiation of growth in the oak–hickory compartment and the demise of the pines.

As in the central Oklahoma grassland model, detailed results require that the general forest compartments be broken down into their component species with autoecological data reflected in their transfer functions. Thus, the climax understory, variously treated above as a pure maple compartment or as containing a mixture of species, should actually have explicit subcompartment variables for the faster-growing taller maples and the shorter dogwoods and redbuds.

Again the problem of dimensionality of the model's dependent variables is raised. Billings' data is presented in terms of "stem density per unit area" as measured by a quadrat method. To provide an insight into the homogeneity of the vegetation, he also lists the frequency f of occurrence of each species as

$$f = 100 \times \frac{\text{number of quadrats containing a species}}{\text{total number of quadrats read}} \tag{38}$$

Clearly, the number of stems of *Andropogon* or *Viburnum* on a site is not directly comparable to the number of pine stems. What has been reflected on the vertical axis of the graphs of model results can best be described as "degree of dominance $\times$ average height of species." The degree of dominance of a species is a qualitative variable which can be extracted from Billings' discussion and density data. Intuitively, it seems

that the curve representing pine should rise higher than the curve representing *Andropogon*, though neither is "more or less dominant" than the other at the height of their seral stage. (This might be disputed, since Dansereau (1957) defines dominance of a species as attainment of "great spatial extent.") For this reason, the parameter "height of species" is included.

V. General Discussion

A. Empirical Data and Random Effects

Many analysts might be dissatisfied with the subjectiveness of the measurements involved in what is ostensibly a mathematical model. Nevertheless, the measurements used are adequate and fulfill the purpose of this preliminary modeling study. The literature, especially the older material where many fundamental concepts are investigated, has a dearth of objectively measured quantitative information suitable for direct use in mathematical models.

One value of the model is to illustrate the need for future studies wherein some variable such as standing crop (in calories per square meter) is the index to vegetation abundance. At the same time, it can be seen that qualitative information is far from incompatible with a model. Accompanying such quantitative data should be measures of the variability of the numbers involved. It is absurd to use a program such as COMSYS 2, requiring relatively large amounts of computer time, to fit coefficients of a model to four significant digits with data having, say, a 20% coefficient of variation.

It is possible to perform a type of sensitivity analysis on the model in which many simulations are completed, each with a set of input parameters selected at random from a collection having a specified probability density. The result will be an approximation to a distribution function for the reponse of the model. Comparison of the variances of empirical data with the model-response variance will yield another measure of model performance.

B. Applications of a Model

The usefulness of a complete model is not limited to a mere graphic representation of normal secondary succession. Properly manipulated, the model could be used to predict successional responses subsequent to fire, drought, application of a selective herbicide or pesticide, severe erosion, or other environmental stress. For example, the Oklahoma model might be specialized to study effects of a selective herbicide. The herbicide

would reduce certain compartment values to near zero, forcing down, in turn, the biomass of those insects dependent upon the species destroyed. This would trigger a chain of events among those predaceous species dependent upon the affected phytophagous insects. At the same time the rate of humus accumulation might be reduced if the plants affected were turf builders and succession would be slowed. Alternatively, if the plants were forbs such as *Solidago*, whose occurrence depends upon the existence of open spaces among bunchgrasses, rate of succession might be less affected. Yet the total percent cover would be reduced, affecting, in turn, soil moisture and triggering a different chain of events. Exactly what might occur is predictable only through construction of the detailed model and simulation of a particular initial occurrence. Such model development for a whole naturally-occurring ecosystem would require intensive literature study, consultations with ecologists of the area, field survey, and considerable mathematical experimentation.

A complete ecosystem model is a vast mathematical machine for deducing the logical consequences of many individual but interacting mechanisms. The individual mechanisms can be understood by a single person but the simultaneous effect of many mechanisms requires the painstaking thoroughness of a computer for analysis. A scientist might then abstract the computer results into useful generalizations about ecosystems.

C. Manpower and Hardware Requirements

The studies reported herein required about six months of half-time effort with some help from student programmers. The work was done in a batch-processing computer environment (using Fortran IV implemented on a Control Data 6400 computer). The use of an interactive computer terminal, time-shared among several users, enables the user to make the many test runs and parameter modifications much more rapidly than is possible in the batch environment. During the lag between program submission and return, the modeler loses touch with his train of thought, even if turnaround time is fast (say, $\frac{1}{2}$ hr). In addition, there is the problem of transportation of the program information to and from the computer center, which further increases effective turnaround time.

The remote terminal method is much more efficient; the information transportation problem is solved electronically. Similar efficiencies can be achieved by using a medium or large scale analog computing system. Unfortunately, analog programming is not as versatile a tool as digital programming; however, once learned, analog methods are very appropriate and efficient for the types of models discussed above.

From an economic point of view, digital terminal fixed costs are of the same order of magnitude as for a medium sized analog facility. Operational costs for the analog are considerably smaller. Bledsoe (1968) discusses these points more thoroughly and provides references on the economics involved.

The Fortran programs used in the numerical solution of the above equations are available from the authors or in an appendix of Bledsoe (1968).

Acknowledgments

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Analog Computer Models of "The Wolves of Isle Royale"

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I. The Plant–Moose–Wolf Food Chain

A. Introduction

Ecologists more and more are describing natural communities as though they were systems in the engineering sense: mutual causal machinery with inputs, outputs, and holistic function. Such systems should, therefore, be amenable to mathematical description and modeling. Engineers, however, have never had to deal with systems of such complexity as those encountered in ecology, and current mathematical tools and perspectives allow for only crude analyses of oversimplified systems or subsystems of the larger ecosystem.

Since methods of describing whole systems in a fashion which would permit completely realistic simulation modeling are not obvious at this time, all mathematical relationships thus far developed deal with one or another of the major subsystems of natural communities. Examples of classes of these major subsystems are mineral cycling and energy flow components, both of which contribute information necessary for proper understanding of the ecosystem as a whole.

In this chapter an energy-flow subsystem of the Isle Royale National Park ecosystem is modeled. This system is the plant–moose–wolf food chain as described in L. David Mech's study, "The Wolves of Isle Royale" (Mech, 1966). The technique will consist in applying various mathematical functions to define energy transfers within this system, and testing the behavior of the resultant systems against known aspects of reality.

The modeling problem was approached by first attempting to simulate steady state conditions on the analog computer based on information contained in Mech's paper. Following establishment of realistic steady states, certain hypotheses about both the analog computer models in use and the actual plant–moose–wolf trophic structure were tested. In making these comparisons, the following considerations of Mech provided guidance:

(1) "The important question is whether wolves merely substitute for other mortality factors or whether they kill more animals than other factors would. The history of Isle Royale moose affords an answer. Before wolves became established, the herd increased to an estimated 1,000 to 3,000 animals in the 1930's, decreased drastically a few years later, and built up again in the late 1940's. The limiting factor was food supply.

(2) "Apparently the Isle Royale wolf and moose populations have reached a state of dynamic equilibrium. Each is relatively stable, so any substantial fluctuation in one probably would be absorbed by the other until another equilibrium is reached.

(3) "If some extraordinary factor suddenly reduced the moose population by half,

the wolves probably would have such difficulty killing enough animals that inferior individuals might not be allowed to share what prey is taken.
(4) "Conversely, if the moose population increased significantly, wolves would find hunting easier and might eat only preferred parts of their prey (Mech, 1966)."

Three implications important in testing our models can be derived from the above considerations:

(1) Peaks in wolf population oscillations should follow peaks in the moose population. That is to say, there will be a lag in the response of wolves to changes in the moose population. The wolf population will reach a peak approximately when the moose population begins to decline from a peak.

(2) If wolves exert some control over size of the moose population, the wolf population should fluctuate less violently than the moose. That is, fluctuations in the wolf population should involve a smaller percent change in population than should occur in the moose population. For example, doubling the moose population would be expected to increase the wolf population, but not to the point of doubling it. If, as Mech suggests, the wolves ate only preferred parts when moose were plentiful, the wolves would then kill many more moose and cause a greater rate of change in the moose population than in their own.

(3) Any general model, which is not to be restricted to present conditions, must have more than one steady state, but also must have a unique steady state for a given set of conditions. (In this chapter, "steady state" will be used to indicate regular periodic nonincreasing or nondecreasing functions as well as constant functions.)

B. Basic Data

Two types of data useful for modeling appear in Mech's paper: the histories of the moose and wolf populations and the amount of food passing through the chain. The histories were a particularly attractive feature because they enabled us to check the time behavior of our models with that actually recorded.

Moose probably reached Isle Royale about 1905 by swimming from Canada. The herd was estimated at 200 animals in 1915. In the years following, the moose herd went through several population oscillations. For some 15 years from 1915 to 1930, the number of animals rose steadily from 200 to an estimated 1000–3000. About this time apparently, the carrying capacity of the environment was exceeded, and a crash occurred. The moose herd dwindled over the next 13 years to a nadir of 171 animals in 1943. Following this low point, the herd once again began to build and went through another smaller oscillation. This oscillation was

reduced in size, presumably because of previous damage to the vegetation by the large herd. A peak of about 800 animals was reached in 1949, and the number declined to about 290 in 1957. During the recovery period after this decline, wolves apparently developed into a significant factor (Fig. 1).

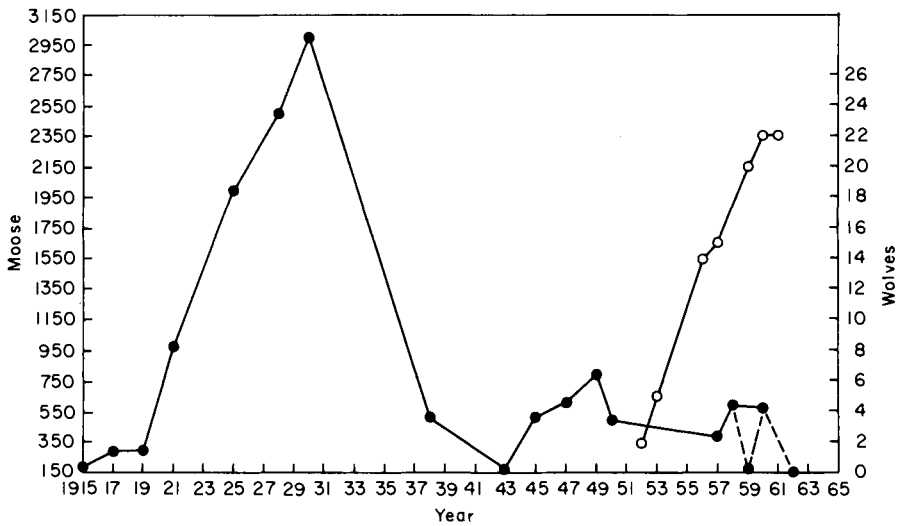

FIG. 1. Histories of the Isle Royale moose (●) and wolf (○) populations.

The existence of wolves on Isle Royale was first definitely established in 1952, although evidence had indicated their earlier presence. The wolf population increased from an estimated two animals in 1952 to at least 22 animals in 1961 (Fig. 1). During the period of Mech's study (1959–1961), wolf–moose interactions were strong. Mech concluded that moose were by far the most important energy source for the wolves, and that the moose and wolf populations had stabilized.

The amount of food passing through the chain was estimated by Mech in several ways. He estimated the weight of vegetation consumed by a moose herd of 600 animals by extrapolating from data on the food consumption of a captive 800-lb moose. The herd was considered to consist of 564 "average" 800-lb moose. He estimated the weight of moose consumed by wolves by examining remains of wolf kills. Wolf weights were estimated by considering an "average" wolf to weigh 72 lb; this figure was applied to a total of 21 "average" wolves on Isle Royale to obtain an estimate of population biomass. The important point to note here is that these calculations lead to a pyramid of energy transfer.

Figure 2 summarizes virtually all of the energy flow data available in the paper which was relevant to modeling the system.

Table I lists the values of system parameters available directly from

TABLE I

KNOWN SYSTEM PARAMETERS

Parameter	Value	Explanation
Area of Isle Royale	210 square miles (544×10^6 m^2)	
Wolf population weight	1512 lb	72 lb/average[a] wolf; 21 average wolves
Weight of moose eaten by wolves per year	89,425 lb	112 average moose; 800 lb/average moose
Weight of vegetation eaten by 112 average moose	1,156,400 lb	
Number of average moose in the herd	564	

[a] An average animal is the weight of one animal adjusted for age and sex distribution.

the paper along with relevant qualifications employed in making the estimates. It can easily be seen from Fig. 2 and Table I that most of the system parameters needed for modeling had to be derived indirectly.

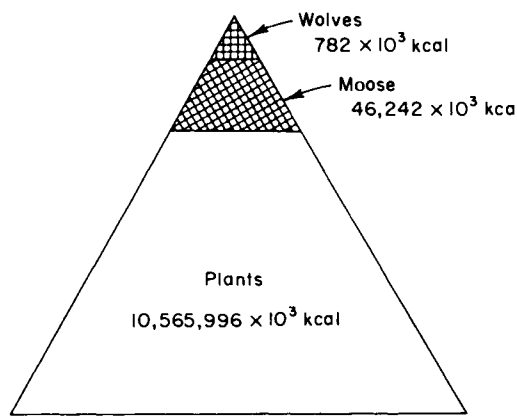

FIG. 2. Pyramid of energy content of Isle Royale plants, moose, and wolves (adapted from Mech, 1966).

C. Derivation of System Parameters

Lack of information on most system parameters required us to estimate needed values. This situation is common in ecological modeling since so few ecosystems have been studied adequately enough to provide measured parameter values. Consequently, our calculated values represent what are probably very gross estimates of actual conditions on Isle Royale. As originally conceived, our model would have contained five compartments: plants, moose, other herbivores, wolves, and decomposers. However, it proved impossible to estimate contents of the other herbivore and decomposer compartments, although we were able to estimate losses to these compartments. As a result, we collapsed our system to a three-compartment plant–moose–wolf model.

1. *Plants*

The important parameters associated with the plant compartment are: energy input, standing crop, respiratory energy loss, loss to other herbivores, loss to moose, and loss to decomposers. Direct information from Mech's paper was available for only one of these parameters—loss to moose. We were therefore obliged to follow an indirect route to the information needed. MacFadyen (1969) reported average net productivity for the northern hemisphere as 1 $kg\,m^{-2}\,yr^{-1}$, 4×10^3 $kcal\,m^{-2}\,yr^{-1}$, or 1.6 % of incident utilizable solar radiation, In addition, average gross productivity was given as 3.0% of incident utilizable solar radiation. These values are certainly high for Isle Royale in Lake Superior, and consequently represent maximum conditions. From these figures, it was possible to calculate average incident utilizable solar radiation by dividing net productivity energy by 0.016 (1.6%). It was then possible to estimate average gross productivity by taking 3.0% of the calculated average incident utilizable solar radiation. This value represents solar radiation actually utilized by plants, and was therefore used as energy input to the plant compartment.

Plant respiration was taken as the difference between gross and net production.

Total herbivore loss was estimated as 10% of net productivity (Odum, 1963). Mech's data yielded a value for loss to moose. This value was calculated by converting pounds of vegetation to kilograms of vegetation, multiplying by the average energy content of 1 kg of plant material (4×10^3 kcal), and dividing by the area of Isle Royale. Loss to other herbivores was taken as the difference between total herbivore loss and loss to moose.

Loss to decomposers was taken as the difference between net productivity and total herbivore loss.

Plant standing crop was the most difficult parameter to estimate, and the following procedure was employed: Total moose browse was estimated as the amount of vegetation that would be consumed by 3000 moose on the basis of Mech's estimate for an average 800-lb moose, plus the amount of vegetation that would be needed to support 171 surviving animals both for a period of one year. This value was then considered arbitrarily to be 1 % of the total plant biomass of Isle Royale.

2. *Moose*

Important parameters associated with the moose compartment are: standing crop, respiration, transfer to wolves, and energy loss through nonassimilation, nonwolf mortality, and remains from wolf kills. Data on standing crop and transfer to wolves were available from Mech's paper. The following procedure was used to calculate the standing crop and is an example of the type of calculations made for wolves also: Pounds of moose were estimated by considering the herd to consist of 564 average 800-lb animals. This value was converted to kilograms, and 20% of the kilogram value was taken as the fresh weight protein content of the moose (see below). The protein content in kilograms was then multiplied by the average energy content of 1 kg of protein, 5.7×10^3 kcal/kg (Brody, 1964), to yield an estimate of energy content of the moose herd. Brody (1964) gives beef protein values ranging from 16.2 to 21.3% fresh weight for various body parts. Therefore, the assumption of 20% overall for moose is probably high, but it helps to compensate for neglected carbohydrate and fat. Since the animals are probably 70–85% water, we feel that this protein value yields an adequate approximation of energy content.

Moose respiration was estimated as 47.5% of ingestion based on white-tailed deer (Smith, 1966). Ingestion, of course, is the energy transfer from plants to moose.

Transfer to wolves was calculated using the weight of moose transferred as given by Mech and the protein equivalent.

The loss attributable to unassimilated energy, nonwolf mortality, and remains from wolf kills was taken as the difference between ingestion and respiration plus transfer to wolves.

3. *Wolves*

The important parameters associated with the wolf compartment are: standing crop, respiration, and loss through nonassimilation and mortality.

Standing crop was calculated from Mech's data employing the protein equivalent.

Respiration was taken as 90% of ingestion, an average value for carnivores (Odum, 1963).

The remaining loss was calculated as the difference between ingestion and respiration.

The preceding calculations assume that no growth is occurring in the system; or put another way, net production is totally dissipated. In addition, all calculations are based on a time period of one year. Table II summarizes the derived estimates of system parameters.

TABLE II

DERIVED SYSTEM PARAMETERS[a]

Forcing	Plant	Moose	Wolf
F_{01} : 7.5×10^3	x_1 : 12×10^3	x_2 : 0.43	x_3 : 0.0014
	F_{10} : 3.5×10^3	F_{20} : 9.2	F_{30} : 0.076
	F_{15} : 3.6×10^3	F_{25} : 10.1	F_{35} : 0.009
	F_{12} : 19.4	F_{23} : 0.085	
	F_{14} : 380.6		

[a] The F's are in kilocalories per square meter per year, and the x's are in kilocalories per square meter.

D. BLOCK DIAGRAM

Figure 3 represents the compartment model of the Isle Royale plant–moose–wolf food chain as defined above. This model is quite obviously a

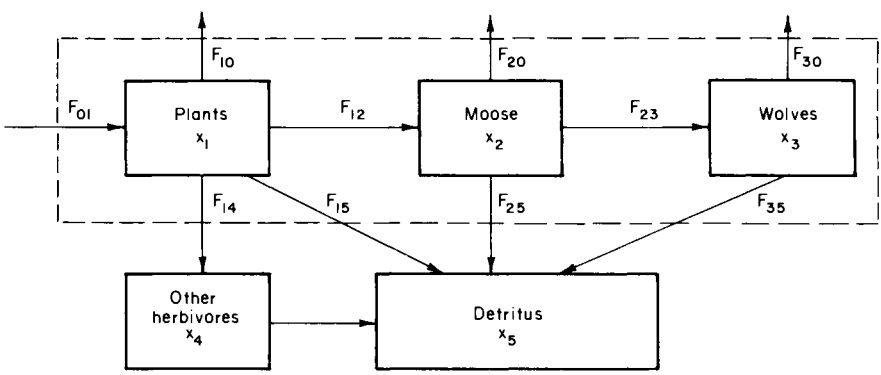

FIG. 3. Block diagram of Isle Royale system.

great oversimplification considering the ecosystem as a whole, but in terms of the predator–prey subsystem, we feel it reflects the actual situation sufficiently well to be utilized in a study of this type. The energy pathways and coupling of compartments are shown in a general way. A major assumption associated with the model is that no factors other than those indicated significantly affect the plant–moose–wolf relationship in terms of energy flow at the system level.

E. General System Equations

General equations of state were developed by considering the balance between energy inputs and losses from each compartment. Thus, referring to Fig. 3, a suitable system of general equations is

$$\begin{aligned} dx_1/dt &= F_{01} - (F_{10} + F_{12} + F_{14} + F_{15}) \\ dx_2/dt &= F_{12} - (F_{20} + F_{23} + F_{25}) \\ dx_3/dt &= F_{23} - (F_{30} + F_{35}), \end{aligned} \tag{1}$$

where x_1 is plants, x_2 is moose, and x_3 is wolves.

The remainder of this chapter will be concerned with consequences of representing these relationships by several different models, as revealed by an analog computer study. The computer used was an EAI TR-20.

II. Description of Models

A. Model Hierarchy

A series of equations describing the fluxes associated with each compartment can be generated. These flux equations can be grouped on the basis of linearity or nonlinearity, as outlined in Section III.G of Chapter 1. Flux functions involving only one compartment (donor or recipient) are generally linear, while functions involving two or more compartments (e.g., donor and recipient jointly) are nonlinear.

Several equations from the Chapter 1 hierarchy were selected and applied to Eqs. (1) to define feeding functions, with the constraint that the feeding function for "other herbivores" was always assumed linear since the content of this compartment was unknown. All nonfeeding fluxes indicated in the block diagram of Fig. 3 were considered to be linear, i.e., the assumed form of these fluxes was a constant fraction of the donor compartment in each case. This pattern was followed for each model. In a more detailed study, nonfeeding fluxes could also be made to depend on more than one compartment or on one compartment in a nonlinear manner.

We assumed a priori, based on the rationale of each formulation as explained in Chapter 1, that models would better approximate reality in a sequence from linear to simple nonlinear to complex nonlinear feeding relations. Consequently, the following three forms were chosen for the feeding functions.

$$F_{ij} = \phi_{ij} x_i \tag{2}$$

$$F_{ij} = \phi_{ij} x_i x_j \tag{3}$$

$$F_{ij} = \phi_{ij} x_i (1 - a_{ij} x_j). \tag{4}$$

The models were tested essentially on the basis of this hierarchy.

B. The Linear Model

The rationale of this donor-controlled formulation of feeding fluxes [Eq. (2)] seems grossly oversimplified for both grazing and predatory cases: the fluxes depend solely on sizes of the donor compartments. Consequently, we believed from the outset that this model would inadequately represent the system, and furthermore would be the poorest of those examined. The primary motivation for exploring it was to test the adequacy of the data and to gain experience in various techniques of analog computer simulation. Yet, because of its usefulness, we returned to it again and again.

The set of differential equations describing the linear system is

$$\begin{aligned} dx_1/dt &= F_{01} - (\rho_{10} + \tau_{12} + \tau_{14} + \mu_{15})\, x_1 = F_{01} - L_1 x_1 \\ dx_2/dt &= \tau_{12} x_1 - (\rho_{20} + \tau_{23} + \lambda_{25})\, x_2 = \tau_{12} x_1 - L_2 x_2 \\ dx_3/dt &= \tau_{23} x_2 - (\rho_{30} + \lambda_{35})\, x_3 = \tau_{23} x_2 - L_3 x_3 \,. \end{aligned} \tag{5}$$

The ρ-coefficients signify respiration rates, τ represents feeding rates, μ mortality, and λ other energy loss rates. The summed loss rate coefficients of each respective compartment are L_1, L_2, and L_3.

Taking flux [$\phi_{ij} x_i$, Eq. (2)] and standing crop (x_i) values calculated previously (Table II), rate constants ϕ_{ij} were evaluated as $\phi_{ij} x_i / x_i$. Table III lists the rate constants calculated in this general manner (i.e., with appropriate modifications for the nonlinear systems) for all models. With all necessary data now available, voltage scaling of the system equations preparatory to analog programming can proceed.

To simplify voltage scaling, a table similar to Table IV, which illustrates calculations for the linear model, is constructed. After the computer variables have been calculated, they are substituted into the

original unscaled differential equations. Amplifier gains then are evaluated by using the scale factor of the left-hand term as a multiplier and using scale factors of the right-hand terms as divisors of their respective terms

TABLE III
RATE CONSTANTS

Constant	Linear	Nonlinear I[a]	Nonlinear II[a]
ρ_{10}	0.292		
μ_{15}	0.300		
τ_{14}	0.0317		
τ_{12}	0.00162	0.00376	0.00181
L_1	0.625		
ρ_{20}	21.43		
λ_{25}	23.49		
τ_{23}	0.198	141.67	0.198
L_2	45.12		
ρ_{30}	54.29		
λ_{35}	6.43		
L_3	60.72		

[a] Blank entries in the nonlinear columns signify the same value as in the linear model.

TABLE IV
VOLTAGE SCALING

State variable (kcal m^{-2})	Estimated maximum (kcal m^{-2})	Scale factor (α_i) (V/kcal m^{-2})	Computer variable (V)
x_1 : 12.0×10^3	24.0×10^3	$10/24 \times 10^3 = 0.417 \times 10^{-3}$	$[0.417 \times 10^{-3} x_1]$
x_2 : 0.43	1.80	$10/1.8 = 5.556$	$[5.556 x_2]$
x_3 : 0.0014	0.0070	$10/0.007 = 1429$	$[1429 x_3]$
Forcing (kcal m^{-2} yr^{-1})	Estimated maximum (kcal m^{-2} yr^{-1})	Scale factor (σ) (V/kcal m^{-2} yr^{-1})	Computer variable (V yr^{-1})
F_{01} : 7.5×10^3	10.0×10^3	$10/10 \times 10^3 = 1 \times 10^{-3}$	$[1 \times 10^{-3} F_{01}]$

(cf. Chapter 1, Section IV. A, for procedural details). The system equations can thus be rewritten as

$$
\begin{aligned}
[0.417 \times 10^{-3}\dot{x}_1] &= \frac{0.417 \times 10^{-3}}{1 \times 10^{-3}}[1 \times 10^{-3}F_{01}] \\
&\quad - \frac{0.417 \times 10^{-3}}{0.417 \times 10^{-3}}(\rho_{10} + \tau_{12} + \tau_{14} + \mu_{15})[0.417 \times 10^{-3}x_1] \\
[5.556\dot{x}_2] &= \frac{5.556}{0.417 \times 10^{-3}}(\tau_{12})[0.417 \times 10^{-3}x_1] \\
&\quad - \frac{5.556}{5.556}(\rho_{20} + \tau_{23}\lambda_{25})[5.556x_2] \\
[1429\dot{x}_3] &= \frac{1429}{5.556}(\tau_{23})[5.556x_2] - \frac{1429}{1429}(\rho_{30} + \lambda_{35})[1429x_3].
\end{aligned}
\tag{6}
$$

Since gains of one and ten are those directly available on the TR-20 analog computer, it is frequently necessary to combine the rate constant with the gain to obtain a number between zero and one that can be set on a potentiometer and appropriately amplified. Varying the setting can still be considered as varying only the rate since the gain is interpreted as constant. However, the potentiometer settings will not correspond to actual rate constants. In addition, the various loss rates can be programmed individually or lumped into a single value. For convenience, loss rates are summed together in the following equations and in the analog computer programs. They are represented by L_i (e.g., Table III), where i indicates the compartment incurring the loss. The final voltage-scaled equations for the linear model are

$$
\begin{aligned}
[0.417 \times 10^{-3}\dot{x}_1] &= 0.417[1 \times 10^{-3}F_{01}] - (1)(0.625)[0.417 \times 10^{-3}x_1] \\
[5.556\dot{x}_2] &= (13{,}324)(0.00162)[0.417 \times 10^{-3}x_1] - (1)(45.12)[5.556x_2] \\
[1429\dot{x}_3] &= (257)(0.198)[5.556x_2] - (1)(60.72)[1429x_3].
\end{aligned}
\tag{7}
$$

The initial condition settings of the various computer variables are now calculated by multiplying the scale factor times the state variable. The forcing must also be multiplied by its gain in order to obtain the correct setting. The program corresponding to Eqs. (7) is shown in Fig. 4a.

Since no time scaling (Chapter 1, Section IV.B) was involved in the calculations, and since all data used were on the basis of one year, one second of computer time corresponds to one year of system behavior.

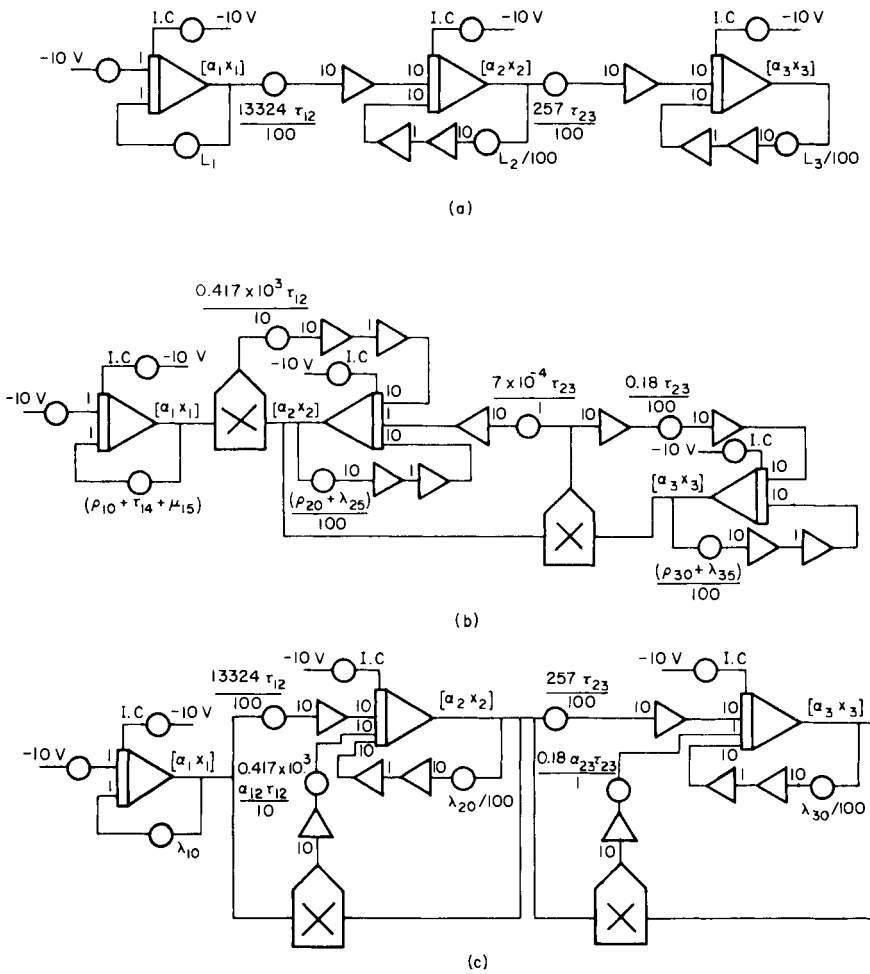

FIG. 4. Analog computer programs of three models. (a) linear model. (b) nonlinear model I. (c) nonlinear model II.

C. NONLINEAR MODEL I

Nonlinear model I represents a system with cross-product interactions between compartments. In the natural system such interactions do, of course, occur, but the problem is how to represent them mathematically in system equations. Equation (3) was used as the form of feeding fluxes. It should be pointed out here that the biological nature of the interaction is not specified by this formulation. It simply states that the

flux depends in some manner on both donor and receiver compartments. The following equations, derived in the same manner as those of the linear system, describe the model:

$$\begin{aligned} dx_1/dt &= F_{01} - (\rho_{10} + \tau_{14} + \mu_{15})\, x_1 - \tau_{12}x_2x_1{}^* \\ dx_2/dt &= \tau_{12}x_2x_1 - (\rho_{20} + \lambda_{25})\, x_2 - \tau_{23}x_3x_2 \\ dx_3/dt &= \tau_{23}x_3x_2 - (\rho_{30} + \lambda_{35})\, x_3 \,. \end{aligned} \tag{8}$$

The analog computer program resulting from these equations is shown in Fig. 4b. The asterisk is explained below.

There are other differences between nonlinear model I and the linear model besides the fact that the former allows interaction between compartments. The feeding-rate constants, τ_{12} and τ_{23}, must be recalculated since they now depend on two compartments. The term marked with an asterisk in Eqs. (8) was dropped from the first equation in programming because its value was too small to be set on a potentiometer. This situation may arise when a flux is small in respect to one compartment, but large in respect to another. Thus, in Eqs. (8), $F_{12} = \tau_{12}x_2x_1 =$ 19.4 kcal m^{-2} yr^{-1}, which is a small fraction of total efflux from the plant compartment ($F_{10} + F_{12} + F_{14} + F_{15} =$ 7500 kcal m^{-2} yr^{-1}, from Table II), but is the total influx to moose [Eq. (1)]. Also, the standing crop of plants is 12,000 kcal m^{-2} versus only 0.43 for moose (Table IV). Thus, $\tau_{12}x_2x_1$ is negligible in the first equation but significant in the second. Dropping it is reflected in the computer program of Fig. 4b.

D. Nonlinear Model II

In nonlinear model II, interaction between compartments again occurs, but differently than in nonlinear model I. This model is based on Eq. (4) which is analogous to the basic Lotka–Volterra competition relation. The nature of the interaction is specified somewhat better here in that its strength can be adjusted by varying a_{ij}, hence the terminology "controlled nonlinear" flow. Equation (4) is an attempt to show that the flux between compartments is primarily a function of the donor compartment, but with a negative feedback correction factor representing compartment interaction. Application of Eq. (4) yields the following descriptive equations:

$$\begin{aligned} dx_1/dt &= F_{01} - \lambda_{10}x_1 - \tau_{12}x_1{}^* + \tau_{12}a_{12}x_2x_1{}^* \\ dx_2/dt &= \tau_{12}x_1 - \tau_{12}a_{12}x_2x_1 - \lambda_{20}x_2 - \tau_{23}x_2 + \tau_{23}a_{23}x_3x_2{}^* \\ dx_3/dt &= \tau_{23}x_2 - \tau_{23}a_{23}x_3x_2 - \lambda_{30}x_3 \,. \end{aligned} \tag{9}$$

The analog computer program resulting from these equations is shown in Fig. 4c.

In this model, values for a_{ij} are unknown for any natural system and were arbitrarily chosen to be 0.25. In addition, a_{ij} was not varied in simulation since the intent was only to obtain a representative behavior for this model. Once again it is necessary to recalculate τ_{12} and τ_{23} on the basis of Eqs. (4). Negligible terms again are dropped, and this is reflected in the computer program of Fig. 4c.

E. Forcings

Energy input to the plant compartment is represented by the system forcing function. Several different types of forcings were employed on each model to observe their effects on system behavior.

The first type was a constant input of the form $F_{01} = k$, the estimate (Table II) of average annual gross productivity. The analog computer programs of Fig. 4 show this type. A constant forcing is adequate to examine the system on an average annual basis, but it cannot be used to generate a realistic yearly cycle of time behavior since gross production varies seasonally.

The second type of forcing used was a "self-generating" input of the form $F_{01} = gx_1$. The plant compartment is driven through a positive feedback loop by a constant fraction of its current energy content. A program to generate this type of forcing is illustrated in Fig. 5a. The self-generating input is realistic for certain kinds of growing systems, but again a yearly cycle is not inherent, and neither is stability.

The third type of forcing was a sinusoidal function of the form $F_{01} = A \sin \omega t$, which varied from zero input to twice the calculated value of the constant forcing. Twice the calculated value was used in order to yield an average value equivalent to the constant forcing. This function offered the possibility of crudely simulating the yearly cycle of energy input to the plant compartment, and was therefore adjusted to a period of one year. An analog program for generating it is shown in Fig. 5b.

III. Time Behavior of Models

A. Free and Forced Responses

Two general characteristics of dynamic systems are their free and forced responses. Free responses result when forcings on a system are zero. Forced responses result when initial conditions of the compartments

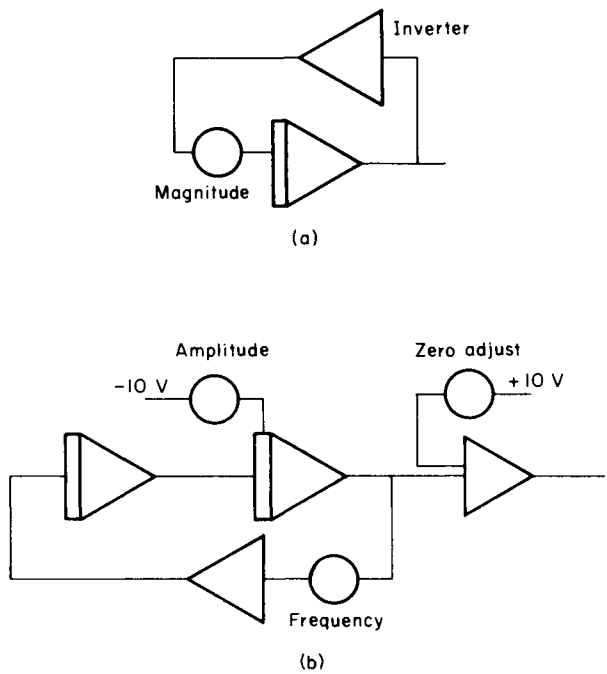

FIG. 5. Programs for (a) self-generating and (b) sinusoidal forcing functions.

are zero, and the system is forced. These responses are components of the general solution of differential equations (Distefano *et al.*, 1967). Figure 6a presents these responses of the linear model. All graphs shown in Figs. 6–8 are taken from actual analog computer outputs as recorded by an XY-plotter. It should be kept in mind that values graphed are scaled, but that the actual values (obtained by utilizing the scale factors α_i) would appear qualitatively the same.

Both free and forced responses shown in Fig. 6a are characteristic of linear behavior. Each compartment goes through a period of transient behavior and approaches a steady state when inputs balance losses. All compartments of the system require about eight years to reach steady state, both in free and forced responses. This is true regardless of whether the constant or sine forcing is used. The phase and amplitude differences which can be observed in this and other sine-forced graphs will be discussed in Section III.D.

Figure 6b shows the only response graph obtainable for nonlinear model I. The free response of this system differs from that of the linear model. Curves for the plant compartment are very similar. However,

the moose and wolf compartments show distinct differences in curvature. Two additional characteristics should be noted. The order in which the compartments approach zero is that which would be expected in nature should the situation ever occur. That is, wolves would disappear when there no longer were sufficient moose to support them and, in turn, the moose would disappear when there was no longer enough vegetation. The time response differs considerably from the linear model. The plant compartment requires longer to get close to zero, whereas both wolves and moose take less time.

No forced response graph for nonlinear model I could be obtained, for two reasons. First, no behavior at all can be generated if the initial conditions are zero because of the double-product feature of Eq. (3) used to couple the compartments. Second, the system is stable only when precisely set at the calculated steady state values. Thus, no values greater than zero but less than initial conditions can be set which will allow a forced response. In essence, nonlinear model I cannot describe a system with a growth phase. In fact, this model does not possess a steady state under the conditions imposed by the Isle Royale data, as will be discussed further below.

Figure 6c illustrates the type of behavior obtained from nonlinear model II. Free and forced responses are both very similar to those of the linear model. Nonlinear model II thus behaves dynamically essentially as a linear model despite the superior biological realism of the controlled-flow rationale [Eq. (4)] on which it is based. This behavior is due to the circumstance that the nonlinear terms remaining in the equation again are of small magnitude when compared with the other terms. If the interaction coefficient (a_{ij}) is increased to a value that makes the term in which it occurs sufficiently large relative to the other terms, behavior of nonlinear model II will depart from the linear response.

B. Steady States

Figure 7a shows the steady state behavior of the linear model with constant and sine forcings. The behavior of the sine-forced system is consistent with that noted earlier for the forced (sine) response. This type of behavior is well known for linear models of this kind.

A self-generating input to the plant compartment was attempted. The plants proved very sensitive to this function (Fig. 8d). Since this input represents positive feedback of some fraction of the compartment's content, the plants increase or decrease unless input exactly balances losses. If the equilibrium value can be set, a steady state similar to that produced by constant forcing results.

Figure 7b shows the "best" behavior that could be obtained from nonlinear model I with self-generating and constant forcings. This system could not be sine-forced at all because it was too sensitive. The oscillations shown are inherent. Only the general form and outcome of the graphs are characteristic because behavior was difficult to duplicate. The system was observed to be so sensitive at several points that very

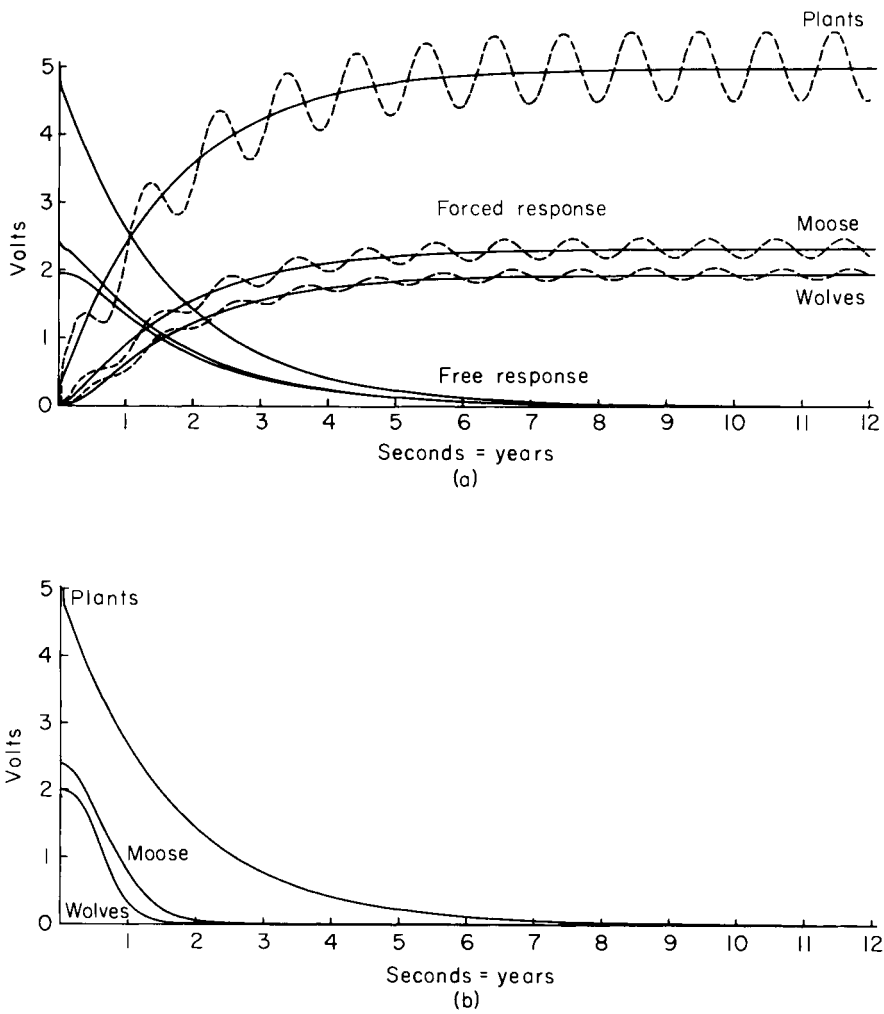

FIG. 6. Free and forced responses. (a) linear model. (b) nonlinear model I.

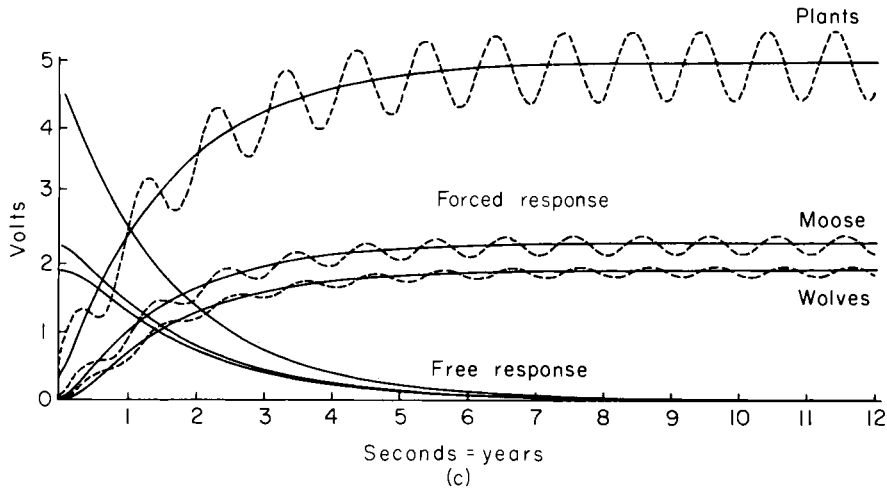

FIG. 6 (c) nonlinear model II. (See text for explanation).

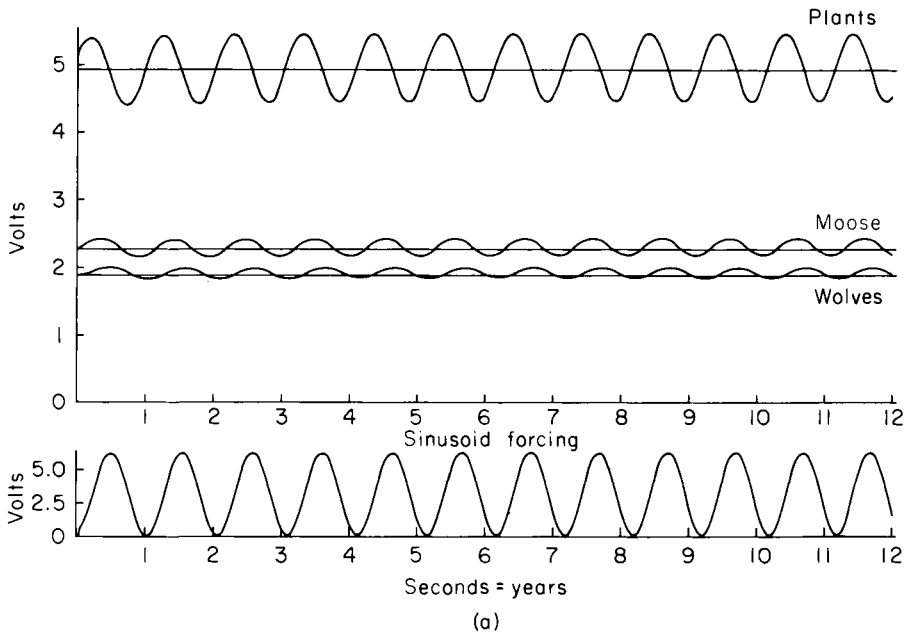

FIG. 7. Steady states. (a) linear model, constant and sine forcing.

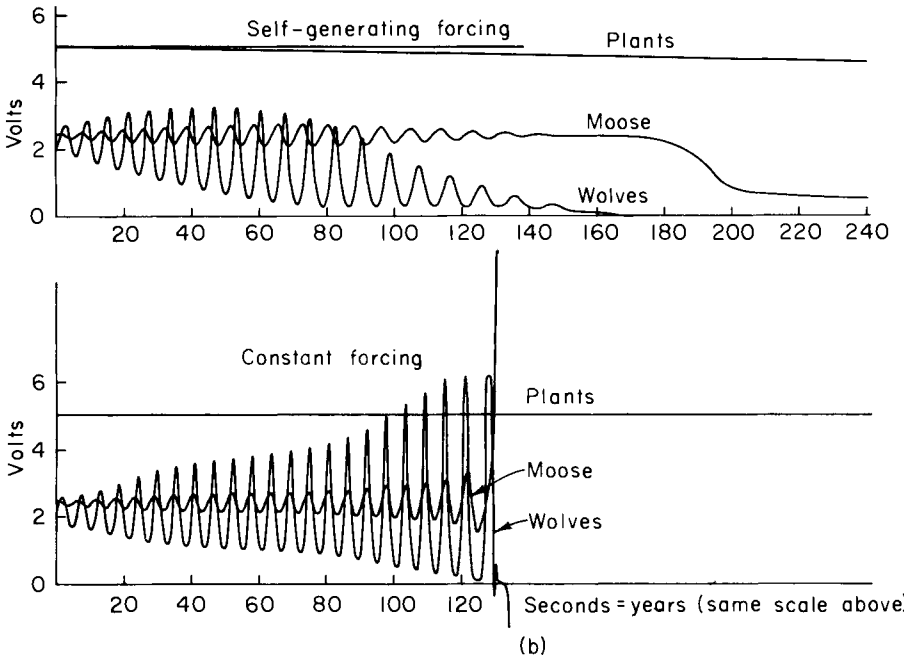

FIG. 7 (b) nonlinear model I, long-term behavior.

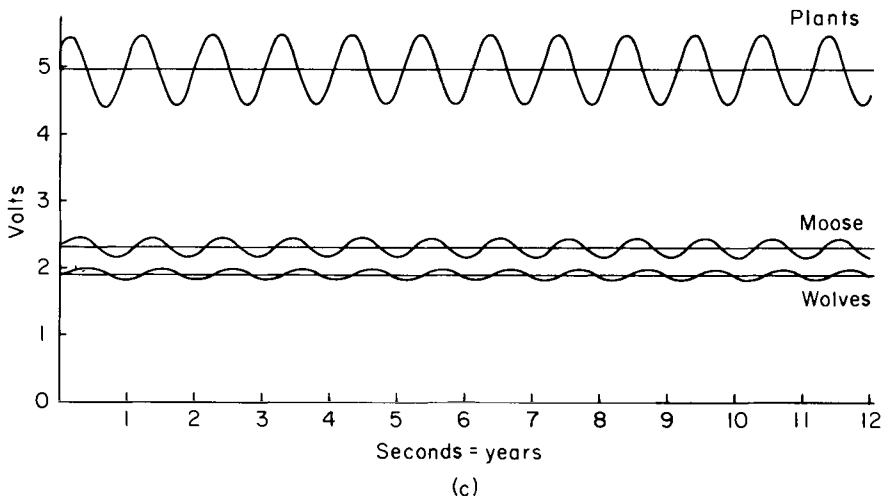

FIG. 7 (c) nonlinear model II.

different behavior could be obtained by changing a key parameter only slightly. Note also that these graphs represent relatively long time behavior. On short time scales behavior appears to stabilize, but this is only because the system has not run long enough either to blow up or run down. In general, if the plant compartment is increasing, even slightly, the system explodes. If the plant compartment is decreasing, the system collapses. Both of these types of behavior are obtained regardless of the type of forcing applied. It is extremely difficult to maintain the plant compartment constant.

Williams (Volume II) states that there is no satisfactory steady state for a self-generating, three-compartment model of the type presented here. Our results substantially agree with this statement, however, on slightly different grounds. While admittedly estimated, our data are derived from a real ecosystem rather than theoretical considerations. This point is important because Williams' analyses show that a system of this type with either a constant forcing or a self-generating forcing has a mathematically definable steady state. We could not produce such a steady state with nonlinear model I, however, because the data do not meet the requirements for stability as mathematically defined.

Figure 7c shows the steady state behavior of nonlinear model II with constant and sine forcings. The behavior again is essentially similar to that of the linear model and, moreover, the self-generating input also produced behavior virtually identical to the linear response.

C. Displacements from Steady State

Several tests involving displacements from steady state were performed on the analog computer. These tests centered on the linear model because nonlinear model I could not be displaced without blowing up and nonlinear model II behaved essentially like the linear model.

Figure 8a shows the type of behavior obtained from the linear model with a constant forcing when the plant compartment was reduced from its initial condition level. Any displacements in the linear model initial conditions always result in return to the same steady state, as is well-known from the theory of linear systems. In addition, uncoupling compartments starting from the last compartment has no effect on the preceding compartments. Thus, when the wolf compartment is uncoupled, plant and moose compartments respond exactly as if the wolves were still connected. This is one of the logic deficiencies of the linear model.

Figure 8b shows the type of behavior obtained if a sine forcing is used. The initial conditions of the plant compartment were adjusted both

above and below the calculated steady state value. Again, as known from linear theory, all compartments return to the same steady state levels. Figures 6a, 7a, and 8a,b summarize the behavior of the linear model with constant and sine forcings.

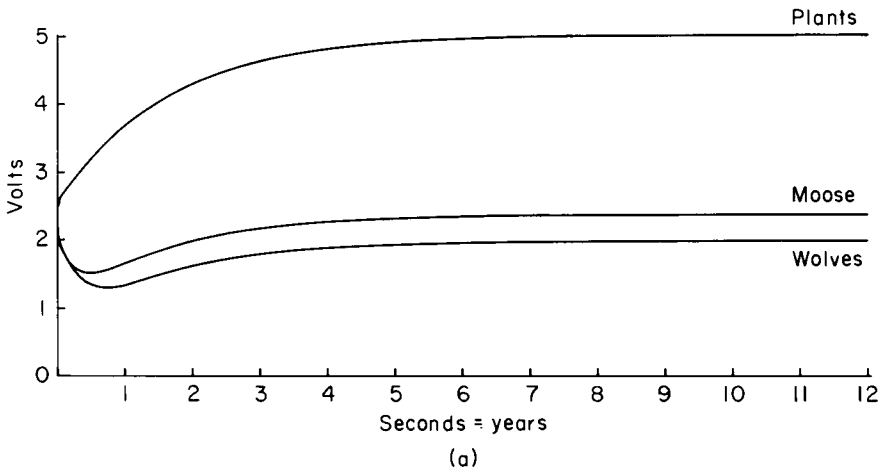

FIG. 8. Displacements from steady state. (a) linear model. Plants reduced by one-half original value.

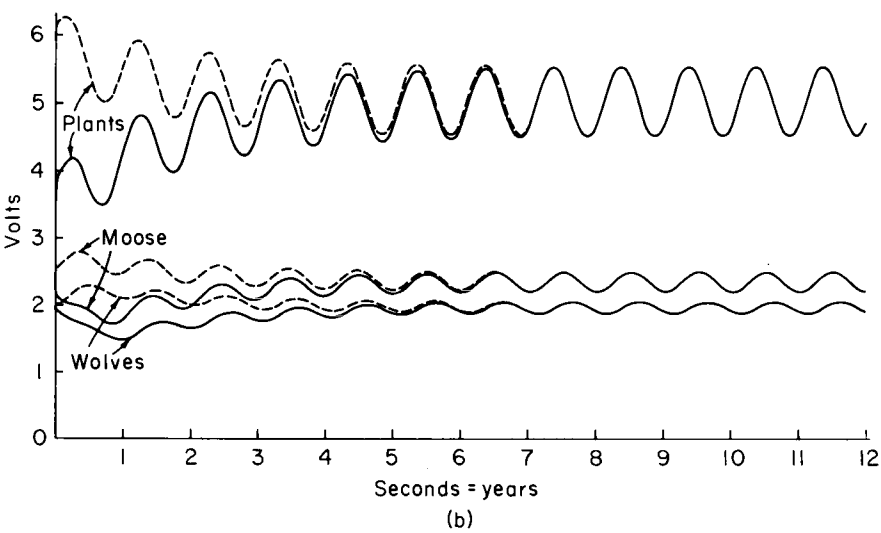

FIG. 8 (b) linear model with sine forcing. Plant compartment increased above and decreased below steady state.

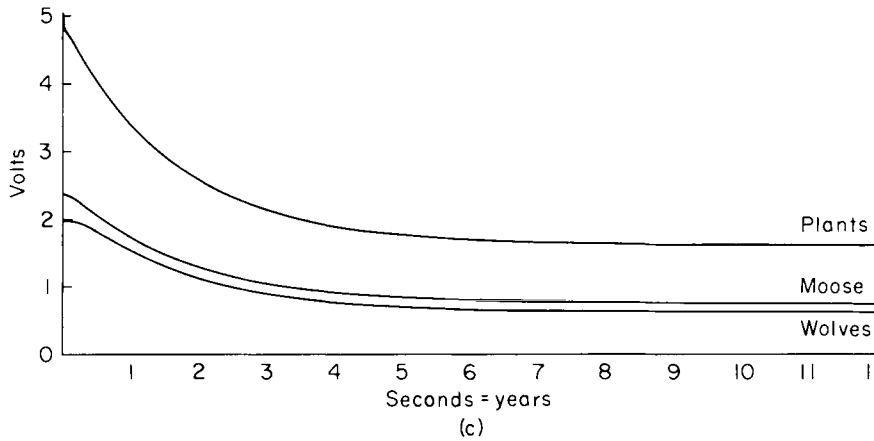

FIG. 8 (c) linear model. Forcings reduced to one-third original value.

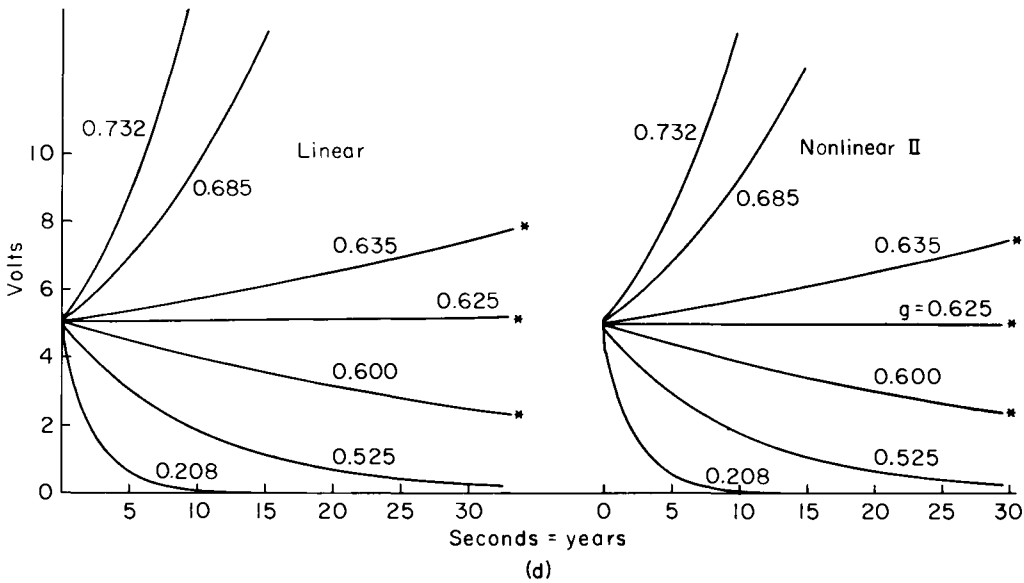

FIG. 8 (d) linear model and nonlinear model II. Self-generating forcing gx_1 plant compartment responses.

Figure 8c illustrates the type of behavior obtained from the linear model by varying the forcing. All compartments come to new steady states, as predicted by steady state solutions of Eqs. (5). Readjustments also occur in the case of sine forcings. Thus, the linear model and

nonlinear model II have many steady states available depending on values of the forcing.

Figure 8d shows results of varying the self-generating inputs to the linear model and to nonlinear model II. This type of behavior was mentioned earlier (Section III.B) when it was noted that the linear system was very sensitive to a self-generating input. This sensitivity is illustrated by the fact that the whole range indicated on the graph is only one-half of full scale forcing input. Furthermore, the three graph lines marked with an asterisk actually represent a range of variation of only 3.5% of full scale. It appears that the plant compartment can be maintained only when the input gx_1 equals the loss L_1x_1 (i.e., $g - L_1 = 0$). This condition also holds for nonlinear model I in that behavior is prolonged the better this condition is met. That is, as $g - L_1$ deviates from zero either positively or negatively by a greater and greater amount, nonlinear model I blows up faster and faster. It thus seems characteristic of self-generating inputs that there is a very narrow range of values which will allow a steady state. An important aspect of the types of forcings used in our models is that the self-generating forcing is density-dependent, whereas the constant and sine forcings are density-independent.

D. Selected Comparisons

It was mentioned earlier (Section III.A) that phase and amplitude differences could be noted in the sine-forced systems. The phase shift occurs in the sequence: plant, moose, wolf. That is, peaks in plant oscillations follow those of the sine forcing in time, moose lag the plants, and wolves lag the moose (Figs. 6a, 7a, and 8a,b). There is, then, a phase shift between the input to each compartment and its responding output. For the type of system modeled, producer–herbivore–carnivore, the phase responses observed are not unrealistic.

Nonlinear model I oscillates intrinsically and it is instructive to examine the phasing of these oscillations (Fig. 7b). In the self-generating system, a phase shift in the moose and wolf compartments occurs such that wolf peaks become aligned with moose troughs. In this situation, the system decays, and both moose and wolf compartments go to zero. With a constant forcing, the phase shift is such that wolf peaks become aligned with moose peaks, the system becomes self-amplifying, and blows up. Also mentioned earlier (Section III.B) was the fact that, regardless of the forcing, the system is unstable, exploding if the plant compartment is increasing, and decaying if it is decreasing. That is, if the plant compartment is increasing wolf peaks become aligned with

moose peaks, and if the plant compartment is decreasing, wolf peaks become aligned with moose troughs.

Amplitude changes can also be noted in the same figures. For the linear model and nonlinear model II the amplitudes of oscillation decrease in the sequence: forcing, plant, moose, wolf. This decrease is absolute in the sense that it holds when scaling effects are taken into account. Oscillations occurring in the inputs are damped in the outputs. But a steady state oscillation is eventually developed in each compartment of these two systems because no further phase shift occurs (i.e., the phase angles are constant, as would be expected in a linear system lacking feedback).

In nonlinear model I, however, amplitude changes occur through time representing both increases and decreases. The self-generating system behavior shown in Fig. 7b does, in fact, show both an increase and a decrease in compartmental amplitudes. Comparing the self-generating and constant forcings, initial oscillations in both cases are quite similar in phase and amplitude. The amplitude is increasing in both cases. However, in the self-generating system (plant compartment decreasing very slightly), the oscillations reach a maximum amplitude, then decline because the phase shift occurs as previously noted. That is, wolf peaks become aligned with moose troughs, and self-damping oscillations are produced. In the constant-forced system (plant compartment increasing very slightly), the amplitude continues to increase until blow-up occurs, again because of the phase relations. That is, wolf peaks become aligned with moose peaks, and self-amplifying oscillations are produced. In the case of this model, the phase angles are not constant and change with time.

IV. Evaluation of Models

The accepted yardstick for judging a model is how well its behavior conforms to that of the real system it is designed to represent. If the correspondence is good over a reasonably wide range of empirical observations, then it is assumed to hold also beyond this range and into the realm of prediction.

Figure 9 depicts the plant–moose–wolf food chain of Isle Royale as an input–output block. The behavior of the system, $y(t)$, is related to forcings $z(t)$, by a "transfer function" H which expresses how the system machinery processes input to generate output

$$y(t) = H \cdot z(t),$$

where H is the output/input ratio, $y(t)/z(t)$.

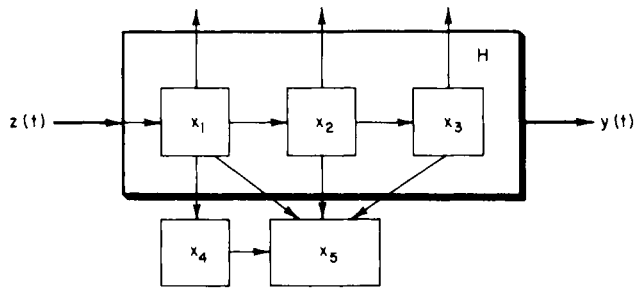

FIG. 9. The Isle Royale system as a functional block.

In Section I.A, three implications for testing models of the Isle Royale system were developed from Mech's considerations of moose–wolf interactions. The first two referred to oscillating systems which were judged to be more realistic than nonperiodic ones. In these, (1) wolf population peaks should lag those of their prey, and (2) the wolves should also fluctuate with smaller amplitudes than moose. The other implication was (3) that a unique steady state should exist for a given set of conditions.

The linear model and nonlinear model II both showed a general capability to satisfy all three of these criteria. Under sinusoidal forcings wolves lagged the moose population and fluctuated with smaller amplitudes. Both models also were "globally stable," i.e., came to new steady states when perturbed either by changes in forcings or parameters. In addition, free and forced response characteristics were reasonable: In Figs. 6a and c it was observed that moose and wolves both took about eight years either to become extinguished or to grow from zero to steady state (both models, incidentally, were capable of reproducing as steady states the observed standing crops of all three compartments). In the actual system it took 12 (1919–30) and 6 (1943–49) years for moose to develop from low to high populations on two occasions when analogs of forced responses could be observed (Fig. 1), and corresponding declines (analogous to free responses) took place in 13 (1930–43) and 8 (1949–57) years, respectively. Similarly, the recorded history of the wolf population shows the essential forced response to have occurred in 8 years (1952–60).

Thus, on the basis of (1) ability to reproduce realistic standing crop levels as steady states, (2) moose–wolf relationships under periodic behavior, (3) reasonableness of free and forced responses, and (4) general

system stability, both the linear model and nonlinear model II appear to be satisfactory representations of the Isle Royale system.

Nonlinear model I, on the other hand, is unacceptable. It did not possess a satisfactory steady state under conditions imposed by the basic data. In periodic behavior, its oscillations were inherent, with phase shifts determined by whether the plants were growing or declining, and the model in general proved unstable. A strict forced response could not be determined, and the free response of both moose and wolves (Fig. 6b) was more rapid than the actual data (Fig. 1) suggest. Hence, nonlinear model I, despite its superior biological logic in terms of representing plant–moose and moose–wolf interactions, must be rejected as a working model of the Isle Royale ecosystem.

To say (above) that the linear model and nonlinear model II are both "satisfactory" means that reasoned relationships between the functional compartments [Eqs. (1) and Fig. 3], and the expression of these relationships in terms of derived numerical parameters (Tables II and III) produced a model with reasonable capability for simulating real system behavior, given appropriate inputs. In other words, the basic kinetic relations H of the system machinery have been captured in the model so that any desired performance $\hat{y}(t)$, e.g., that of Fig. 1, could be obtained by forcing the system with an appropriate input $z(t)$. However complex the latter, it can in principle always be found

$$z(t) = H^{-1} \cdot \hat{y}(t)$$

although its biological significance possibly may be obscure.

Several questions remain in evaluating the relative merits of nonlinear model II and the linear model, both of which have similar dynamic responses over the range investigated. Nonlinear model II is biologically more appealing for several reasons. It is based on a traditional formulation of ecological interaction [Eq. (4)]. It acknowledges and represents that if the predator is removed, this will (unlike in the linear model) have an effect on the prey, and these in turn on the plants. This is basic biology, and to exclude it from a model of trophodynamics is to appear to be patently unrealistic. On the other hand, little was actually gained operationally in terms of dynamic characteristics or useful parameters to justify introducing the mathematical complications of a "superior" rationale. The fact is that in this case more is lost in moving beyond the realm of linear theory, which is technically the best-understood in systems science, than is gained by introducing nonlinear logic, since differences between the two models that do not begin to appear until outside the range of available data cannot be evaluated anyway. The linear model at

least has a complete theory behind it. In substituting other data into these models, however, one may find that their behaviors diverge. The feeding relations qualitatively may be identical with those of Isle Royale, but changes in parameter values might possibly alter the basic behavior pattern of nonlinear model II. This attribute of nonlinear model II illustrates that model behavior can depend upon system parameters.

Thus, the problem of balancing mathematical and biological considerations in simulation and systems analysis modeling in ecology has no general resolution at this time. It would seem that "empirical simulation" approaches which proceed purely on the basis of biological considerations, such as the experimental components analysis method of Holling (1965, 1966), produce no guarantees that "transfer" blocks based on selected mathematical functions and connected in complex patterns of mutual causality will, with fidelity, reproduce behavior of natural systems. It would almost be better to know with certainty the extent and conditions under which an oversimplified but theoretically understood model will *not* duplicate the real system's response.

When a model is "oversimplified" is not entirely clear either. For example, the following characteristics may not be altogether unreasonable to expect as properties of many ecological systems. Consider, in the system of Fig. 9, responses to two different inputs, z_1 and z_2 .

$$y_1(t) = H \cdot z_1(t)$$
$$y_2(t) = H \cdot z_2(t).$$

If both inputs are applied together, then

$$y(t) = H \cdot (z_1(t) + z_2(t)),$$

and if $y(t) = y_1(t) + y_2(t)$, the system H is said to have the property of *additivity*. Further, if some multiple m of an input is applied to the system, the response is

$$y_3(t) = H \cdot mz_1(t).$$

If $y_3(t) = m \cdot y_1(t)$, then the system is said to have the property of *homogeneity*.

These two properties are not so unreasonable as potential characteristics of a large class of ecological systems over a wide range of dynamic behavior: Additivity asserts that the response to a sum of inputs equals the sum of the separate responses to each; homogeneity says that the response to a constant multiple of any input equals the response to the input multiplied by the same constant:

$$H(m_1z_1(t) + m_2z_2(t)) = m_1Hz_1(t) + m_2Hz_2(t).$$

These two properties together comprise the *principle of superposition*, which is both necessary and sufficient in systems science to define a linear system.

Thus, it remains for the future to assess the relative merits of simple versus complex models and to evolve a general rationale for ecological simulation and systems analysis. In the present case of the Isle Royale ecosystem, simple models appear to embody many of the essential dynamic features that are of interest to the functional ecologist.

Acknowledgments

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10

Computer Simulation of Energy Flow in Cedar Bog Lake, Minnesota Based on the Classical Studies of Lindeman*

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* See Lindeman (1941a, b; 1942).

I. Introduction

In his final paper, "The trophic–dynamic aspect of ecology," Raymond Lindeman (1942) gave a new direction to ecological research by demonstrating the importance and broad applicability of two concepts, trophic level and energy flow, in the analysis of ecosystems. In this paper Lindeman also introduced some lasting ideas concerning energy flow—that the productivity of a lake is lowest during its senescence, and that the efficiency with which the energy in a given trophic level is transferred to the next trophic level increases with successive levels. Much of the information for this paper was drawn from his previous studies (Lindeman, 1941a,b) of the ecosystem in a shallow Minnesota pond, Cedar Bog Lake.

This chapter describes an attempt to convert Lindeman's ideas and observations concerning the flow and accumulation of energy in the Cedar Bog Lake ecosystem into a mathematical model. The purpose behind this attempt was to gain insight into the construction of ecosystem models. The model probably has little similarity to the ecosystem which Lindeman studied because only a fraction of the information needed to simulate accurately the Cedar Bog Lake ecosystem was available in Lindeman's publications or elsewhere, and these gaps in information were filled by means of educated guesses. Accordingly, the resulting model cannot yield any great insights into the functioning of ecosystems. However, an account of its construction may be of assistance to others in the development of workable ecosystem models. The detailed examination of Lindeman's data which the modeling required also led to a reevaluation of certain of his ideas.

II. Lindeman's Study of Cedar Bog Lake

The data on the ecosystem in Cedar Bog Lake were obtained from 36 surveys irregularly spaced over a period of four years (Lindeman, 1941b). Lindeman identified and measured the standing crop of most of the common macroscopic organisms and many of the microscopic forms. He also investigated the food habits of many of the organisms and in part diagrammed these as a fairly complex network system (Fig. 1). His description of the ecosystem mentions additional groups of organisms and pathways not included in this figure. The data on standing crop were grouped into eight categories, nannoplankton, net plankton (plant), benthic plants (and their epiphytes), zooplankton (chiefly rotifers), browsers (snails, insect larvae, etc.), plankton predators (*Chaoborus*

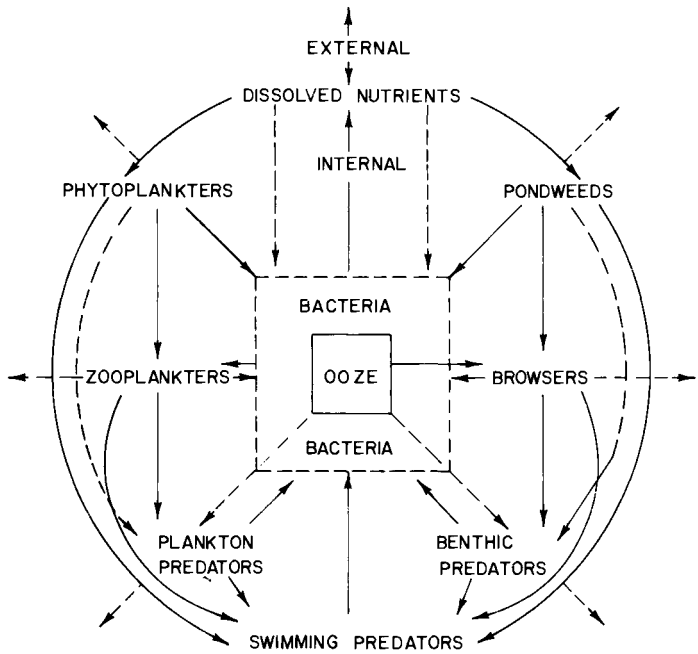

FIG. 1. Food cycle relationships in Cedar Bog Lake (after Lindeman, 1941b).

larvae), benthic predators (insects and leeches), and swimming predators (insects, leeches, and fish). The annual net production (in grams wet weight per square meter) of each of the categories except benthic plants was obtained by multiplying the average standing crop by its estimated number of turnovers per year. These estimates were drawn from the literature and from Lindeman's observations on the life histories of the organisms. Annual net production of the benthic plants was assumed equal to the average maximum standing crop. These values in terms of weight were converted to calories per square centimeter by use of factors drawn from the literature and pooled into a simple, unbranched system with three trophic levels, producer, primary consumer (herbivore), and secondary consumer (carnivore) (Table I and Fig. 2). He apparently felt that his data was insufficient to implement the more complicated network system suggested by his study of food habits.

In the trophic–dynamic paper Lindeman (1942) added to his previously obtained values for production (now called "uncorrected productivity") estimates of the losses due to respiration and predation, and called the sums "corrected productivity" (Table I). He divided the calories ingested by the consumer trophic levels into "predation," the amount assimilated,

TABLE I

MEAN ANNUAL VALUES FOR ENERGY FLOW (cal $cm^{-2}yr^{-1}$) IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartment	Net or uncorrected productivity	Respiration	Predation	Decomposition	Gross or corrected productivity
Nannoplankton	16.7				
Net phytoplankton	9.1				
Pond weeds	44.6				
Plants	70.3	23.4	14.8	2.8	111.3
Zooplankton	6.1				
Browsers	0.8				
Herbivores	7.0	4.4	3.1	0.3	14.8
Plankton predators	0.8				
Benthic predators	0.2				
Swimming predators	0.3				
Carnivores	1.3	1.8	0.0	0.0	3.1

[a] Values taken from the data of Lindeman (1941b, 1942).

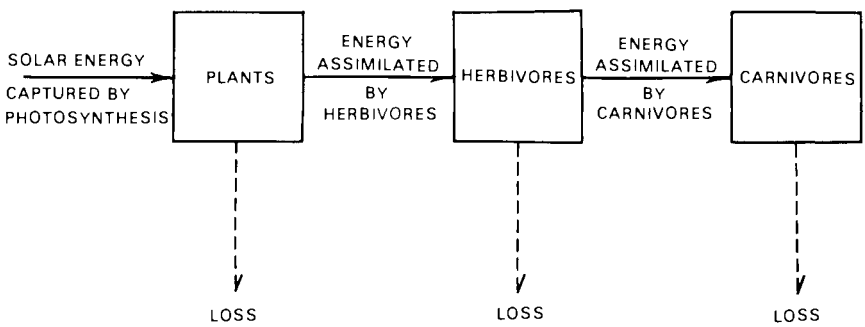

FIG. 2. Lindeman's (1941b) analysis of energy flow in the Cedar Bog Lake ecosystem.

and "decomposition," the amount not assimilated. From comparison of the corrected productivity of each trophic level with the energy available to it either from the sun or from the preceeding trophic level, he calculated progressive efficiencies (Table II); his values for these are still widely quoted. Lindeman finally compared his corrected productivities and progressive efficiencies for Cedar Bog Lake with corresponding values for Lake Mendota, Wisconsin [calculated from the data of Juday (1940)] and with other data in the literature, and drew generalizations concerning the behavior of ecosystems.

TABLE II

EFFICIENCY WITH WHICH ENERGY AVAILABLE IN A TROPHIC LEVEL IS TRANSFERRED TO THE SUCCEEDING TROPHIC LEVEL[a]

Transfer	Percent efficiency (1941b)	Percent efficiency (1942)
Plant/sun	0.1	0.1
Herbivore/plant	9.6	13.3
Carnivore/herbivore	18.5	22.3

[a] From the data of Lindeman (1941b, 1942).

The importance of Lindeman's work lies in the concepts he developed and not in the data from which the concepts were abstracted nor in the precise methods by which the data were obtained and analyzed. The data is scanty. In Cedar Bog Lake only the standing crop of organisms was measured. All values for net production and respiration of the various trophic levels were estimates drawn from the literature and from general observations on the pond and its biota. These values thus appear to be little more than educated guesses.

His mode of calculating total or gross production is also seriously in error, as pointed out previously by Slobodkin (1962). Lindeman's uncorrected productivity or turnover $\times$ standing crop is equivalent to yield or net production. Losses to predation are a part of yield and thus should not be added to net production when computing gross production. In addition no consideration was given to production in the form of reproduction, i.e., eggs, etc., or to the loss in observable benthic plant production due to grazing.

III. General Approach to Modeling the Cedar Bog Lake Ecosystem

It is thus clear that there are too many gaps in the observational data in Lindeman's papers to construct an energy flow model for the ecosystem existing in Cedar Bog Lake, and there is little in other publications on the area (Marshall, 1964) to fill these gaps. Models described below are based on Lindeman's picture of average values for energy flow in Cedar Bog Lake. His values, reasonable or unreasonable, are accepted as far as possible and altered only when they contain some obvious and easily corrected error in logic or arithmetic. Quantities needed for the construction of these models and not available in the literature were given reasonable arbitrary values.

The final nonlinear network model of the Cedar Bog Lake ecosystem was developed in a series of steps. First a linear model of Lindeman's simple, plant–herbivore–carnivore ecosystem was prepared by abstracting the necessary data from his papers. Next, the values for this unbranched system were reworked into a network model in which the compartments were joined in the manner which seemed most compatible with Lindeman's opinions and data. Next this linear model was converted into a simple nonlinear model involving only donor compartment $\times$ recipient compartment transfers. Then environmental effects, temperature, light, and time of year, were introduced, and finally the behavior of the model was stabilized by replacing many of the simple nonlinear transfers with more complex nonlinear functions. Simulation of the three-compartment linear system was done on an EAI TR-48 analog computer; the simulation of the various network systems was accomplished with a digital computer by use of a matrix type program, COMSYS 1 (Bledsoe and Olson, 1970).

IV. A Linear Three-Compartment System

A. Structuring the System

Figure 3 portrays a forced linear system analogous to Lindeman's plant–herbivore–carnivore ecosystem. The value of each compartment is equal to the average standing crop of the corresponding trophic level. The system is considered to be in a dynamic equilibrium such that the

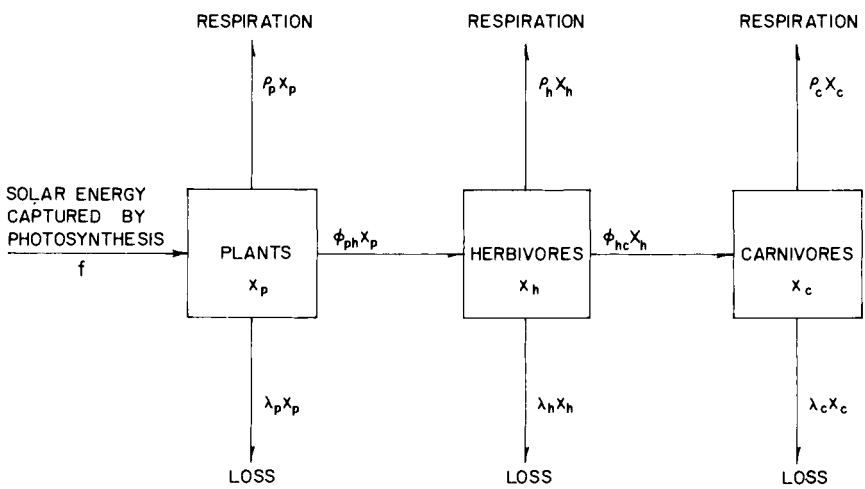

FIG. 3. A forced linear model of energy flow in a plant–herbivore–carnivore ecosystem.

input per unit time into each compartment equals the loss from it. The input for the system, the forcing function, is the light energy utilized in photosynthesis, which, of course, equals gross photosynthesis. Some of this energy which enters the plant compartment via photosynthesis is dissipated in respiration and some transferred to the next trophic level, the herbivores; the remainder, thus, must be lost in some unspecified manner. This loss might, for example, be to the metabolism of bacteria and other decomposers, or to sediment which is gradually filling the pond. However, no particular set of destinations is implied. The loss flow is not part of Lindeman's formulation, but is necessary for balancing outflow against input. Energy transferred into the herbivores similarly is either dissipated in respiration, transferred into the next trophic level, or drained away as loss. Energy transferred into the final trophic level, the carnivores, is removed either as respiration or loss. In a linear system the amounts transferred or lost per unit time from a compartment are expressed as fractions of the standing crop in the compartment, and these fractions are called "transfer rates." The amount transferred along any given path per unit time is thus the product of standing crop $\times$ a transfer rate (Fig. 3). Calculation of the forcing functions and transfer rates is a central problem in developing a linear model.

B. Calculating the Forcing Functions and Transfer Rates

Numerical values for the forcing function and transfer rates needed to complete this linear model were obtained from Lindeman's data in seven steps. First, usable data (values for net production and rates of turnover) were summarized (Table III) and mean standing crops of all but benthic plants were calculated by dividing net production by turnovers per year. Second, respiration flows for the carnivores were calculated by multiplying net production by 1.40 (Lindeman, 1942, p. 404), and were added to the values for net production to obtain gross productions. Since there were no secondary carnivores in the system, all carnivore net production was relegated to the loss flows. Third, an arithmetic inconsistency was eliminated from the herbivore data (Table I) by arbitrarily adding 0.1 cal cm^{-2} to zooplankton net production. Respiration rates and gross productions for the herbivores were then calculated in the same manner as for the carnivores, except that respiration was assumed equal to 0.623 $\times$ net production flow (Lindeman, 1942, p. 403). Net production of the herbivore level was divided into transfer (or predation), a flow equal to the gross production of the succeeding carnivore level, and a remainder, loss. Predation within the two parts of the herbivore level, zooplankton and browsers, was assumed propor-

TABLE III

VALUES FOR THE CONSTRUCTION OF A THREE-COMPARTMENT LINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartment	Net production (cal cm^{-2} yr^{-1})	Number of turnovers (yr^{-1})	Average standing crop (cal cm^{-2})	Transfer (ϕ)		Respiration (ρ)		Loss (λ)		Gross production	
				Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})
Solar energy										118, 625	
Net phytoplankton	9.1	36.5	0.249	1.4	5.80	3.1	12.3	7.6	30.7	12.2	48.8
Nannoplankton	16.7	36.5	0.458	2.7	5.80	5.6	12.3	14.1	30.7	22.3	48.8
Benthic plants	46.2	2.0	23.1	7.3	0.32	15.2	0.66	38.9	1.68	61.4	2.66
Plants	72.0	—	23.8	11.4	0.48	23.9	1.00	60.6	2.55	95.9	4.03
Zooplankton	6.2	26.0	0.238	2.7	11.3	3.9	16.4	3.5	14.7	10.1	42.4
Browsers	0.8	2.0	0.400	0.4	0.89	0.5	1.25	0.4	1.11	1.3	3.25
Herbivores	7.2	—	0.638	3.1	4.85	4.4	6.90	3.9	6.12	11.4	17.87
Plankton predators	0.8	3.0	0.267	0.0	0.0	1.11	4.16	0.8	3.00	1.91	7.16
Benthic predators	0.2	2.0	0.100	0.0	0.0	0.28	2.80	0.2	2.00	0.48	4.80
Swimming predators	0.3	1.0	0.300	0.0	0.0	0.41	1.37	0.3	1.00	0.71	2.37
Carnivores	1.3	—	0.667	0.0	0.0	1.80	2.70	1.3	1.95	3.10	4.65

[a] Values taken from the data of Lindeman (1941b, 1942).

tionate to their net productions. Fourth, Lindeman's value for benthic plant production was augmented by the loss due to browsers. The correction, 1.25 × browers' gross production, was based on Lindeman's (1942, p. 405) estimate of 20% indigestible matter in pond weeds, and increased benthic plant production by less than 4%. In addition, the average standing crop of benthic plants was assumed to be one-half the annual net production; this yielded an arbitrary turnover rate of twice per year. Fifth, the flows for respiration, gross production, predation, and loss were calculated for the producer level in the same manner as for the herbivore level. Respiration was computed as 0.333 × net production, because this corresponds to Lindeman's (1942, Table 2) calculations. It is, however, contrary to his statement (1942, p. 403) that plant respiration is one-third of gross photosynthesis. Sixth, the forcing functions, here amounts of light energy utilized in photosynthesis, were set equal to the gross plant productions. Lastly, transfer rates were obtained by dividing each flow by the standing crop of its donor compartment.

C. The Completed Model

Values for the forcing functions, standing crops, and transfer rates (Table III) were assembled into a model depicting annual energy flow in Cedar Bog Lake (Fig. 4). This model can be expressed mathematically by its system equations [Eqs. (1)–(3) and Table IV], differential equations describing change with time in the values of the compartments.

$$\text{Plant} \quad \begin{aligned} \dot{X}_p &= f - (\rho_p + \lambda_p + \phi_{ph})\, X_p \\ &= 95.9 - (1.00 + 2.55 + 0.48)\, X_p \end{aligned} \tag{1}$$

$$\text{Herbivore} \quad \begin{aligned} \dot{X}_h &= \phi_{ph} X_p - (\rho_h + \lambda_h + \phi_{hc})\, X_h \\ &= 0.48 X_p - (6.90 + 6.12 + 4.85)\, X_h \end{aligned} \tag{2}$$

$$\text{Carnivore} \quad \begin{aligned} \dot{X}_c &= \phi_{hc} X_h - (\rho_c + \lambda_c)\, X_c \\ &= 4.85 X_h - (2.70 + 1.95)\, X_c\,. \end{aligned} \tag{3}$$

In every case change equals input into the compartment minus loss from it. With the system at steady state and change equal to zero, system equations serve no immediate purpose. However, when a model is used to simulate change in a natural system, for example, seasonal cycles in abundance, the system equations provide a means for computing these changes.

Solar radiation which forms the input into the system was, of course, not constant throughout the year, but rather followed an approximately

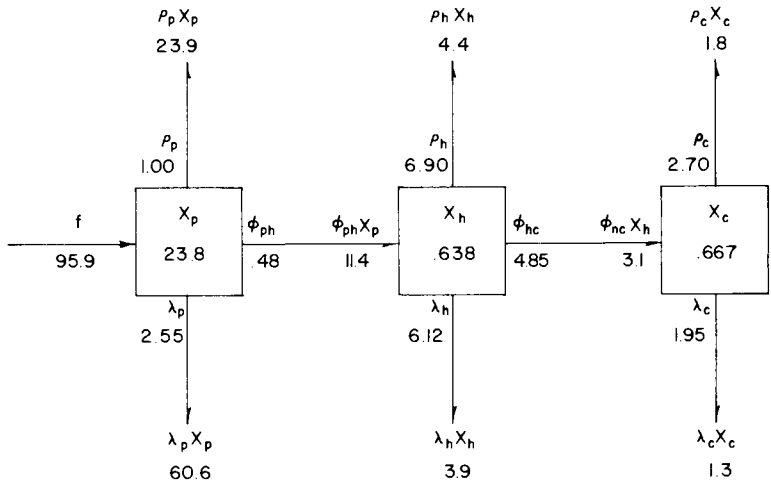

FIG. 4. A three-compartment forced linear model of energy flow in the Cedar Bog Lake ecosystem. The value for each flow rate (per year) is placed near the base of its arrow, and the value for the flow generated (calories per square centimeter per year) near the tip of the arrow. In the compartment is the value for average standing crop (calories per square centimeter).

TABLE IV

FORCING FUNCTION AND FLOW RATES FOR A THREE-COMPARTMENT LINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartment	Photosynthesis (f) (cal cm^{-2} yr^{-1})	Transfer rate (ϕ) (yr^{-1})	Respiration rate (ρ) (yr^{-1})	Loss rate (λ) (yr^{-1})
Plants X_p	95.9	0.48	1.00	2.55
Herbivores X_h		4.85	6.90	6.12
Carnivores X_c			2.70	1.95

[a] Values computed from Eqs. (1)–(3).

sinusoidal cycle. The amplitude of this fluctuation at Cedar Bog Lake was taken from data on a nearby area, Lake Mendota, Wisconsin (Juday, 1940). Lindeman used Juday's data to estimate the annual solar input into Cedar Bog Lake. The annual cycle in solar radiation was simulated with Eq. (4) in which t is time in radians, a year equals 2π radians and the yearly cycle begins, i.e., $t = 0$, at the vernal equinox.

$$f = 95.9 \times (1 + 0.635 \times \sin t). \tag{4}$$

The operation of this linear three-compartment system with a sinusoidally fluctuating input was simulated on an analog computer. The compartments showed small sinusoidal fluctuations in value (Fig. 5) in no way

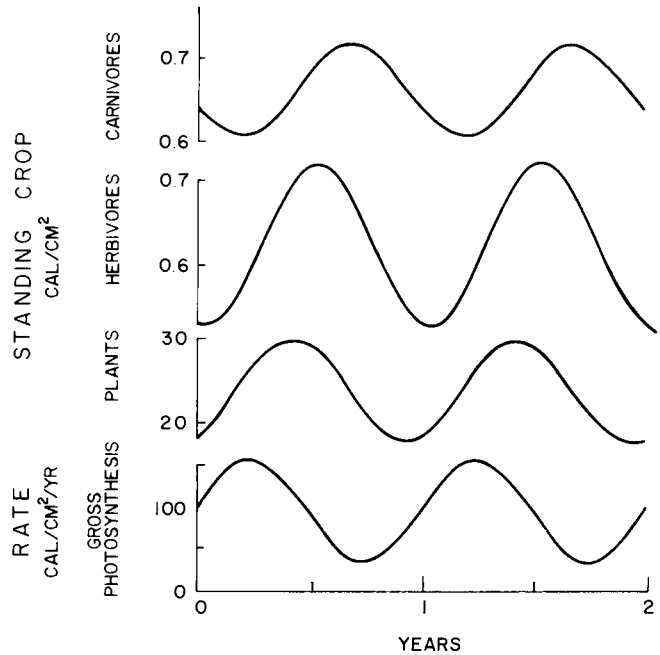

FIG. 5. Behavior of the three-compartment forced linear model of energy flow in the Cedar Bog Lake ecosystem. Fluctuations in standing crop in the compartments are induced by sinusoidal fluctuation in the forcing function, gross photosynthesis. The fluctuation in the forcing function corresponds to the seasonal cycle in insolation.

comparable in either amplitude or time of maxima and minima with the observed behavior of the Cedar Bog Lake ecosystem. This linear system, while adequate as a bookkeeping device to balance input and outflow, made no provision for the interactions between groups of organisms which generate so much of the dynamic behavior of ecosystems.

V. A Ten-Compartment Network System

A. STRUCTURING THE SYSTEM

Lindeman's (1941b) observations on the qualitative food cycle relations of Cedar Bog Lake were converted to a network system (Fig. 6)

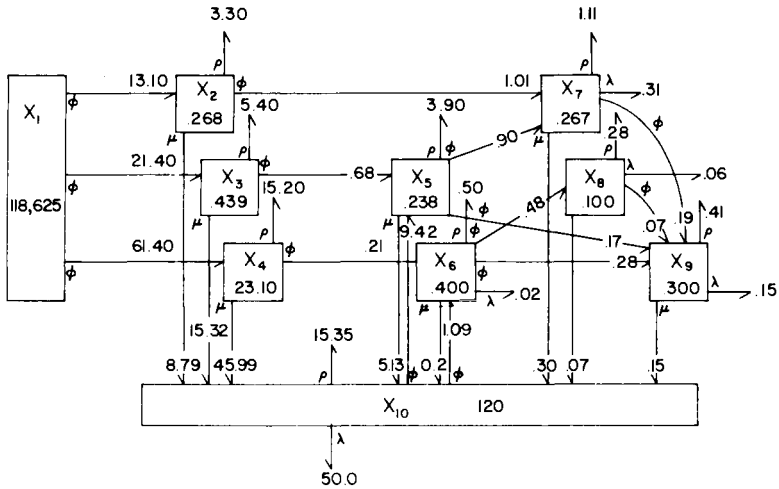

FIG. 6. A ten-compartment forced linear model of energy flow in the Cedar Bog Lake ecosystem. The values near the arrows and the value in compartment 1 are flows (calories per square centimeter per year). Values in the other compartments are average standing crops (calories per square centimeter).

similar to that in Fig. 1. Compartments and flows were excluded from the network if there were no usable data on them (e.g., a neuston compartment and a flow from browsers to plankton predators), or if Lindeman considered them of minor importance (e.g., air breathing tetrapods), or if energy transfer was not involved (e.g., dissolved nutrients). A ten-compartment system resulted. Solar energy was treated as a compartment because this facilitated subsequent use of the digital computer program, COMSYS 1, for simulation of the system. The flow from net plankton to plankton predators (turning them into omnivores) was based on a statement that *Chaoborus*, the chief component of the plankton predators, feed in part on *Ceratium*, the chief component of the net plankton. The zooplankton were chiefly rotifers, organisms too small to feed on *Ceratium*; therefore there was no flow from net plankton to zooplankton. Flows from the ooze, i.e., the sediment underlying the lake, to the zooplankton and the browsers were based on statements that both groups fed indiscriminately on living and dead organic matter. Flows from plankton and benthic predators to swimming predators (converting them to top carnivores) were based on Fig. 1 and statements that the former two were preyed on by the latter.

B. Calculating the Flows and Transfer Rates

The numerical values needed to convert this network into a linear system were drawn as far as possible from Table III. Additional calculations were made to estimate values for the ooze compartment, to divide loss (other than respiration) from the living components of the system (compartments 2–9) into two parts, loss to the ooze (μ) and loss to outside the system (λ), and to determine the individual input flows for compartments receiving more than one input.

Lindeman gave the ooze at the bottom of the pond a central position in the food web (Fig. 1) but provided little information concerning the ooze. Accordingly the necessary values for including ooze in this network system were created through a series of assumptions. The maximum depth in the ooze accessible to the browsers was assumed to be 2 cm. The ooze compartment thus consists of the upper 2 cm of sediment; this layer of dead organic matter and its associated microorganisms is treated as a unit. The material forming the upper 2 m of sediment is 97% water (Lindeman, 1941a). Assuming a specific gravity of one, the upper 2 cm contain 600 g m^{-2} organic matter. The caloric content of this organic matter was assumed to be somewhat below that of any of the pond organisms (Lindeman, 1941b, Table III) and set at 2000 cal g^{-1}. Thus the caloric content of the 2-cm layer available to the browsers was 120 cal cm^{-2}. Feeding by the zooplankton was assumed limited to the upper 1 mm of sediment; therefore the caloric content of the portion of ooze accessible to zooplankton was 6 cal cm^{-2}.

The respiration of ooze was estimated in a single experiment in which ooze was treated as sewage, and its biological oxygen demand obtained by techniques described in "Standard Methods for the Examination of Water and Sewage," 1936 edition (Lindeman, 1941b, p. 650). The biological oxygen demand of the ooze is given as 4.7 mg O_2/liter/50 mg dry sediment/5 days, at 20 C. The size of bottles used in this measurement is not stated, so they are assumed to be the size specified in "Standard Methods," 300 ml. This assumption yielded a respiration of 0.0056 mg O_2/mg dry sediment/day. Assuming an average temperature of 10 C and a Q_{10} of 2.5, the respiration at the average temperature was 0.002 mg O_2/mg dry sediment/day. The ooze compartment contains 30 mg cm^{-3} dry sediment. Assuming that only the upper 1.0 mm of ooze is involved in respiration, daily respiration for the ooze is 0.006 mg O_2 cm^{-2}. Using Ivlev's (1934) value of 3.38 cal/mg O_2, this is a flow of 7.4 cal cm^{-2} yr^{-1}.

Cedar Bog Lake was underlain with 10 m of postglacial sediment; the lower 8 m were consolidated peat and marl and the upper 2 m uncon-

solidated ooze (Lindeman, 1941a). Radiocarbon dating (Flint and Deevey, 1951) indicated that the deepest deposits in Cedar Bog Lake are approximately 8000 yr old. Assuming that the upper 2 m of unconsolidated ooze was relatively recent, the average rate of deposition for consolidated sediment was 1 m/1000 yr. Assuming that the consolidated sediment was 75% water, 2 m of unconsolidated material would compress to 24 cm, and thus represent 240 years' accumulation. This 2-m layer contained 12,000 cal cm^{-2}. The rate of sediment accumulation was thus 12,000 cal/cm^2 per 240 yr, or 50 cal cm^{-1} yr^{-1}. This value represented one of the losses (λ) from the ecosystem.

The other loss from the ecosystem was based on the consideration that aquatic insects have aerial stages in which they travel widely and suffer heavy mortality. Since the quantity of insects leaving the pond and dying at some distance from it was undoubtedly greater than the quantity hatched elsewhere which died over the pond, insect emergence represented a net loss. Fish which form the bulk of the swimming predators may be captured by birds, and thus also removed from the ecosystem. Therefore the compartments made up preeminently of insects or fish, the browsers and the plankton, benthic and swimming predators, were assumed to be points at which energy left the ecosystem through a loss flow (λ). In the absence of any information on the relative magnitude of the two losses, μ and λ, the total loss from each of the four compartments was divided about equally between them (Table V). The remaining compartments representing plants and zooplankton were considered having loss only to the ooze.

To calculate the flows into compartments receiving multiple inputs, feeding was assumed to be unselective, i.e., feeding by a recipient compartment on each of its donor compartments was directly proportionate to the standing crop of that donor. Thus, since the standing crop of nannoplankton was 0.439 cal cm^{-2} and the standing crop of ooze (available to zooplankton) was 6.0 cal cm^{-2}, zooplankton drew 0.439/6.439 of their sustenance from plankton and 6.000/6.439 from detritus. This approach was applied to all compartments (except ooze) with multiple inputs: zooplankton, browsers, plankton predators, and swimming predators (Fig. 6 and Table V).

The resulting model achieved by combining the data of Lindeman with these many assumptions had an annual flow into the ooze (i.e., the gross production for the ooze) of 75.77 cal cm^{-2} and losses from the ooze of 67.82 cal cm^{-2}. This difference was eliminated by increasing ooze respiration from 7.4 to 15.35 cal cm^{-2}, which is equivalent to assuming that the upper 2.1 mm of ooze, rather than 1.0 mm are involved in respiration.

TABLE V

VALUES FOR THE CONSTRUCTION OF A TEN-COMPARTMENT MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM

Compartment		Net production (cal cm^{-2} yr^{-1})	Number of turnovers (yr^{-1})	Average standing crop (cal cm^{-2})	Transfer (ϕ)		Respiration (ρ)		Loss ($\lambda + \mu$)		Gross production	
					Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})
Solar energy	X_1										118,625	
Net phytoplankton	X_2	9.8	36.5	0.268	1.01	3.77	3.30	12.30	8.79	32.73	13.1	48.8
Nannoplankton	X_3	16.0	36.5	0.439	0.68	1.56	5.40	12.30	15.32	34.94	21.4	48.8
Benthic plants	X_4	46.2	2.0	23.1	0.21	0.0091	15.20	0.66	45.99	1.99	61.4	2.66
Plants		72.0	—	23.8	1.90	0.08	23.90	1.00	70.10	2.95	95.9	4.03
Zooplankton	X_5	6.2	26.0	0.238	1.07	4.48	3.90	16.40	5.13	21.52	10.1	42.4
Browsers	X_6	0.8	2.0	0.400	0.76	1.90	0.50	1.25	0.04	0.10	1.3	3.25
Herbivores		8.0	—	0.638	1.83	2.87	4.40	6.90	5.17	8.10	11.4	17.87
Plankton predators	X_7	0.8	3.0	0.267	0.19	0.71	1.11	4.16	0.61	2.29	1.91	7.16
Benthic predators	X_8	0.2	2.0	0.100	0.07	0.71	0.28	2.80	0.13	1.30	0.48	4.80
Swimming predators	X_9	0.3	1.0	0.300	—	—	0.41	1.37	0.30	1.00	0.71	2.37
Carnivores		1.3	—	0.667	0.26	0.39	1.80	2.70	1.04	1.56	3.10	4.65
Ooze	X_{10}	60.42	0.50	120.0	10.42	0.087	15.35	0.127	50.0	0.416	75.77	0.63

C. The Completed Model

The final linear model, summarized in Fig. 6, Eqs. (5)–(14), and Tables V and VI was tested on a digital computer and achieved the computed steady state values for the compartments.

$$\dot{X}_1 = 365 \times 325 = 118,625 \tag{5}$$

$$\dot{X}_2 = f_{12} - X_2(\rho_2 + \mu_2 + \phi_{27}) \tag{6}$$

$$\dot{X}_3 = f_{13} - X_3(\rho_3 + \mu_3 + \phi_{35}) \tag{7}$$

$$\dot{X}_4 = f_{14} - X_4(\rho_4 + \mu_4 + \phi_{46}) \tag{8}$$

$$\dot{X}_5 = \phi_{35}X_3 + \phi_{10,5}X_{10} - X_5(\rho_5 + \mu_5 + \phi_{57} + \phi_{59}) \tag{9}$$

$$\dot{X}_6 = \phi_{46}X_4 + \phi_{10,6}X_{10} - X_6(\rho_6 + \mu_6 + \lambda_6 + \phi_{68} + \phi_{69}) \tag{10}$$

$$\dot{X}_7 = \phi_{27}X_2 + \phi_{57}X_5 - X_7(\rho_7 + \mu_7 + \lambda_7 + \phi_{79}) \tag{11}$$

$$\dot{X}_8 = \phi_{68}X_6 - X_8(\rho_8 + \mu_8 + \lambda_8 + \phi_{89}) \tag{12}$$

$$\dot{X}_9 = \phi_{59}X_5 + \phi_{69}X_6 + \phi_{79}X_7 + \phi_{89}X_8 - X_9(\rho_9 + \mu_9 + \lambda_9) \tag{13}$$

$$\dot{X}_{10} = \mu_2X_2 + \mu_3X_3 + \mu_4X_4 + \mu_5X_5 + \mu_6X_6 + \mu_7X_7 + \mu_8X_8 + \mu_9X_9 - X_{10}(\rho_{10} + \lambda_{10} + \phi_{10,5} + \phi_{10,6}). \tag{14}$$

Although the model maintained in general the flows and average compartment values specified by Lindeman (Table I), inclusion of the ooze compartment and the assumption of nonselectivity in feeding made the model both quantitatively and qualitatively different from his plant–herbivore–carnivore system. Since the ooze compartment contained most of the organic matter in the ecosystem, the herbivores fed chiefly on ooze and the plant production thus went chiefly to the ooze rather than directly to the herbivores. The major food chain was thus plant–detritus–herbivore–carnivore. The assumption of nonselectivity also directs most of the zooplankton net production into detritus and most of the browser net production into carnivores, because browsers have a greater standing crop than zooplankton although a much smaller net production (Table V).

VI. Conversion of the Linear System to a Nonlinear System

A. Structuring the System

The linear model was converted to a nonlinear model by altering control of the flows which could reasonably be thought dependent on the size of both donor and recipient compartments or on the size of the recipient compartment alone (Fig. 7). These were the flows into all the

TABLE VI

FORCING FUNCTIONS AND FLOW RATES FOR A TEN-COMPARTMENT LINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartment		Forcing (f)	Transfer(ϕ)		Respiration (ρ)	Loss to ooze (μ)	Loss to outside (λ)
		Flow (cal cm^{-2} yr^{-1})	Path	Rate (yr^{-1})	Rate (yr^{-1})	Rate (yr^{-1})	Rate (yr^{-1})
Net phytoplankton	X_2	13.1	2, 7	3.77	12.3	32.73	
Nannoplankton	X_3	21.4	3, 5	1.56	12.3	34.94	
Benthic plants	X_4	61.4	4, 6	0.0091	0.66	1.99	
Zooplankton	X_5		5, 7	3.77	16.4	21.52	
			5, 9	0.71			
Browsers	X_6		6, 8	1.2	1.25	0.05	0.05
			6, 9	0.71			
Plankton predators	X_7		7, 9	0.71	4.16	1.13	1.16
Benthic predators	X_8		8, 9	0.71	2.80	0.70	0.60
Swimming predators	X_9				1.37	0.50	0.50
Ooze	X_{10}		10, 5	0.078	0.127		0.416
			10, 6	0.0091			

[a] Values computed from Eqs. (6)–(14).

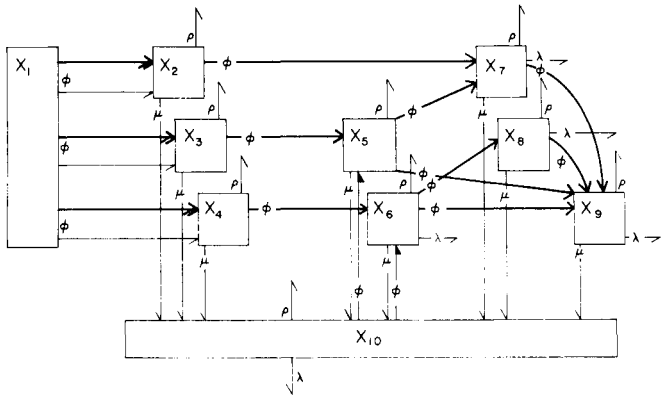

FIG. 7. A ten-compartment nonlinear model of energy flow in the Cedar Bog Lake ecosystem. Flow linear with donor compartment controlling ——→; flow approximately linear with recipient compartment controlling ——▶; simple nonlinear flow ——→; complex nonlinear flow ——↛.

living compartments, the forcing functions (f) and all transfers (ϕ), i.e., all transfers between compartments except transfers into the ooze; the ooze was not considered living in the same sense as compartments 2–9 even though it contained microorganisms and had a respiration flow. The remaining flows, respiration (ρ), loss to the ooze (μ), and loss to outside (λ), were more reasonably left linear with the donor compartment controlling.

B. Selecting Transfer Functions and Calculating Their Constants

The steady state equilibrium of the linear system (Fig. 6) was preserved in the nonlinear system. With the compartments at their steady state values, the nonlinear functions and constants yielded flows identical to those of the linear system. The flow into each plant compartment was divided into two parts, a small flow linear with the donor compartment, solar energy, and nonlinear flow two or three orders of magnitude larger under steady state conditions (Fig. 7, Eqs. (16)–(18), and Table VII). The linear flow was considered to represent the residuum of plant tissue, e.g., spores, seeds, or rhizomes, always present and ready to commence growth regardless of the presence or absence of actively photosynthesizing plant material in its compartment. The linear flow thus prevented plant compartments from ever being driven to zero and permanently destroyed. Values for the residuum b were calculated (as described below) so that at steady state they generated flows ($\phi b X_1$) of

TABLE VII

FLOW RATES, SELF-INHIBITIONS, AND RESIDUUMS FOR A TEN-COMPARTMENT NONLINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartment		Transfer (ϕ) Path	Transfer (ϕ) Rate (yr^{-1})	Respiration (ρ) Rate (yr^{-1})	Loss to ooze (μ) Rate (yr^{-1})	Loss to outside (λ) Rate (yr^{-1})	Self-inhibition (a) Rate (yr^{-1})	Residuum (b) Rate (yr^{-1})
Net phytoplankton	X_2	1, 2	0.000474	12.3	32.73		0.520	0.000178
Nannoplankton	X_3	1, 3	0.000549	12.3	34.94		0.572	0.000154
Benthic plants	X_4	1, 4	0.0000315	0.66	1.99		0.0126	0.0794
Zooplankton	X_5	3, 5	6.55	16.40	21.52			
		10, 5	42.4					
Browsers	X_6	4, 6	0.0228	1.25	0.05	0.05		
		10, 6	3.25					
Plankton predators	X_7	2, 7	14.1	4.16	1.13	1.16		
		5, 7	14.1					
Benthic predators	X_8	6, 8	12.0	2.80	0.70	0.60		
Swimming predators	X_9	5, 9	2.37	1.37	0.50	0.50		
		6, 9	2.37					
		7, 9	2.37					
		8, 9	2.37					
Ooze	X_{10}			1.27		0.416		

[a] Values computed from Eqs. (16)–(24).

0.01 into the phytoplankton compartments and 0.3 into the benthic plants (Fig. 7).

The nonlinear transfer rates for the plants were divided into two parts, $\phi X_1 X_2$ and $(\phi X_1 X_2) \times (-aX_2)$. The first term represents a nonlinear flow controlled by the product of donor $\times$ recipient, and the second term the degree to which the population size of the recipient inhibits that flow (cf. Chap. 1. III. G). This formulation, in which the flow into population X is a function of $X(1 - aX)$, is based on equations for interaction between competing species (Gause and Witt, 1935). The inclusion of terms for self-inhibition is supported by the fact that plant populations as they grow inhibit themselves through shading, reduction of available nutrients, etc. The constant a represents the amount by which each unit of plant population reduces the quality of the environment and thus the ability of each unit of plant population to capture solar energy. The constants ϕ and a were calculated for each plant compartment such that they—in conjunction with b—yielded the average gross production with the average standing crop (Table V) and a gross production equal to respiration at a standing crop approximating the largest value listed by Lindeman (1941b).

The regulation of flows from ooze to herbivores appeared entirely dependent on sizes of the herbivore compartments because the large amount of organic matter in the ooze provided herbivores with a food supply far beyond their needs. The problems in setting reasonable values for the rates of flow into the herbivore compartments were resolved by assuming that the herbivores ate living plants in proportion to their availability, and ate detritus to an extent sufficient to meet the remainder of their nutritional needs [Eqs. (19)–(20)]. The nonlinear transfer rates from living plants to herbivores (Table VII) were obtained by dividing the linear rates by the size of the recipient (herbivore) compartments. The flow rates from ooze to herbivores were obtained by setting ϕ's equal to the gross productions of herbivore compartments. The flows from ooze were made equal to the standing crop of herbivore compartments $\times$ their needs, i.e., their gross productions minus flows from living plants, or

$$(\phi_{\text{ooze,herbivore}}) - (\phi_{\text{plant,herbivore}} X_{\text{plant}} X_{\text{herbivore}})$$

The nonlinear flows in the carnivore compartments (plankton predators were still considered a member of this group despite their omnivorous diet) were computed simply by dividing each linear flow by the size of its recipient compartment. Observations by Holling (1966) on predator–prey relationships among invertebrates suggest that the resulting flow

into the predators, prey $\times \phi \times$ predator, approximated the behavior of some natural populations [Eqs. (21)–(23)].

C. The Completed Model

The completed nonlinear model is summarized below in Eqs. (15)–(24) and in Fig. 7 and Table VII.

$$X_1 = 118{,}625 \tag{15}$$

$$\dot{X}_2 = X_1\phi_{12}[b_2 + X_2(1 - a_2X_2)] - X_2(\rho_2 + \mu_2 + \phi_{27}X_7) \tag{16}$$

$$\dot{X}_3 = X_1\phi_{13}[b_3 + X_3(1 - a_3X_3)] - X_3(\rho_3 + \mu_3 + \phi_{35}X_5) \tag{17}$$

$$\dot{X}_4 = X_1\phi_{14}[b_4 + X_4(1 - a_4X_4)] - X_4(\rho_4 + \mu_4 + \phi_{46}X_6) \tag{18}$$

$$\dot{X}_5 = X_5[\phi_{35}X_3 + (\phi_{10.5} - \phi_{35}X_3) - (\rho_5 + \mu_5 + \phi_{57}X_7 + \phi_{59}X_9)] \tag{19}$$

$$\dot{X}_6 = X_6[\phi_{46}X_4 + (\phi_{10.4} - \phi_{46}X_4) - (\rho_6 + \mu_6 + \lambda_6 + \phi_{68}X_8 + \phi_{69}X_9)] \tag{20}$$

$$\dot{X}_7 = X_7[\phi_{27}X_2 + \phi_{57}X_5 - (\rho_7 + \mu_7 + \lambda_7 + \phi_{79}X_9)] \tag{21}$$

$$\dot{X}_8 = X_8[\phi_{68}X_6 - (\rho_8 + \mu_8 + \lambda_8 + \phi_{89}X_9)] \tag{22}$$

$$\dot{X}_9 = X_9[\phi_{59}X_5 + \phi_{69}X_6 + \phi_{79}X_7 + \phi_{89}X_8 - (\rho_9 + \mu_9 + \lambda_9])] \tag{23}$$

$$\begin{aligned}\dot{X}_{10} = {} & \mu_2X_2 + \mu_3X_3 + \mu_4X_4 + \mu_5X_5 + \mu_6X_6 + \mu_7X_7 + \mu_8X_8 + \mu_9X_9 \\ & - [X_{10}(\rho_{10} + \lambda_{10}) + X_5(\phi_{10.5} - \phi_{35}X_3) + X_6(\phi_{10.6} - \phi_{46}X_4)].\end{aligned} \tag{24}$$

The stability of this model was tested with constant solar energy input and the following initial conditions: the ooze at its average value, the nannoplankton at five times its average value, and the remaining compartments at one-half their average values. Much of the model proved both sluggish and unstable (Fig. 8). Net plankton, zooplankton, and plankton predators oscillated both widely and slowly (approximately 1 cycle/yr). Browsers first increased greatly, and then dropped to less than the initial condition. Benthic predators first increased markedly and then were almost exterminated. Swimming predators, the top carnivores, increased irregularly and at the end of the computer run, simulating 4 yr, were 20 times their initial value. Benthic plants slowly increased, but after the simulated 4 yr were still 4% below their calculated steady state value. Nannoplankton was the sole compartment which moved promptly to approximately the desired standing crop and stayed there. The model obviously needed further modification to simulate an ecosystem.

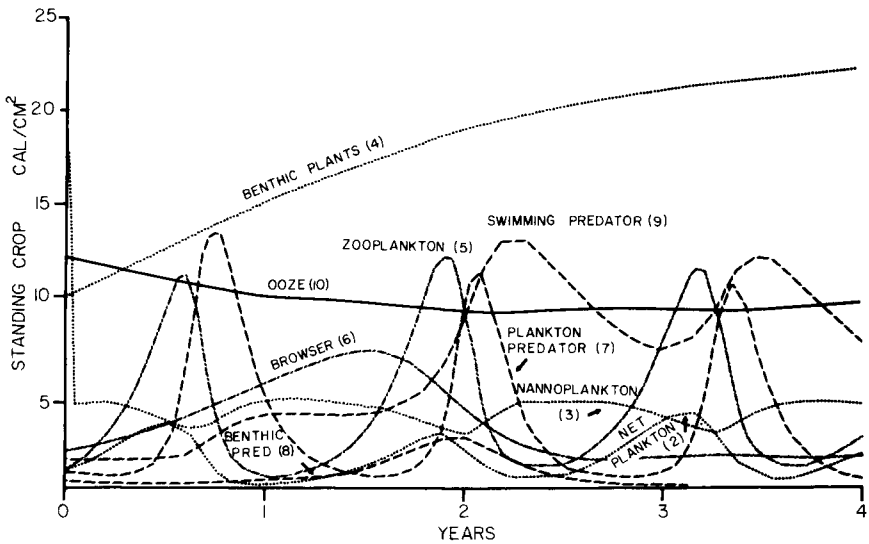

FIG. 8. Behavior of the ten-compartment nonlinear model (Eqs. (15)–(24) and Table VII) started with the ooze compartment at its average value, nannoplankton at five times its average value, and the remaining compartments at half their average values. Values on the ordinate for the ooze are multiplied by 0.1, for benthic plants by 1.0, and for the remaining compartments by 10.0.

VII. Controlling the Nonlinear Model

Control of the nonlinear model was achieved in two steps. The flux into swimming predators was regulated first by changing it from the general form $\phi X_1 X_2$ to $(\phi X_1 X_2) \times (1 - aX_2)$, thereby adding a term for self-inhibition like that used with the plant compartments [Eq. (36)]. The constants a and ϕ were selected to yield the average flow at the average standing crops of recipient and donor compartments, a flow approximating respiration of the recipient at the average standing crop of the donors, and the maximum standing crop which Lindeman observed for the recipient.

This modified nonlinear model had markedly improved behavior. Expansion of the swimming predator compartment was partially controlled and both browser and benthic predator compartments maintained larger populations. Net phytoplankton, zooplankton, and plankton predator compartments continued to oscillate widely in response to one another. The low plankton predator value allowed net plankton and zooplankton to increase. This increased food supply caused plankton

predators to increase, driving down net plankton and zooplankton. The flows into both zooplankton and plankton predator compartments were controlled with terms for self-inhibition, in the same manner as the flows into swimming predators [Eqs. (32) and (34)]. Besides stabilizing the model by causing the compartments to move to their equilibrium values with minimum oscillation, this modification of the nonlinear transfers also increased the speed with which equilibrium was approached. The presence of the inhibition term in the controlled nonlinear relationship necessitated increases of 12% to 40% in the transfer rates ϕ (Table VIII). Control of the flows into browsers and benthic predators seemed unnecessary because the remainder of the model was controlled and thus served as a mechanism to regulate those compartments.

The stable and responsive model obtained through modification of the equations for three compartments was suitable for reworking into a final form. Its general structure was preserved (see Fig. 10) despite the many changes in the system equations necessitated by the introduction of seasonal cycles in light and temperature.

VIII. The Addition of Environmental Effects

Effects of the annual cycle in light and temperature were introduced into the model by rewriting the equations defining the system. The amount of insolation was considered to affect only the plants and to affect them in a one-to-one manner. Insolation ranged from about 16,392 cal cm^{-2} during July to 3586 during December. This seasonal cycle was approximated by introducing a sine function into the solar energy compartment [Eq. (25)] similar to that used previously with the three-compartment linear model

$$X_1 = 118{,}625(1.00 + 0.635 \times \sin t). \tag{25}$$

Lindeman provided little temperature data for Cedar Bog Lake, so the values of Dineen (1953) for a similar nearby pond were used. Dineen's pond reached 27–29 C in July and, like Cedar Bog Lake, was frozen from about December to April. The temperature cycle was simulated with a modified sine function [Eq. (26)] in which negative values generated by the sine curve were set equal to 0 C.

$$C = \begin{cases} 11.00 + 1.37 \times \sin(t - 30) & \text{when computed } C \geqslant 0 \\ 0 & \text{when computed } C < 0. \end{cases} \tag{26}$$

TABLE VIII

FLOW RATES, SELF-INHIBITIONS, AND RESIDUUMS FOR A TEN-COMPARTMENT CONTROLLED NONLINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartments		Transfer (ϕ) Path	Transfer (ϕ) Rate (yr^{-1})	Respiration (ρ) Rate (yr^{-1})	Loss to ooze (μ) Rate (yr^{-1})	Loss to outside (λ) Rate (yr^{-1})	Self-inhibition (a) Rate (yr^{-1})	Residuum (b) Rate (yr^{-1})	Average standing crop (cal cm^{-2})	Gross production (cal cm^{-2} yr^{-1})
Net phytoplankton	X_2	1, 2	0.000474	12.3	32.73		0.520	0.000178	0.249	37.54
Nannoplankton	X_3	1, 3	0.000549	12.3	34.94		0.572	0.000154	0.361	46.59
Benthic plants	X_4	1, 4	0.0000315	0.66	1.99		0.0126	0.0794	18.9	126.45
Zooplankton	X_5	3, 5	7.42	16.40	21.52		0.520		0.133	10.21
		10, 5	47.4				0.444			
Browsers	X_6	4, 6	0.0228	1.25	0.05	0.05			0.387	2.01
		10, 6	3.25							
Plankton predators	X_7	2, 7	15.8	4.16	1.13	1.16	0.418		0.330	5.56
		5, 7	15.8				0.418			
Benthic predators	X_8	6, 8	12.0	2.80	0.70	0.60			0.096	0.79
Swimming predators	X_9	5, 9	3.38	1.37	0.50	0.50	1.00		0.392	1.44
		6, 9	3.38				1.00			
		7, 9	3.38				1.00			
		8, 9	3.38				1.00			
Ooze	X_{10}			0.122		0.416			242.0	153.31

[a] Values were obtained from Eqs. (29)–(37).

Temperature was considered to act uniformly on all the flows in the model, except loss from the ooze to the permanent sediment. This loss to the sediment was considered unaffected by temperature. The action of temperature was assumed to be a multiplication of the flows by a Q_{10} factor, symbolized in the equations by Q. A Q_{10} of 2.25 was selected, and 10 C taken as the reference temperature, i.e., temperature at which Q equalled one.

$$Q = 2.25^{[(C-10)/10]}. \tag{27}$$

It seemed unlikely that the seasonal change in light and temperature could oscillate the benthic plant compartment between approximately zero in winter and its summer maximum because turnover for this compartment was relatively slow. A third environmental factor was therefore added; loss from benthic plants to the ooze (μ_4), was multiplied by a factor, kx_1, reflecting the change in daily insolation. This factor was set equal to 1 — cosine time (1 yr = 2π rad).

$$kx_1 = 1 - \cos t. \tag{28}$$

Thus, the loss rate from benthic plants to the ooze, ($kx_1 \times \mu_4$), ranged from zero at the vernal equinox to twice the steady state value of μ_4 at the autumnal equinox. The variation in the loss rate seemed justified because benthic plants were growing in the spring and dying in the fall under similar conditions of light and temperature. This environmentally regulated model is summarized in Eqs. (25)–(37), Table VIII, and Fig. 9.

$$X_1 = 118{,}625(1.00 + 0.635 \sin t) \tag{25}$$

$$\dot{X}_2 = Q[\phi_{12}X_1(b_2 + X_2(1 - a_2X_2)) - X_2(\rho_2 + \mu_2 + \phi_{27}X_7(1 - a_7X_7))] \tag{29}$$

$$\dot{X}_3 = Q[\phi_{13}X_1(b_3 + X_3(1 - a_3X_3)) - X_3(\rho_3 + \mu_3 + \phi_{35}X_5(1 - a_{35}X_5))] \tag{30}$$

$$\dot{X}_4 = Q[\phi_{14}X_1(b_4 + X_4(1 - a_4X_4)) - X_4(\rho_4 + kx_1\mu_4 + \phi_{46}X_6)] \tag{31}$$

$$\begin{aligned}\dot{X}_5 = {} & QX_5[\phi_{35}X_3(1 - a_{35}X_5) + (\phi_{10,5}(1 - a_{10,5}X_5) - \phi_{35}X_3(1 - a_{35}X_5)) \\ & - (\rho_5 + \mu_5 + \phi_{57}X_7(1 - a_7X_7) + \phi_{59}X_9(1 - a_9X_9))]\end{aligned} \tag{32}$$

$$\begin{aligned}\dot{X}_6 = {} & QX_6[\phi_{46}X_4 + (\phi_{10,6} - \phi_{46}X_4) - (\rho_6 + \mu_6 + \lambda_6 + \phi_{68}X_8 \\ & + \phi_{69}X_9(1 - a_9X_9))]\end{aligned} \tag{33}$$

$$\begin{aligned}\dot{X}_7 = {} & QX_7[\phi_{27}X_2(1 - a_7X_7) + \phi_{57}X_5(1 - a_7X_7) - (\rho_7 + \mu_7 + \lambda_7 \\ & + \phi_{79}X_9(1 - a_9X_9))]\end{aligned} \tag{34}$$

$$\dot{X}_8 = QX_8[\phi_{68}X_6 - (\rho_8 + \mu_8 + \lambda_8 + \phi_{89}X_9(1 - a_9X_9))] \tag{35}$$

$$\begin{aligned}\dot{X}_9 = {} & QX_9[\phi_{59}X_5(1 - a_9X_9) + \phi_{69}X_6(1 - a_9X_9) + \phi_{79}X_7(1 - a_9X_9) \\ & + \phi_{89}X_8(1 - a_9X_9) - (\rho_9 + \mu_9 + \lambda_9)]\end{aligned} \tag{36}$$

$$\dot{X}_{10} = Q[\mu_2 X_2 + \mu_3 X_3 + kx_1\mu_4 X_4 + \mu_5 X_5 + \mu_6 X_6 + \mu_7 X_7 + \mu_8 X_8 + \mu_9 X_9 - (\phi_{10,5} X_5(1 - a_{10,5} X_5) - \phi_{35} X_3 X_5(1 - a_{35} X_5) + \phi_{10,6} X_6 - \phi_{46} X_4 X_6 + \rho_{10} X_{10})] - \lambda_{10} X_{10} . \quad (37)$$

In addition to faulty seasonal cycles and average standing crops, the model had about twice the proper energy flow (Table VIII). This flow which stemmed from an average Q_{10} factor (Q) of 1.55 was not, however, accompanied by a proportionate elevation in the content of any of the

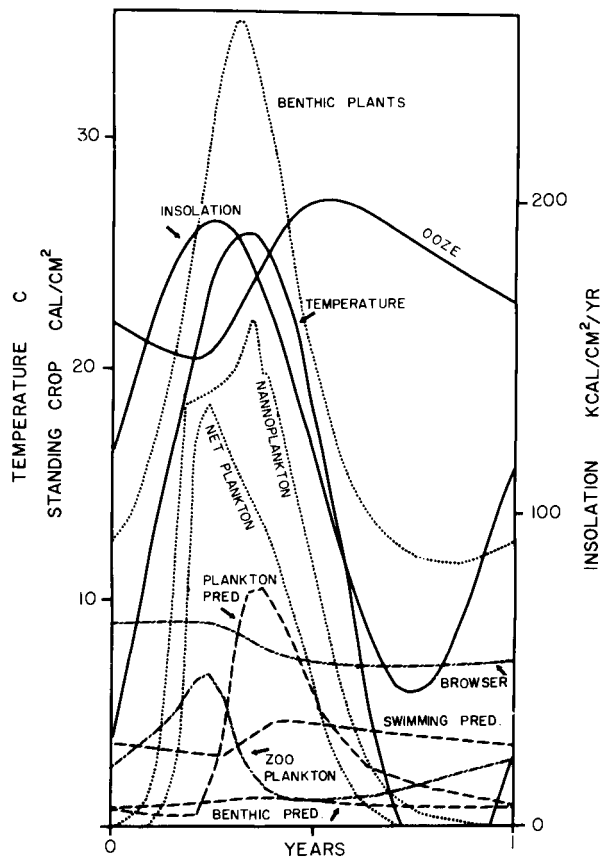

FIG. 9. Behavior of the ten-compartment, environmentally regulated, controlled nonlinear model (Eqs. (25), (26), and (29)–(37), and Table VIII). The year starts at the vernal equinox. Values on the ordinate for the ooze are multiplied by 0.1, for insolation, temperature and benthic plants by 1.0, for the predator compartments by 10.0, and for the remaining compartments by 20.0.

compartments except the ooze because, as mentioned above, temperature acted uniformly on all flow rates except loss from the ooze.

IX. Final Adjustment of the Model

A. General Approach

This environmentally regulated controlled nonlinear model was adjusted by a trial-and-error technique (i.e., many computer runs) to approximate parts of Lindeman's picture of the Cedar Bog Lake ecosystem. The degree of approximation was evaluated by the accuracy with which the models duplicated (1) average size of the compartments as listed in Table V, (2) total yearly energy flow (gross production) of the compartments as listed in Table V, and (3) seasonal cycles in compartment size where such cycles were explicitly mentioned by Lindeman. To facilitate the evaluation of trial models by these criteria, the COMSYS 1 program was modified to compute for the final year of simulated four-year runs the average value of each compartment, the total amount transferred, and the average flow rate of each flow. The initial simulated three years of operation permitted the model to approach equilibrium before the recording of flows and standing crops was begun.

The total flow through the model was first reduced by bringing the average value for the Q_{10} factor down from 1.55 to approximately one (1.033). This was done by changing the reference temperature for the calculation of Q from 10 C to 15 C, i.e., by replacing Eq. (26) with

$$Q = 2.25^{[(c-15)/10]}. \tag{38}$$

This change, however, brought the total energy flow from about 100% too great down only to about 50% too great; the model incorporating this change is referred to below as the "15-degree" model.

B. Plants

Adjustment of two of the primary producer compartments, nannoplankton and benthic plants, required much experimentation. The nannoplankton had 50% too great a gross production, 11% too small an average standing crop and a seasonal cycle reversed from that observed by Lindeman in Cedar Bog Lake. In the model the influx into nannoplankton was in part a direct function of available solar energy, and thus the seasonal cycle in nannoplankton standing crop followed the solar energy cycle (Fig. 9). The reverse cycle, with highest standing crop when solar energy was low, observed by Lindeman in Cedar Bog Lake

was obtained by changing the equation defining solar energy influx. The presence of a large standing crop during the period of minimum solar energy suggested that nannoplankkton utilized low levels of light at least as effectively as high levels. Accordingly, the energy influx into nannoplankton was disconnected from the seasonal solar energy cycle and instead was based on a uniform amount of solar energy equal to the annual average insolation rate. The reduction in nannoplankton standing crop coincided with the increase in net plankton standing crop, suggesting that the net plankton inhibit the nannoplankton. Accordingly the inhibition term of the equation defining influx into nannoplankton was made a function of the standing crop of both net plankton and nannoplankton, and the transfer and inhibition constants readjusted to this change [Eq. (39) and Table IX].

$$\dot{X}_3 = Q[325\phi_{13}(b_3 + X_3(1 - a_3(X_2 + X_3))) - X_3(\rho_3 + \mu_3 + \phi_{35}X_5(1 - a_{35}X_5))]. \tag{39}$$

These changes brought the average standing crop within 3% of the desired value, and in doing so depressed the gross production 39% below its desired value (Table X). In a population whose standing crop is negatively correlated with temperature, the bulk of the population's metabolism will occur when the Q_{10} factor is much less than one. Thus with the nannoplankton—or any similar population in this model—the gross production finally obtained will be less than that initially proposed on the basis of average standing crop. The reverse is, of course, true of populations whose abundance is positively correlated with temperature.

In the 15-degree model benthic plants had a slight excess of gross production (being most abundant in summer) and approximated the desired standing crop, but fluctuated between a midsummer maximum 50% higher than the average and a midwinter minimum 50% lower than the average. The desired seasonal cycle—approximately zero from late fall through early spring, a maximum reached in midsummer and maintained until October, and an abrupt drop back to the winter level during October and November—was reached only by radically altering the initial assumptions for the compartment. A more pronounced seasonal cycle than that obtained with the 15-degree model required both more rapid growth during spring and summer and more rapid death during the fall. More rapid growth was obtained by multiplying the transfer rate, ϕ_{14}, for the 15-degree model by 12/5 (Table IX) because appreciable growth by the benthic plants should be limited to five months per year. Similarly, since the loss from the benthic plants to the ooze occurred mainly during two months of the year, the loss rate.

μ_4, was multiplied by 12 for the 60 days following the autumnal equinox, and set at an arbitrary trivial value of 0.1 during the remainder of the year. The loss rate was multiplied by 12 rather than by 6 because the average biomass from which the loss took place was about one-half that at the beginning of the loss period. Since the loss rate was no longer related to temperature, this rate was disconnected from the Q_{10} factor.

$$\dot{X}_4 = Q[\phi_{14}X_1(b_4 + X_4(1 - a_4X_4)) - X_4(\rho_4 + \phi_{46}X_6)] - \mu_4X_4 . \qquad (40)$$

Finally, the self-inhibition coefficient was adjusted by trial-and-error to obtain the desired annual gross production (Table IX). The average standing crop in the final model, 11.1 cal cm^{-2} (Table X), was less than half that in the initial formulation of the Cedar Bog Lake model (Table III), in part because the benthic plants were abundant only in warm weather when the Q_{10} factor is greater than one, and in part because of an erroneous assumption in the initial formulation. It was assumed initially that the annual average standing crop lay midway between the maximum and minimum. However, the minimum persists for about seven months and the maximum for but two months per year; accordingly the annual average should have been considerably less than the mean of maximum and minimum. In the final model kx_1, the factor reflecting change in amount of insolation, was thus discarded, and the portion of the computer program used to calculate kx_1 was modified into a clock to control the switching between the two loss rates to the ooze. The factor kx_1 was made a cosine function [Eq. (41)] and examined with an IF statement—such that if kx_1 were less than or equal to 0.14, $\mu_4 = 24$, but if kx_1 were greater than 0.14, $\mu_4 = 0.1$.

$$kx_1 = 1 + \cos(t - 30). \qquad (41)$$

The net plankton compartment required no adjustment [Eq. (29)]. In the 15-degree model its average standing crop was 7% below the desired value, but its gross production was nearly twice that of the linear model (Table V). This excess flow was the result of maximum abundance in warm weather and a decision to aim for duplication of the average standing crop of the linear model (Table V) in preference to its annual gross production. The adjustment of the plankton predator compartment (described below) further slightly elevated both the average standing crop and gross production of net plankton.

C. Herbivores

Like the net plankton, neither of the herbivore compartments required any direct adjustment. The browsers were satisfactory in the 15-degree

TABLE IX

FLOW RATES, SELF-INHIBITION, AND RESIDUUMS FOR A TEN-COMPARTMENT, ENVIRONMENTALLY REGULATED, CONTROLLED NONLINEAR MODEL OF ENERGY FLOW IN THE CEDAR BOG LAKE ECOSYSTEM[a]

Compartments		Transfer (ϕ) Path	Transfer (ϕ) Rate (yr^{-1})	Respiration (ρ) Rate (yr^{-1})	Loss to ooze (μ) Rate (yr^{-1})	Loss to outside (λ) Rate (yr^{-1})	Self-inhibition (a) Rate (yr^{-1})	Residuum (b) Rate (yr^{-1})
Net phytoplankton	X_2	1, 2	0.000474	12.3	32.73		0.520	0.000178
Nannoplankton	X_3	1, 3	0.000721	12.3	34.94		0.539	0.000117
Benthic plants	X_4	1, 4	0.000759	0.66	0.1[b]		0.0244	0.0333
					24.0[b]			
Zooplankton	X_5	3, 5	7.42	16.40	21.52		0.520	
		10, 5	47.4				0.443	
Browsers	X_6	4, 6	0.0228	1.25	0.05	0.05		
		10, 6	3.25					
Plankton predators	X_7	2, 7	15.8	4.16	1.13	$1.16 \times Q^{2.4}$	0.418	
		5, 7	15.8				0.418	
Benthic predators	X_8	6, 8	12.0	2.80	0.70	0.60		
Swimming predators	X_9	5, 9	3.38	1.37	0.17[c]	0.50	1.00	
		6, 9	3.38		1.70[c]		1.00	
		7, 9	3.38				1.00	
		8, 9	3.38				1.00	
Ooze	X_{10}			0.122		0.416		

[a] Calculated from Eqs. (29), (32), (33), (35), (39), (40), (42)–(44).

[b] $\mu_4 = 0.1$ if $T <$ Sept. 22 or $>$ Nov. 21, $kx_1 > 0.14$
$= 24.0$ if $T \geqslant$ Sept. 22 and $\leqslant$ Nov. 21, $kx_1 \leqslant 0.14$.

[c] $\mu_9 = 0.17$ if C > 0
$= 1.70$ if C $= 0$.

TABLE X

VALUES FOR THE FLOW AND ACCUMULATION OF ENERGY IN THE CEDAR BOG LAKE ECOSYSTEM GENERATED BY A TEN-COMPARTMENT, ENVIRONMENTALLY REGULATED, CONTROLLED NONLINEAR MODEL[a]

Compartment		Net production (cal cm^{-2} yr^{-1})	Number of turnovers (yr^{-1})	Average standing crop (cal/cm^2)	Transfer (ϕ)		Respiration (ρ)		Loss ($\lambda + \mu$)		Gross production	
					Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})	Flow (cal cm^{-2} yr^{-1})	Rate (yr^{-1})
Solar energy	X_1										118, 625	
Net phytoplankton	X_2	19.77	68.41	0.289	2.00	6.92	6.68	23.09	17.77	61.43	26.45	91.43
Nannoplankton	X_3	9.71	22.67	0.428	0.42	0.98	3.27	7.64	9.29	21.70	12.98	30.31
Benthic plants	X_4	42.82	3.85	11.130	0.19	0.02	13.65	1.23	42.63	3.83	56.47	5.07
Plants		72.30	—	11.847	2.61	0.22	23.60	1.99	69.69	5.88	95.90	8.09
Zooplankton	X_5	6.54	27.71	0.236	1.08	4.58	4.17	17.64	5.46	23.14	10.71	45.38
Browsers	X_6	0.79	1.95	0.405	0.75	1.85	0.52	1.28	0.04	0.10	1.31	3.23
Herbivores		7.33	—	0.641	1.83	2.85	4.69	7.32	5.50	8.58	12.02	18.75
Plankton predators	X_7	1.81	7.04	0.257	0.19	0.72	1.10	4.29	1.62	6.30	2.91	11.32
Benthic predators	X_8	0.19	2.02	0.094	0.07	0.71	0.27	2.85	0.12	1.32	0.46	4.89
Swimming predators	X_9	0.31	1.06	0.293	—	—	0.41	1.41	0.31	1.04	0.72	2.46
Carnivores		2.31	—	0.644	0.26	0.40	1.78	2.76	2.05	3.18	4.09	6.35
Ooze	X_{10}	60.84	0.51	118.791	11.41	0.10	14.22	0.12	49.43	0.42	75.06	0.63

[a] The values for transfer represent transfer into compartments other than ooze. The rates for each compartment are the quotients of its flows divided by the average standing crop, and thus correspond to the linear rates in Table V.

model. The low average standing crop and gross production of the zooplankton in the 15-degree model were corrected by adjustment of the plankton predators.

D. Carnivores

The excessive gross production and average standing crop of the plankton predators had undesirable effects not only on zooplankton but also on the swimming predators. The summer maximum of the net plankton produced a slightly delayed maximum in the plankton predators at a time when Lindeman reported that the plankton predators were near their minimum—apparently due to emergence of adult stages. This increase in plankton predators not only acted directly to reduce the zooplankton below the desired level but caused an increase in the swimming predators which still further reduced the zooplankton. The plankton predators were forced into the desired seasonal cycle (summer minimum and winter maximum) and average standing crop by making their loss rate to the outside a function of the Q_{10} factor ($\lambda_7 \times Q^{2.4}$).

$$\dot{X}_7 = QX_7[\phi_{27}X_2(1 - a_7X_7) + \phi_{57}X_5(1 - a_7X_7) - (\rho_7 + \mu_7 + \lambda_7Q^{2.4} + \phi_{79}X_9(1 - a_9X_9))]. \tag{42}$$

Thus, the loss rate to the outside was maximum in summer, the period of maximum emergence, and minimum in winter. This change, which corrected the average standing crop and the seasonal cycle, only slightly reduced the excessive gross production. Minimum standing crop implied minimum self-inhibition. The combination of high temperature, abundant food, and minimum self-inhibition generated a large flow of energy into the plankton predators, despite their small standing crop. The large flow was drained away via loss to the outside, maintaining the small standing crop. This elevated gross production resulted from imposing the basic assumptions of the model onto a population which undergoes its minimum value when its food is abundant.

Although standing crop and gross production of the swimming predators were satisfactory following the adjustment of the plankton predators, the seasonal cycle of the swimming predators still had a summer minimum and a winter maximum. Lindeman reported an opposite cycle and attributed the winter loss to deoxygenation of the water following freezing of the pond. The rate for loss from the swimming predators to the ooze was made a function of water temperature such that adout three-fourths of the annual loss occurred during the three months that the pond was frozen (i.e., while the water was 0 C) and one-fourth

during the remainder of the year. This was done by separating the loss rate μ_9 from Q and attaching it to an IF statement such that the loss rate was 1.70 when the water temperature was 0 C and 0.17 when the temperature was above 0 C.

$$\dot{X}_9 = QX_9[\phi_{59}X_5(1 - a_9X_9) + \phi_{69}X_6(1 - a_9X_9) + \phi_{79}X_7(1 - a_9X_9) + \phi_{89}X_8(1 - a_9X_9) - (\rho_9 + \lambda_9)] - \mu_9X_9 . \quad (43)$$

Like the browsers on which they fed, the benthic predators approximated the desired values for standing crop and gross production in the 15-degree model. Reduction of the size of the swimming predator compartment through adjustment of the plankton predators slightly elevated the standing crop and gross production of the benthic predators and produced a still closer agreement between the desired values and those obtained.

E. Ooze

The ooze compartment also required no special adjustment.

$$\dot{X}_{10} = Q[\mu_2X_2 + \mu_3X_3 + \mu_5X_5 + \mu_6X_6 + \mu_7X_7 + \mu_8X_8] + \mu_4X_4 + \mu_9X_9 - Q[\phi_{10,5}X_5(1 - a_{10,5}X_5) - \phi_{35}X_3X_5(1 - a_{35}X_5) + \phi_{10,6}X_6 - \phi_{46}X_4X_6 + \rho_{10}X_{10}] - \lambda_{10}X_{10} . \quad (44)$$

Once the other compartments were adjusted—benthic plants in particular—the ooze approximated the standing crop and gross production of the linear model.

F. The Final Model

This final model is summarized in Eqs. (25), (26), (38), (41), (29), (39), (40), (32), (33), (42), (35), (43), (44), Figs. 10 and 11, and Tables IX and X.

$$X_1 = 118{,}625(1.00 + 0.635 \sin t) \quad (25)$$

$$C = \begin{cases} 11.00 + 1.37 \sin(t - 30) & \text{when computed } C \geqslant 0 \\ 0 & \text{when computed } C < 0 \end{cases} \quad (26)$$

$$Q = 2.25^{[(C-15)/10]} \quad (38)$$

$$kx_1 = 1 + \cos(t - 30) \quad (41)$$

$$\dot{X}_2 = Q[\phi_{12}X_1(b_2 + X_2(1 - a_2X_2)) - X_2(\rho_2 + \mu_2 + \phi_{27}X_7(1 - a_7X_7))] \quad (29)$$

$$\dot{X}_3 = Q[325\phi_{13}(b_3 + X_3(1 - a_3(X_2 + X_3))) - X_3(\rho_3 + \mu_3 + \phi_{35}X_5(1 - a_{35}X_5))] \quad (39)$$

$$\dot{X}_4 = Q[\phi_{14}X_1(b_4 + X_4(1 - a_4X_4)) - X_4(\rho_4 + \phi_{46}X_6)] - \mu_4X_4 \tag{40}$$

$$\dot{X}_5 = QX_5[\phi_{35}X_3(1 - a_{35}X_5) + (\phi_{10,5}(1 - a_{10,5}X_5) - \phi_{35}X_3(1 - a_{35}X_5)) - (\rho_5 + \mu_5 + \phi_{57}X_7(1 - a_7X_7) + \phi_{59}X_9(1 - a_9X_9))] \tag{32}$$

$$\dot{X}_6 = QX_6[\phi_{46}X_4 + (\phi_{10,6} - \phi_{46}X_4) - (\rho_6 + \mu_6 + \lambda_6 + \phi_{68}X_8 + \phi_{69}X_9(1 - a_9X_9))] \tag{33}$$

$$\dot{X}_7 = QX_7[\phi_{27}X_2(1 - a_7X_7) + \phi_{57}X_5(1 - a_7X_7) - (\rho_7 + \mu_7 + \lambda_7Q^{2.4} + \phi_{79}X_9(1 - a_9X_9))] \tag{42}$$

$$\dot{X}_8 = QX_8[\phi_{68}X_6 - (\rho_8 + \mu_8 + \lambda_8 + \phi_{89}X_9(1 - a_9X_9))] \tag{35}$$

$$\dot{X}_9 = QX_9[\phi_{59}X_5(1 - a_9X_9) + \phi_{69}X_6(1 - a_9X_9) + \phi_{79}X_7(1 - a_9X_9) + \phi_{89}X_8(1 - a_9X_9) - (\rho_9 + \lambda_9)] - \mu_9X_9 \tag{43}$$

$$\dot{X}_{10} = Q[\mu_2X_2 + \mu_3X_3 + \mu_5X_5 + \mu_6X_6 + \mu_7X_7 + \mu_8X_8] + \mu_4X_4 + \mu_9X_9 - Q[\phi_{10,5}X_5(1 - a_{10,5}X_5) - \phi_{35}X_3X_5(1 - a_{35}X_5) + \phi_{10,6}X_6 - \phi_{46}X_4X_6 + \rho_{10}X_{10}] - \lambda_{10}X_{10}\,. \tag{44}$$

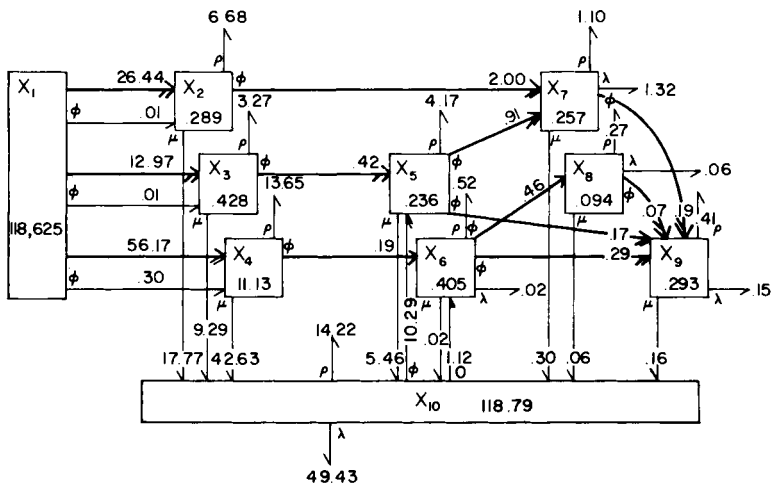

FIG. 10. The final nonlinear model of energy flow in the Cedar Bog Lake ecosystem. The values near the arrows and the value in compartment 1 are flows (calories per square centimeter per year). Values in the other compartments are average standing crops (calories per square centimeter). Flow linear with donor compartment ——→; flow approximately linear with recipient compartment — —▶; simple nonlinear flow ——→; complex nonlinear flow ⟶→; complex nonlinear flow independent of donor compartment ——▶.

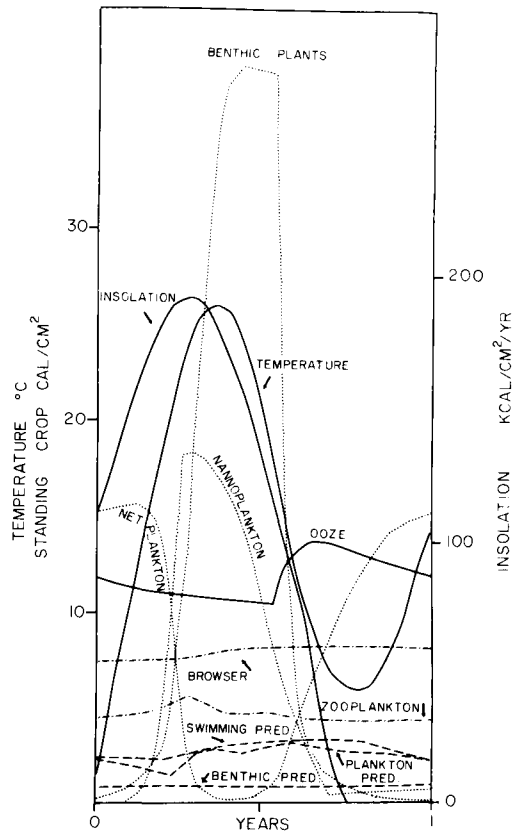

FIG. 11. Behavior of the final model (Eqs. (25), (26), (29), (32), (33), (35), (38)–(44), and Table IX). The year starts at the vernal equinox. Values on the ordinate for the ooze are multiplied by 0.1, for insolation, temperature and benthic plants by 1.0, for the predator compartments by 10.0, and for the remaining compartments by 20.0

In response to simulated annual cycles in light, temperature, and season, this model yielded annual cycles in the energy flow and standing crop of its compartments. Lindeman's data and descriptive comments suggested the form of the seasonal cycles in the standing crops of five of the compartments, benthic plants, net plankton, nannoplankton, plankton predators, and swimming predators, and these cycles were to some degree duplicated by the model. All the compartments of the model approximated the average standing crops suggested by Lindeman's

data. Except for benthic plants, the average standing crops lay within 7% (average 3%) of those initially calculated (Tables V and X). The average standing crop of benthic plants was about half that originally calculated, but this represented an initial misconstruing of Lindeman's observations rather than a failure of the model. The model also yielded gross productions in most compartments within a few percent of the calculated values (Tables V and X). Three compartments, net plankton, nannoplankton, and plankton predators, could not be adjusted to yield both the desired average standing crop and the desired gross production. By control of input, the phytoplankton compartments were forced into pronounced seasonal cycles in standing crop correlated either inversely or directly with temperature. The average metabolic rates for these populations were thus either much greater or much less than the metabolic rates occurring at the mean effective temperature of the ecosystem. The model, however, is based on the concept that the annual average metabolic rate for a population approximates the rate at the mean effective temperature of the system. The plankton predator compartment had excessive gross production despite the fact that it was forced into a seasonal cycle in standing crop inversely correlated with temperature. The difference between this compartment and the phytoplankton compartments lay in the manner in which standing crop was controlled. The plankton predators were regulated by manipulating loss from the compartment rather than input into it. The small standing crop minimized self-inhibition, and this combined with high temperature and abundant food generated a large input during the summer despite the small standing crop at this time.

When summed by trophic level, the deviations from desired values for gross production somewhat cancelled one another (Table X). The final model yielded average gross productions of 95.9, 12.1, and 4.1 cal/cm^2 yr^{-1} for primary producers, herbivores and carnivores, respectively. Lindeman's data (Table III) suggested gross productions of 95.9, 12.0, and 3.1 cal cm^{-2} yr^{-1}, respectively, for these trophic levels.

X. Utility of the Model

Although the various models of energy flow in the Cedar Bog Lake ecosystem are in part based on data, none of them can be employed in speculations concerning the nature of ecosystems—because the principal foundation for much of this modeling was educated guesses. The final model has pedagogical rather than analytical value. This model possesses desirable attributes, stability, and responsiveness to simulated environ-

mental changes, and thus offers insights into the construction of workable nonlinear ecosystem models.

The ten-compartment nonlinear models functioned passably well even when relationships between compartments were very imperfect, and showed considerable stability when subjected to extensive tinkering. This stability is probably derived from three decisions in the initial structuring of the model: (1) unselective feeding, (2) the interposition of an ooze compartment between the plants and the herbivores, and (3) an ooze to herbivore flow controlled solely by the herbivores. Unselective feeding directed most of the plant production into the ooze which then served as a reservoir for plant production. The presence of this reservoir and a recipient-controlled flow from it gave the herbivores an almost unlimited food supply, precluding any important direct interaction between the plants and herbivores. Thus, fluctuations in the plant compartments had minimal effect on the herbivore compartments, and vice versa. With abundant food available to herbivores, their regulation became a function of carnivore abundance. The ecosystem was thus split into two largely isolated parts, the plants and the animals, and the animals split into the subordinate herbivores and the dominant carnivores. The plankton predators which fed directly on net phytoplankton consumed only 10% of the net production of this compartment and therefore had little effect on it. This dividing of the ecosystem into isolated parts gave the model stability and simplified its adjustment. The plant and animal ends of the system could be simultaneously subjected to experimentation, and imperfect behavior by one part of the model, buffered by the ooze compartment, was not transmitted throughout the system.

The regulation of nonlinear flows with self-inhibition functions gave the model both stability and increased responsiveness. The presence of some restraint on the nonlinear flows appears essential in the constructing of workable nonlinear models. The first nonlinear models of the Cedar Bog Lake ecosystem lacked adequate control of the interaction among compartments. The stimulus provided by the annual variation in solar energy caused some compartments to fluctuate widely in response to one another. With the interaction (i.e., the flows among compartments) regulated by self-inhibition, the compartmental values remained within suitable bounds and responded smoothly to the annual energy cycle.

Since each nonlinear flow has the ability to produce far-reaching effects in a model and requires complex regulation, the construction of a nonlinear model is speeded and simplified by minimizing the number of nonlinear flows, and as far as possible separating them from one another. This separation can be effected by interposing between two nonlinear

flows either a large compartment with slow turnover or two compartments joined by a linear flow. Both methods were used in the Cedar Bog Lake model.

One aspect of the final model serves no useful purpose. The residuums do not save any of the plant compartments from extinction because none are so threatened. Even at their lowest standing crops the plant compartments receive no more than 1 to 5% of their input via the residuums.

XI. Reconsideration of Lindeman's Work

Lindeman's conclusion that the productivity of lakes is lowest during senesence was based on his comparison of two bodies of water, Cedar Bog Lake and Lake Mendota (Wisconsin). Neither his own study of Cedar Bog Lake nor Juday's (1940) study of Lake Mendota contained any measurements of plant production. In both studies phytoplankton production was inferred from data on standing crop by use of arbitrary rates of turnover, and the rates used do not agree with current notions. Data of Kristiansen and Mathiesen (1964) on the phytoplankton of a small Danish lake, for example, suggest an annual gross production at the most favorable depth at least 274 times the average standing crop. Cedar Bog Lake is shallow enough to be illuminated to the bottom. Assuming—as Lindeman did—that net production is three-fourths of gross production, this yields an average turnover time of 1.8 days. Use of such a turnover time would have increased the estimates of phytoplankton production in Cedar Bog Lake by five-fold. Lindeman appears also to have underestimated benthic plant production. He equated annual production of pond weeds and their epiphytes with the maximum standing crop. These algal epiphytes presumably turned over more often than once a year. Since values of zero were recorded during the winter it is likely that his measurements of standing crop did not include roots, and these are often a substantial part of total plant biomass (Westlake, 1966). Lindeman also ignored the emergent plants, *Typha* and *Decodon*, in his measurements of biomass in Cedar Bog Lake. Comparisons of plant productivity by Westlake (1963) indicate that the productivity of lakes rises during senescence. Submerged pond weeds are on the average at least as productive as fresh-water phytoplankton communities, and emergent species—which characterize the transition from aquatic to terrestrial—are far more productive than phytoplankton.

When reworked into a network system, the observations of Lindeman no longer support his suggested general principle that the efficiency with which energy assimilated by one trophic level is transferred to the next

increases with successive trophic levels. Lindeman is correct to the extent that the efficiency of the first transfer, i.e., the efficiency with which solar energy is captured via photosynthesis, is low in natural communities. Neither studies of other ecosystems (Kozlovsky, 1967), nor the network model of the Cedar Bog Lake ecosystem (Table XI), show any consistent increase in the efficiencies of the transfers for succeeding levels.

TABLE XI

EFFICIENCY WITH WHICH ENERGY ASSIMILATED BY TROPHIC LEVELS IS TRANSFERRED TO A SUCCEEDING TROPHIC LEVEL[a]

Transfer	Percent efficiency	
	Linear model	Final model
Plants/sun	0.1	0.1
Browser/benthic plant + ooze	0.9	1.0
Zooplankton/nannoplankton + ooze	10.4	12.2
Plankton predator/net plankton + zooplankton	8.2	7.8
Benthic predator/browser	36.9	35.1
Swimming predator/browser + zooplankton + plankton predator + benthic predator	5.1	4.7

[a] From data for the ten-compartment linear model (Table V) and from the results obtained with the final nonlinear model (Table X).

The fact that nearly thirty years of research have revealed flaws in some of the conclusions Lindeman drew from his pioneer study in no way detracts from the stature and importance of his work. His basic conclusion, that trophic level and energy flow are key factors in the analysis of ecosystems, stands.

Acknowledgments

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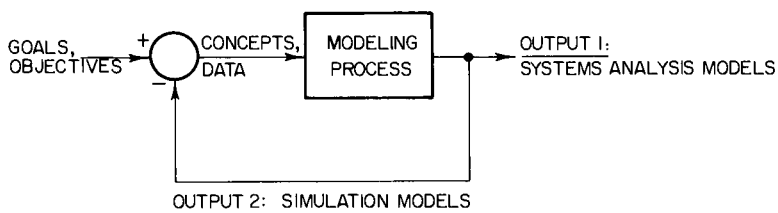
Coda

Nothing seems more natural, perhaps, after a half century or so of biological analysis devoted to understanding organisms by understanding their parts, than to try in synthesis to put the understood parts back together again. This rationale has dominated the modeling represented in this volume, which might be characterized as "mechanistic" modeling. It doesn't work—not yet—especially not for ecosystems, and the fundamental wisdom of attempting to achieve realistic simulations by stringing together large sets of arbitrarily derived equations representing mechanisms seems open to question. As H. T. Odum [1971. "Environment, Power and Society." Wiley (Interscience), New York] has suggested, it is difficult to see a forest when the trees stand out so clearly; perhaps what we need is smoked glass in our macroscope.

Modeling spans a spectrum from *isomorphic* formulations, in which components and interactions of systems are captured on a one-to-one basis, to *homomorphic* representations where details are collapsed many-to-one into lumped variables and parameters. The former emphasize realism and detail, while the latter grade into abstraction and generality. The trick of effective modeling is somehow to strike a balance between the two extremes that is appropriate for what should be explicitly defined goals and objectives. Moreover, within a given investigation different models may serve different purposes, and the title of this book is intended to suggest that these may broadly be considered *simulation* and *systems analysis*. Models for simulation tend to be realistic and concerned with details (isomorphic), whereas systems analysis models may possibly lean more to the abstract (homomorphic). The general cybernetic model for feedback control can be used to diagram how these two approaches might logically complement one another in a given macrosystem study.



Output 1 corresponds to the ultimate objective of performing a systems analysis on a general model representing the "core" dynamic characteristics of the real system. The analysis may include transient and frequency response, sensitivity analysis, stability, optimization, etc., and it is suggested that for many purposes, particularly when the system is in a well-defined operating state, linear models may serve usefully to express the general features of that state. Output 2, on the other hand, is associated more with realism and the simulation rationale. Mechanistic models, linear or nonlinear, may be studied for their heuristic value in refining concepts and identifying data needs. Simulation models do not have to reproduce dynamic behavior realistically to be useful in the feedback loop; the thought that goes into them may be their greatest value.

In accordance with this scheme, the first section of Volume II presents a series of papers concerned more with dynamic analysis of ecosystems than with simulation. This is followed by sections on theory and applications, culminating in a visionary chapter outlining the exciting prospects for ecological systems modeling in the future.

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