

This work was supported partially by the German "Fonds der Chemischen Industrie". Computer simulations were executed on the IBM 7094 of the "Deutsches Rechenzentrum" in Darmstadt, Germany.

REFERENCES

- BAK, T. A. (1963). "Contributions to the Theory of Chemical Kinetics". New York: W. A. Benjamin, Inc.
- DENBIGH, K. G., HICKS, M. & PAGE, F. M. (1948). *Trans. Faraday Soc.* **44**, 479.
- HEARON, J. Z. (1953). *Bull. math. Biophys.* **15**, 121.
- LOTKA, A. J. (1910). *J. phys. Chem. Ithaca* **14**, 271.
- MEIXNER, J. (1949). *Z. Naturf.* **4a**, 594.
- MOORE, M. J. (1949). *Trans. Faraday Soc.* **43**, 1088.
- SUGITA, M. (1961). *J. theor. Biol.* **1**, 415.

J. theor. Biol. (1970) **27**, 207-220

Interspecific Competition, Predation and Species Diversity

J. D. PARRISH AND S. B. SAILA

*Graduate School of Oceanography, University of Rhode Island,
Kingston, Rhode Island 02881, U.S.A.*

(Received 5 May 1969, and in revised form 10 October 1969)

A review was made of some mathematical population models and their applications to problems of interspecific competition and predator-prey relationships. These were considered in relation to some observations and experiments suggesting local increases in species diversity under predation in competitive situations. A mathematical model of a three-species trophic subweb was developed and examined critically. Model results indicated that the equilibrium assumptions postulated in previous models may be unrealistic, and that local species diversity may indeed increase with predation under some competitive conditions.

1. Introduction

Gause (1935) and Gause & Witt (1935) have demonstrated from the mathematical formulation of a theory of competition that the outcome of equal competition between two species, subsisting on a common resource at a constant trophic potential in a homogeneous closed environment, depends only on the initial proportions of the two species. In a number of instances, experimental and observational research has shown that when several species are in approximately the same ecological niche, competing for a common resource, the most capable species becomes dominant and the others become extinct. Gause's (1935) formulation also predicts this result for two unequally competing species. The idea of one species to a niche has become known (in ecological literature) as Gause's Principle.

Hutchinson (1961) pointed out that differential predation on competing species may theoretically permit some diversification of prey. Recently Paine (1966) suggested that predation, under some circumstances at least, may tend to increase species diversity locally in competitive situations. He theorized that with predation acting on both (or all) competing species, total resource utilization is decreased and both weaker and stronger species may survive in the resulting situation which is less resource-limited. He explored these ideas by observing species diversity vs. trophic structure (i.e. numbers and kinds of predators and numbers and kinds of prey) in some intertidal

communities of marine invertebrates, and found a positive correlation between high species diversity and increased predation. He also experimented by removing the major predator from an intertidal community and observed its change from a 15-species to an 8-species system during a period of less than two years.

Paine's experiments and observations are intuitively appealing and seem to suggest an ecological outcome of predation in natural systems, in addition to that of maintaining populations (such as the Kaibab deer) in stable equilibrium. However, from the limited data at hand it does not appear intuitively clear what the outcome of predation will be on a given competitive situation involving more than one prey species. It might be argued that predation, if it imposes an additional depressing effect equally on both (or all) competing species, severely lowers the population growth potential of both or all species. Thus the competitive differences resulting may act to eliminate the weaker species at an even earlier time than without predation. Other hypotheses might be postulated, but it seems unreasonable to attempt to predict the consequences of the dynamic interactions of three or more populations without constructing and testing an analytical model of the system. It is the object of this paper to consider a model of the dynamic interactions of a three-species population consisting of one predator and two prey organisms. It is suggested that although the model is applied to only a restricted and somewhat hypothetical situation, model construction and analysis provide additional insight and understanding of complex phenomena not attainable by observation and intuition alone.

2. Background

The usual approach to the study of the dynamics of competition has involved the logistic type equations of Lotka-Volterra (Volterra, 1928). Volterra developed a variety of expressions describing the relationships between species. These include a generalized expression which (when utilized with proper coefficients and proper signs) provides some indication of the results of interactions between two species including: mutualism, proto-cooperation, competition and predation. He also developed a more complete model of competition between two species which may be expressed as:

$$\frac{dN_1}{dt} = [\varepsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2]N_1, \quad (1)$$

$$\frac{dN_2}{dt} = [\varepsilon_2 - \alpha_{21}N_1 - \alpha_{22}N_2]N_2, \quad (2)$$

where N_1 and N_2 are the numbers of species 1 and species 2, respectively,

ε_1 and ε_2 are intrinsic rates of natural increase (biotic potential), α_{11} and α_{22} are coefficients representing intraspecific checks on rate of increase, α_{12} and α_{21} are coefficients of decrease or increase of a species due to interaction with the other species.

This system of equations was utilized by Larkin (1963) to describe interspecific competition and exploitation effects in natural fisheries. Larkin considered the properties of equations (1) and (2) under an equilibrium condition based on the assumption that both the rates of population change are simultaneously zero, i.e. ($dN_1/dt = 0$ when $dN_2/dt = 0$). He solved the resulting simultaneous algebraic equations to provide the following expressions for N_1 and N_2 at the equilibrium:

$$N_1 = \frac{\alpha_{22}\varepsilon_1 - \alpha_{12}\varepsilon_2}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \quad (3)$$

$$N_2 = \frac{\alpha_{11}\varepsilon_2 - \alpha_{21}\varepsilon_1}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \quad (4)$$

Equations (3) and (4) are particularly convenient since they contain only constant coefficients. Larkin (1963) then used these relations to determine the combinations of the coefficients for which one or the other of the two species would go to extinction and the conditions under which both would persist. It appears from an examination of his results that both species can persist indefinitely only when the numerical values of the coefficients are such as to provide equal rates when the numbers of both species are equal. In any event, all of Larkin's conditions for indefinite survival of both species include offsetting competitive advantages for the two species. In the present paper, the well-defined case of a definite competitive advantage for one species will be considered without the assumption of an equilibrium where both rates of population change are zero.

Larkin also made use of the relations described above by adding an exploitation or fishing rate (c_1 and c_2) which represents a fixed fraction of the instantaneous population of each species. He then considered equilibrium as the point of maximum sustainable yield and calculated that yield Y_1 from:

$$Y_1 = c_1 N_1 = c_1 \left[\frac{\alpha_{22}(\varepsilon_1 - c_1) - \alpha_{12}(\varepsilon_2 - c_2)}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \right] \quad (5)$$

$$Y_2 = c_2 N_2 = c_2 \left[\frac{\alpha_{11}(\varepsilon_2 - c_2) - \alpha_{21}(\varepsilon_1 - c_1)}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} \right]. \quad (6)$$

From equations (5) and (6), curves depicting Y_1 as $f(c_1)$ for various values of c_2 , and Y_2 as $f(c_2)$ for various C_1 were plotted.

With reference to predation, the basic Volterra (1928) model of two interacting species, wherein species N_3 preys on species N_1 is as follows:

$$\frac{dN_1}{dt} = [\varepsilon_1 - \alpha_{13}N_3]N_1, \quad (7)$$

$$\frac{dN_3}{dt} = [-\varepsilon_3 + \alpha_{31}N_1]N_3, \quad (8)$$

where the terms are defined as in equations (1) and (2).

Equations (7) and (8) have a serious limitation in the real world because without predation the prey increases without limit, and conversely the predator becomes extinct in the absence of prey. The form of these equations permits analytical solution and Doi (1962) has used these in an analog computer simulation model. This system of equations describes a lagged cyclic behavior with phase displacement of predator and prey, and is inherently unstable.

Larkin (1966) modified Volterra's model of predator-prey relationships in a manner similar to Kostitzin (1939) by adding a self-limiting term to the prey and introducing a modified predator expression as follows:

$$\frac{dN_1}{dt} = [\varepsilon_1 - \alpha_{11}N_1 - \alpha_{13}N_3]N_1, \quad (9)$$

$$\frac{dN_3}{dt} = [\varepsilon_3 - \alpha_{33}N_3 + \alpha_{31}N_1]N_3. \quad (10)$$

Again, considering the "equilibrium" case (where $dN_1/dt = 0$ when $dN_3/dt = 0$) he solved for N_1 and N_3 in terms of constant coefficients. By applying a percentage exploitation (fishing) to the predator/prey system and deriving sustained yield expressions similar to equations (5) and (6), he achieved results of the same general type as those for two competing species.

3. The Model

To consider the effects of predation on species diversity of competing species, a three-species model or "trophic subweb" is a minimum requirement. It would obviously be more realistic to deal with more species of predator as well as prey. However, with the data available, such an increase in complexity might provide no increase in insight.

The Lotka-Volterra competition equations [equations (1) and (2)] were used for competing species N_1 and N_2 and a modified Volterra predator-prey equation [equation (13)] was used for species N_3 , which is a predator preying on N_1 and N_2 . The equations for the three species "trophic subweb" model which describe competition between species 1 and species 2, with species 3

preying on both are:

$$\frac{dN_1}{dt} = [\varepsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3]N_1, \quad (11)$$

$$\frac{dN_2}{dt} = [\varepsilon_2 - \alpha_{22}N_2 - \alpha_{21}N_1 - \alpha_{23}N_3]N_2, \quad (12)$$

$$\frac{dN_3}{dt} = [-\varepsilon_3 + \alpha_{31}N_1 + \alpha_{32}N_2]N_3, \quad (13)$$

where ε_i ($i = 1, 2, 3$) are the intrinsic rates of increase or decrease (biotic potential), $\alpha_{11}, \alpha_{12}, \alpha_{13}, \alpha_{21}, \alpha_{22}, \alpha_{23}, \alpha_{31}, \alpha_{32}$ represent the intraspecific and interspecific coefficients similar to previous equations.

For equations (11), (12) and (13) the "equilibrium" state can be formally considered by setting $dN_1/dt = 0$, $dN_2/dt = 0$ and $dN_3/dt = 0$. Solution of the above equations then provides the following expressions for "equilibrium" numbers of each species:

$$N_1 = \frac{-\alpha_{23}\alpha_{32}\varepsilon_1 + \alpha_{13}\alpha_{32}\varepsilon_2 + \alpha_{12}\alpha_{23}\varepsilon_3 - \alpha_{13}\alpha_{22}\varepsilon_3}{-\alpha_{11}\alpha_{23}\alpha_{32} + \alpha_{13}\alpha_{21}\alpha_{32} + \alpha_{12}\alpha_{23}\alpha_{31} - \alpha_{13}\alpha_{22}\alpha_{31}}, \quad (14)$$

$$N_2 = \frac{\varepsilon_3 - \alpha_{31}N_1}{\alpha_{32}}, \quad (15)$$

$$N_3 = \frac{\varepsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2}{\alpha_{13}} = \frac{\alpha_{32}\varepsilon_1 - \alpha_{12}\varepsilon_3 + [\alpha_{12}\alpha_{31} - \alpha_{11}\alpha_{32}]N_1}{\alpha_{13}\alpha_{32}}. \quad (16)$$

Since these expressions are in terms only of constant coefficients, the number of individuals are readily calculated. The numbers thus predicted agree with those which the N_i appear to be approaching after a long period of time in the model results to be presented. It was impossible to examine all possible combinations of coefficients which might satisfy equations (14), (15) and (16) mathematically. Furthermore, the difficulties in ecological interpretation of most coefficient combinations would not appear to justify the effort involved. The combinations of coefficients used in this study are of ecological interest, and the "equilibrium" predicted by equations (14) to (16) occurs when the number of one of the competing species, N_2 , approaches zero and, the number of the other, N_1 , approaches its maximum. However, this condition is not the only point of interest ecologically. Even though eventual extinction of the weaker species is predicted, it is not obvious from the steady-state formulation when this will occur, nor is it possible to determine how predation affects the period of time involved. In order to obtain answers to these questions, the dynamics of the system must be studied.

4. Model Results

A continuous systems modeling program (IBM, 1968) was written to solve this system of simultaneous non-linear differential equations (Appendix A) on an IBM 360/50 Data Processing System.

The program was utilized with assumed model coefficients which were believed to have some direct bearing on Paine's (1966) problem. In this model species 1 and species 2 compete, and comparisons are made of populations of these species with and without predation by species 3. To relate to Paine's case, the subweb might be assumed to consist of the acorn barnacles *Balanus glandula* and *Tetraclita squamosa* competing for space and the starfish *Pisaster ochraceus* eating them. The model coefficients were varied over a fairly wide range compatible with the data at hand which was estimated primarily from Paine (1966) and Thorson (1956).

The first computer run involved equal competition and no predation (i.e. $\alpha_{13} = \alpha_{31} = \alpha_{32} = 0$, $N_3 = 0$). The results of this run are shown in Fig. 1. The scales on this and all following figures are similar. That is, time

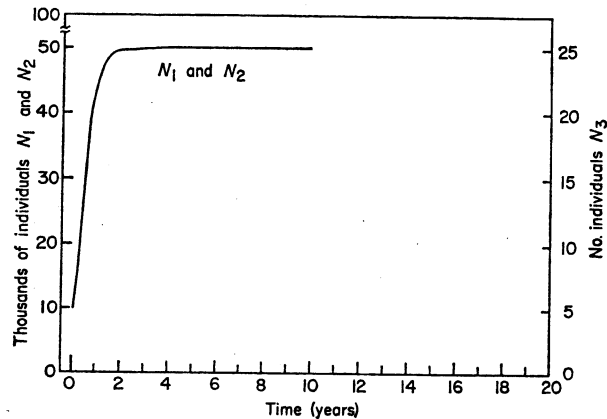


FIG. 1. Results of simulated equal competition between two species and no predation.

in years is shown on the abscissa and the numbers of N_1 and N_2 ($\times 10^3$) are shown on the left-hand ordinate and the numbers of the predator are shown on the right ordinate. Lines (curves) for each species are labeled on the figure. From Fig. 1 it is apparent that the two species increase together. They asymptotically approach some maximum and persist indefinitely. This first run involved equal competition, and ecologically it is not reasonable to expect exactly this condition in the real world.

INTERSPECIFIC COMPETITION

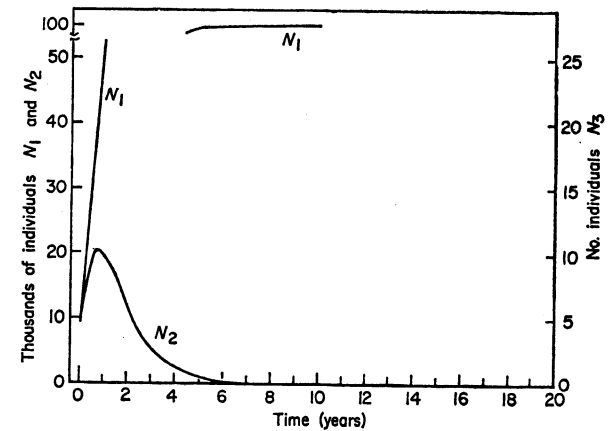


FIG. 2. Results of simulated competition between two species ($\epsilon_2 = 0.7\epsilon_1$) with no predation.

In Fig. 2 the results of a case involving no predation but giving species 1 a competitive advantage are shown. The advantage to species 1 was given by making its intrinsic rate of increase higher than that of species 2 (i.e. ϵ_2 is 30% less than ϵ_1). The results in Fig. 2 clearly show that species 2 would be virtually extinct after 10 years (only six individuals remaining). The break in the numbers of species 1 relates to data lying within the compressed left ordinate scale.

If species 3 (the predator) is added to the system described above with equal predation on both species, the results are as shown in Fig. 3. Both

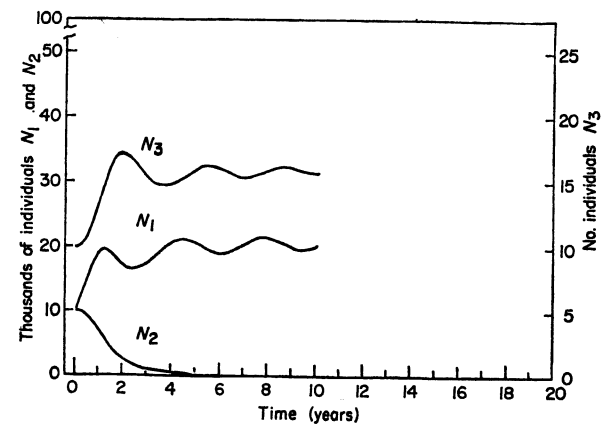


FIG. 3. Results of simulated competition between two species ($\epsilon_2 = 0.7\epsilon_1$) with equal predation on both species.

N_1 and N_2 are considerably lower than in the previous figure (Fig. 2). N_2 is reduced to one individual after 10 years. There are cyclic oscillations of both N_1 and N_3 , with N_3 lagging N_1 . The results resemble a damped Volterra predation equation with reference to N_1 and N_3 .

Next the competitive advantage of species 1 was reduced by making ϵ_2 (the intrinsic rate of increase) only 10% less than ϵ_1 , with no predation. The results are shown in Fig. 4. From this figure it is evident that N_2 does better for a while and appears to persist for a longer time, but eventually becomes extinct. If we superimpose the same predation as used previously (Fig. 3), the results are as shown in Fig. 5. It is evident that N_2 again dies out faster

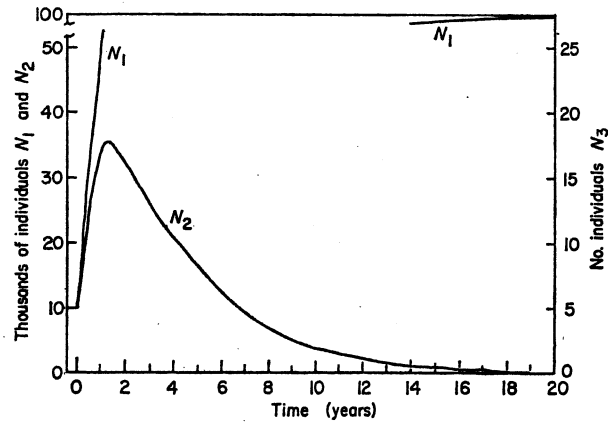


FIG. 4. Results of simulated competition between two species ($\epsilon_2 = 0.9\epsilon_1$) with no predation.

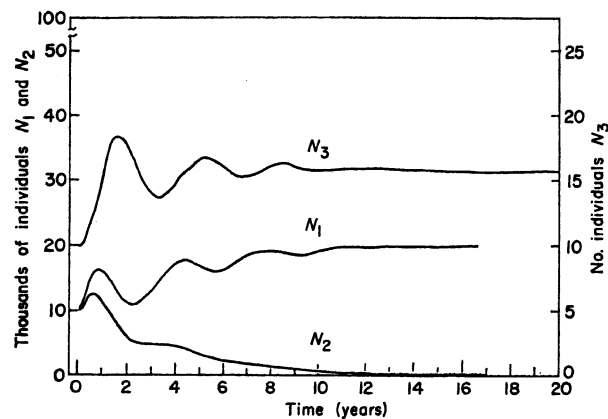


FIG. 5. Results of simulated competition between two species ($\epsilon_2 = 0.9\epsilon_1$) with equal predation on both species.

under predation. The results of the simulation modeling thus far do not indicate that predation (under the competitive conditions described) has any tendency to increase relative survival and thus increase species diversity. Up to this point only the ϵ coefficients, which relate to intrinsic rates of increase, were altered.

The next approach involved giving species 1 a competitive advantage manifested in a self-limiting factor. The coefficient α_{11} was set at a value 10% less than α_{22} . With all other factors equal and similar to those above and without predation, the model results shown in Fig. 6 were obtained.

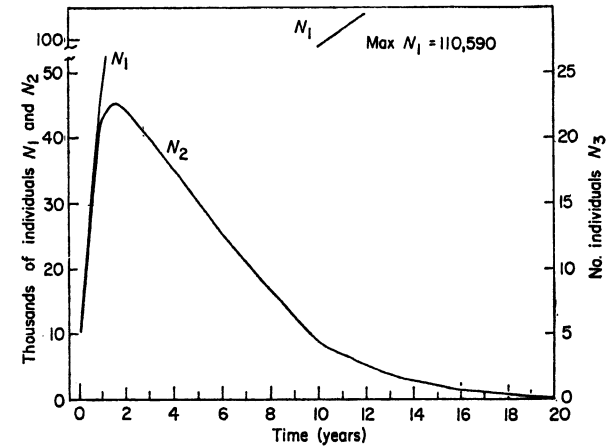


FIG. 6. Results of simulated competition between two species ($\alpha_{11} = 0.9\alpha_{22}$) with no predation.

The results show only that N_2 persists somewhat longer than under the conditions of Fig. 4. If we now add a predator to the system, the results are as shown in Fig. 7. This figure illustrates dramatic changes in the relative populations of N_1 and N_2 after a few years. Also, the much greater absolute numbers of N_2 even after 20 years, are of interest. It seems that under the conditions described, N_2 is virtually extinct in 20 years without predation (Fig. 6). On the other hand, under identical conditions, except with predation, N_2 is at a relatively high numerical value with little indication of change over the time span considered (Fig. 7).

Another competitive coefficient examined was the limiting effect of the other competing species (α_{12} and α_{21}). If α_{12} is reduced to 10% less than α_{21} , it is found that N_2 survives better and remains larger compared to N_1 even after several years. Figure 8 illustrates the case of α_{12} being 10% less

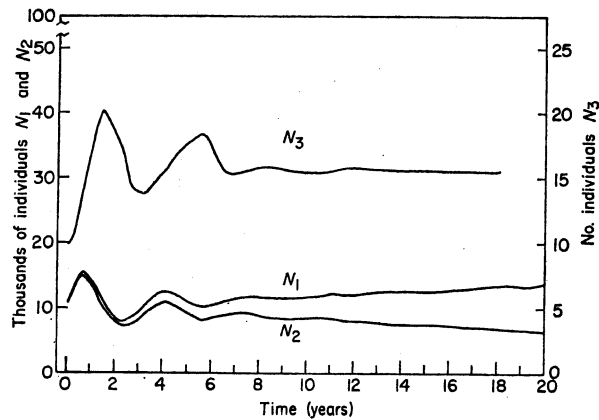


FIG. 7. Results of simulated competition between two species ($a_{11} = 0.9a_{22}$) with equal predation on both species.

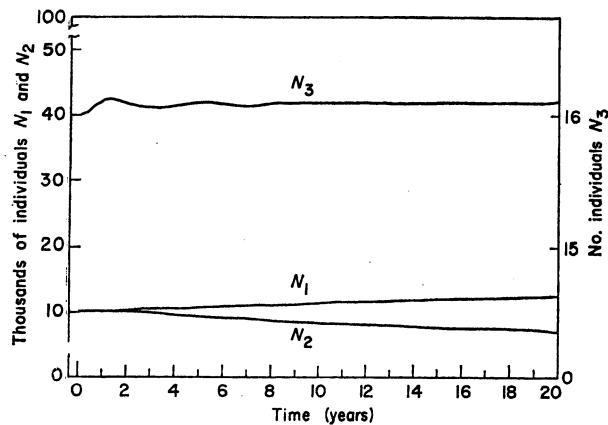


FIG. 8. Results of simulated competition between two species ($a_{12} = 0.9a_{21}$) with equal predation on both species.

than the other coefficients with equal predation on both species. Also, this figure illustrates a case where the system is started near "equilibrium": where the values of dN_1/dt , dN_2/dt and dN_3/dt are not large at time zero. In the other figures the system was initialized with relatively large positive values of dN_1/dt and dN_2/dt . The larger initial values better illustrate the possible dynamics of the system and are also believed to be reasonable values in the real world. In Fig. 8 some of the oscillations of the system are eliminated by modifying the initial conditions. In this case the value of

N_3 (predator) was increased from 10 to 16 at time zero. It should be pointed out that the basic effect of predation is not changed. Runs with and without early oscillations show very nearly the same N_1 and N_2 after 20 years. The positive effect of predation on N_2 is still apparent. It is also apparent that the predator still shows small cycles, and dN_1/dt and dN_2/dt cycle as well.

5. Discussion

Although it would be possible to exercise the model under other sets of conditions, the results to date are adequate to lend support to Paine's hypothesis. Figure 9 is a summary of results. In this figure the ratio N_1/N_2 is plotted on a logarithmic scale vs. time on a linear scale. N_1/N_2 can be considered a crude index number related to the inverse of species diversity in the models. That is, as the ratio N_1/N_2 increases, the species diversity tends to decrease. At some extremely high value of N_1/N_2 species 1 would

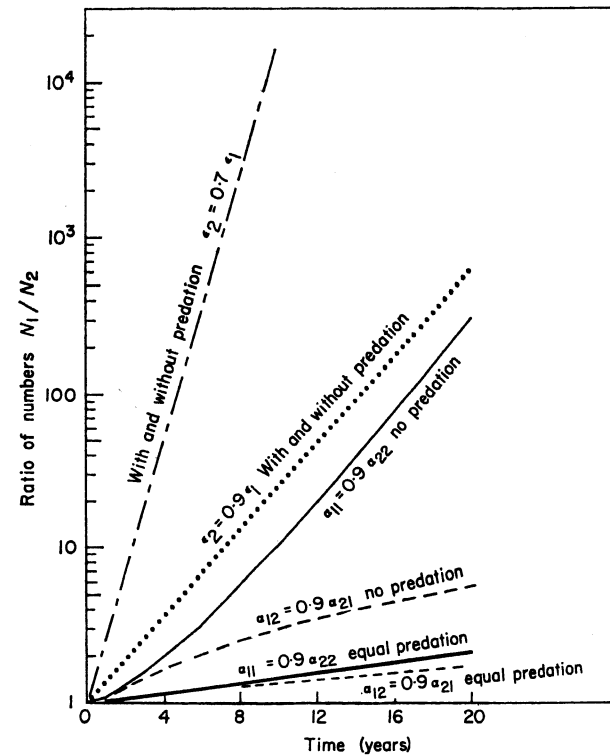


FIG. 9. Theoretical time history of species diversity as measured by the ratio N_1/N_2 under the various conditions studied.

be completely dominant and species 2 would be scarcely measurable. At this point the ecosystem would effectively have decreased from three species to two. From Fig. 9 it is evident that when N_1 has a competitive advantage in its biotic potential ε_1 , predation greatly decreased total numbers but did not affect the ratio N_1/N_2 . In the case where N_1 has a competitive advantage in α_{11} (its self-limiting factor), predation can greatly decrease the ratio. After 20 years we found that $N_1/N_2 \approx 310$ without predation and $N_1/N_2 \approx 2.15$ with predation. For the time span considered it is suggested that this difference indicates a greater species diversity with predation than without predation.

The overall results of the modeling with several combinations of values of model coefficients, as indicated by the figures, showed a tendency toward "equilibrium" only as N_2 tended toward zero. Gause's Principle of "one niche—one species" persists when there are no perturbations by influences outside the model and when measured on an evolutionary time scale. However, these studies clearly indicate that two species may theoretically persist in the same niche under predation for a much longer time than they would without predation. With a proper choice of model coefficients this time span of coexistence may be very long on a humanly observable scale.

It is also possible to consider the outcomes of some simple models of competition between two species with predation by deriving analytical expressions describing the rate of change of N_1/N_2 (or $\log N_1/N_2$) as a function of time. The following expressions were derived:

$$\frac{d[\log N_1/N_2]}{dt} = \varepsilon_1 - \varepsilon_2 + (\alpha_{21} - \alpha_{11})N_1 + (\alpha_{22} - \alpha_{12})N_2 + (\alpha_{23} - \alpha_{13})N_3. \quad (17)$$

For the general case, this expression [equation (17)] is still difficult to handle. However, for the simple competitive examples considered the expressions become more tractable. If all the α coefficients are equal for the two species, the simplified expression can be integrated to give:

$$N_1/N_2 = N_1/N_{2(\text{initial})} e^{(\varepsilon_1 - \varepsilon_2)t}. \quad (18)$$

Equation (18) is an expression for the ratio N_1/N_2 as a function of time. N_1/N_2 was unity initially in the computer runs with the ε coefficients as constants. It can be seen from equation (18) that predation cannot affect this expression, and this is of course a check on the validity of the computer analysis. Now if all coefficients are equal except α_{11} , equation (17) becomes:

$$\frac{d[\log N_1/N_2]}{dt} = [\alpha_{21} - \alpha_{11}]N_1 \quad (19)$$

which describes competition only in α_{11} with no predation or equal predation. Equation (19) describes the rate of change of $\log N_1/N_2$. The ratio N_1/N_2 increases when $\log N_1/N_2$ increases, and $\log N_1/N_2$ is a linear function

of N_1 . With predation, N_1 is smaller and therefore the rate of increase of the ratio is smaller. Similarly, if all coefficients are equal except α_{12} , equation (17) simplifies to:

$$\frac{d[\log N_1/N_2]}{dt} = [\alpha_{22} - \alpha_{12}]N_2. \quad (20)$$

In equation (20) the rate of increase of the ratio N_1/N_2 is a function of N_2 . With predation N_2 is also smaller. Hence, the rate of increase of the ratio is also smaller.

6. Conclusions

The results obtained from this model study lend qualified support to Paine's (1966) theory of increased local species diversity under predation. These results also demonstrate that the effects of predation upon diversity among competing species depend heavily upon the nature of the competition.

To a resource manager the concept of a balanced or equilibrium population is measured in terms of a relatively short time scale. For example, Silliman (in press) has developed analog computer models of competing fish species which are compared with empirical data for relatively short periods of time (i.e. a few decades, at most). The theory enunciated by Paine and examined further in this report may have considerable application in resource management studies—especially those related to aquatic resources. It is suggested, for example, that critical studies of the characteristic decline of fishing in newly-established ponds and reservoirs over time may demonstrate how selective removal of predators results in a decline in species diversity and later overpopulation by one or more of the competing forage species. Work on fish populations in small ponds, such as that summarized by Swingle (1953) may lend itself to comparisons of Paine's hypothesis with empirical data.

It is recognized that the model developed in this report is idealized, and this limitation has often been justly emphasized in criticisms of analytical population dynamics models. However, the system modeling technique (CSMP) used in the report lends itself to much more complex models which can include such effects as seasonal cycles, spawning, catastrophic mortality, etc. The limitation to realism of systems examined now appears to rest with the biological data available and not with the analytical tools.

REFERENCES

- DOI, T. (1962). *Bull. Tokai reg. Fish Res. Lab.* 32, 49.
 GAUSE, G. F. (1935). *Actual. scient. ind.* 277, 1.
 GAUSE, G. F. & WITT, A. A. (1935). *Am. Nat.* 69, 596.

- HUTCHINSON, G. E. (1961). *Am. Nat.* **95**, 137.
 IBM, 1968. System/360 Continuous System Modeling Program (360A-CX-16X) User's Manual H20-0367-2.
 KOSTITZIN, V. A. (1939). "Mathematical Biology." London: Harrap.
 LARKIN, P. A. (1963). *J. Fish. Res. Bd. Can.* **20**, 647.
 LARKIN, P. A. (1966). *J. Fish. Res. Bd. Can.* **23**, 379.
 PAINE, R. T. (1966). *Am. Nat.* **100**, 65.
 SILLIMAN, R. P. (1969). *Trans. Am. Fish. Soc.* **98**, 560.
 SWINGLE, H. S. (1953). *Bull. Ala. agric. Exp. Stn.* **274**, 1.
 THORSON, G. (1958). In "Perspectives in Marine Biology", p. 67 (A. A. Buzzati-Traverso, ed.). University of California Press.
 VOLTERRA, V. (1928). *J. Cons. perm. int. Explor. Mer.* **3**, 1.

Appendix A

SAMPLE CSMP COMPUTER PROGRAM FOR SOLUTION OF A SINGLE CASE

****CONTINUOUS SYSTEM MODELING PROGRAM****
 PROBLEM INPUT STATEMENTS

```
INITIAL
INCON      IC1 = 10000-0, IC2 = 10000-0, IC3 = 10-0
PARAM      E1 = 3-22, A11 = 3-22E-05, A12 = 3-22E-05, A13 = 0-0, E2 = 3-22, ...
            A21 = 3-22E-05, A22 = 3-22E-05, A23 = 0-0, E3 = 0-0, ...
            A31 = 0-0, A32 = 0-0

DYNAMIC
            N1DOT = N1*(E1-A11*N1-A12*N2-A13*N3)
            N1 = INTGRL(IC1, N1DOT)
            N2DOT = N2*(E2-A21*N1-A22*N2-A23*N3)
            N2 = INTGRL(IC2, N2DOT)
            N3DOT = N3*(-E3 + A31*N1 + A32*N2)
            N3 = INTGRL(IC3, N3DOT)

PRTPLT
TIMER      N1(N2,N3,N1DOT), N2(N1,N3,N2DOT), N3(N1,N2,N3DOT)
END
PARAM      FINT IM = 10-0, OUTDEL = -05

END
STOP

OUTPUT VARIABLE SEQUENCE
N1DOT N1      N2DOT N2      N3DOT N3
OUTPUTS INPUTS PARAMS INTEGERS + MEM BLKS FORTRAN DATA CDS
10(500) 27(1400) 16(400) 3+ 0= 3(300) 7(600) 11
```

A Stochastic Development of the Reversible Michaelis-Menten Mechanism

P. J. STAFF

*The University of New South Wales,
 Kensington, New South Wales, Australia*

(Received 14 October 1968, and in revised form 9 October 1969)

A stochastic model for the reversible one substrate-one intermediate-one product enzymic mechanism is developed, from which an exact solution is found for the bivariate distribution of substrate and product at equilibrium. As the marginal distributions of all species are available, equilibrium properties of the system are examined. An approximation method is demonstrated which utilizes the deterministic prediction, negligibly different from the stochastic mean, in providing an approximation for the variance of the enzyme variate. Calculation of the moments of substrate and product is simplified by relationships derived in terms of the enzymic mean and variance. In systems of physical interest, where the numbers of reactant molecules are large, the relative fluctuations are small.

1. Introduction

The classical mathematical formulations for analysing and studying kinetic data of chemical and biochemical reactions are deterministic in nature. In these models, the concentrations of the components are continuous mathematical variables expressible as real-valued functions of the time after initiation of the reaction. The transformations of individual molecular species and complexes are thus traced en masse, as the description is not sufficiently refined to treat individual molecular events. Of course, random fluctuations, which would necessarily occur from physico-chemical arguments, are not accounted for in the predictions given by the deterministic approach and for their consideration, one must turn to the corresponding stochastic approach. In the early part of this century, Michaelis & Menten (1913) established the hypothesis that the mechanism of enzyme catalysis in which substrate is converted to product, could be described by the stoichiometric equations



where, E, S, ES, P represent the enzyme, substrate, enzyme-substrate and