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EXPLOITATION EFFECTS UPON INTERSPECIFIC RELATIONSHIPS IN MARINE ECOSYSTEMS[1]

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ABSTRACT

Due to man's continuing efforts to extract greater harvests of marine organisms from the world ocean, it is becoming increasingly important to be able to predict the consequences of exploitation on complex assemblages of organisms. These assemblages, or ecosystems, consist of predator and prey organisms in various interacting combinations. Preliminary evidence available from studies of marine invertebrate communities in coastal areas has indicated that removal of grazing herbivores or predators at various levels results in lower species diversity and greater instability of the ecosystem. In order to permit a quantitative evaluation of the effects of various rates and types of exploitation on interspecif relationships, model ecosystems were constructed utilizing a subset of graph theory as applied to network analysis. A basic ecological trophic unit was formulated, and these units were combined to form more complex model ecosystems. In particular, a hypothetical four species system of interacting predator and prey organisms was analyzed to demonstrate the consequences of varying certain model coefficients, especially rates of exploitation. It was shown that nonselective exploitation tended to maintain stability of the system better than highly selective exploitation. A hypothetical example of an empirical approach for examining changes in community structure was also demonstrated.

Much of the present theory of fisheries science as well as many practical fisheries management techniques are based on the concept of a single species or unit stock (Beverton and Holt, 1957; Ricker, 1958). This approach continues to be useful in describing and predicting the behavior of fisheries consisting primarily of a single species. Recently, Walters (1969) developed a deterministic computer simulation model for determining optimum harvest strategies based on a unit stock. However, modern fishing seems to be progressing toward exploitation on many species of the larger animals in aquatic ecosystems. To some extent this is due to the tendency toward reduction to meal of many species of fishes. Some obvious areas for the future development of marine fisheries will be in tropical or subtropical waters, such as parts of the Indian Ocean as well as the southeast and southwest Atlantic. These areas are characterized by a relatively greater diversity of species than the traditional fishing grounds of north-temperate regions. It can reasonably be expected that some species will be exploited intensively from them. It therefore seems desirable to attempt to better understand trophic relations of ecosystems consisting of several interacting species in order to develop management techniques for these systems. This increased understanding includes the effects of various kinds of exploitation strategies as well as environmental perturbations on these ecosystems. It is suggested that stresses applied to ecosystems may produce somewhat similar effects, regardless of their origin.

Some of the large volume of literature concerning diversity and stability in terrestrial as well as aquatic ecosystems has been reviewed at a recent symposium (Woodwell and Smith,

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1969). One of the generalizations which appeared to emerge from the symposium was that ecosystems characterized by high species diversity tended to be relatively stable. Elton (1958) has shown that if a predator has several alternate prey species to utilize, it will persist even if one of the prey becomes very scarce. Thus, it seems as if there is some correlation between diversity and stability.

In the case of marine invertebrates, there is some observational evidence (Paine, 1963) to indicate that marine predators at high levels in the food chain feed on more species of prey than do those on lower levels. Observations, such as the above mentioned, have led some ecologists to suggest that high level predators might contribute more to community stability than the lower level predators.

Removal of predators from rocky shore invertebrate communities (Paine, 1966) resulted in a reduction of the species diversity of the animal community. In addition, removal of grazing herbivores from rocky shores has resulted in the rapid growth of some of the formerly eaten plant species and a change in community composition toward lower species diversity (Jones, 1948; Southward, 1964; Paine and Vadas, 1969). The observations and experiments of Paine (1966) also indicated that diversity among competing species of marine invertebrates could be decreased by removal of predators in some instances. A theoretical dynamic analysis (Parrish and Saila, 1970) of a trophic subweb using Lotka-Volterra type interactions offered some support to Paine's conclusions.

With the exception of some pioneering conceptual work by Larkin (1963, 1966) in describing models for interspecific competition and exploitation applied to natural fisheries, very little seems to have been done in an effort to predict the effects of man's activities on aquatic communities consisting of several interacting species. One of the reasons for this appears to lie in the degree of complexity required to establish and express all the basic interrelationships in such a system (Mann, 1969). Recently, Menshutkin (1969) suggested graph theory as a useful tool for minimizing some of the difficulties of constructing models of interacting systems if certain simplifying assumptions, such as linearity and steady-state conditions, could be tolerated. Recognizing that any set of mathematical equations represents at best a crude approximation of the actual behavior of complex ecosystems and that empirical values of coefficients for complex models are largely unavailable, we have proceeded under the assumption that the simplest models should first be explored and carefully evaluated before proceeding to more elaborate formulations. In addition, it is believed that the simplicity of the methods described herein may enhance their utility, especially when considering the initial effects of exploitation or environmental modification on interacting ecosystems.

The objectives of this work were to: (a) introduce a subset of graph theory as used in network analysis; (b) describe a graph theoretic formulation of a basic ecological trophic unit, and to demonstrate some effects of predation and exploitation on model ecosystems consisting of these units; and (c) demonstrate some other uses of graph theory with a view toward stimulating further interest in its applications.

BACKGROUND AND DEVELOPMENT

By definition, a graph is a set of vertices (nodes) connected by a set of edges (branches). If the graph has polarity or direction, the edges have arrows, and the graph is said to be directed. In this report we are concerned only with directed graphs. Two very simple directed graphs are illustrated in Figure 1.

The ecological graphs utilized herein are based largely on graph theoretical techniques of network analysis, for which the theory has been clearly and concisely presented by Mason and Zimmermann (1960). To analyze a network, each edge connecting two vertices is given a coefficient, a "transfer function" or "branch transmission." The "transmission" from one vertex A to a distant one C can then be expressed as a combination of these individual coefficients. The important principle is that the value of any vertex is the sum of the directed inputs, regardless of the outputs. In the very simple case of Fig-

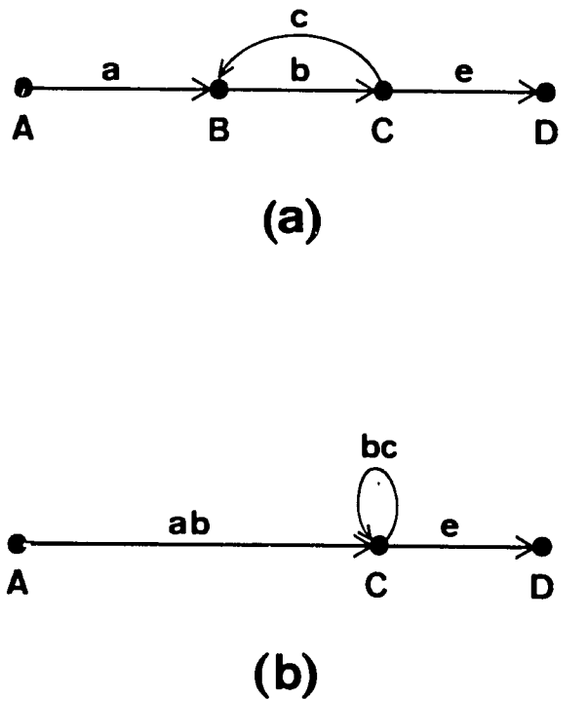


FIGURE 1.—An illustration of two simple directed graphs. A "self-loop" is shown in part (b) of the figure.

ure 1(a), the value of B is equal to the input from A plus the input from C:

$$B = aA + cC. \quad (1)$$

Similarly, the value of C is equal to the only input:

$$C = bB. \quad (2)$$

Substituting B from Equation (1) into Equation (2) and solving for C gives:

$$C = \frac{abA}{1-bc}. \quad (3)$$

Thus the ratio of the value of C to the value of A is:

$$\frac{C}{A} = \frac{ab}{1-bc}, \quad (4)$$

which is the transmission from A to C. This type of term is used later as a biomass ratio or "trophic efficiency."

It can easily be seen that the graph in Figure 1 simply represents a set of linear algebraic equations. Such sets of equations can, of course, be solved classically. However, solution by inspection of some graphs or parts of graphs is possible. For example, in the graph of Figure 1(a), observe that:

$$C = (a \times b) \times A + (c \times b) \times C. \quad (5)$$

The graph can be simplified to that shown in Figure 1(b). A "self-loop" has been created that has the effect of making the value of C to be $\frac{1}{1 - \text{loop transmission coefficient}}$ times what it would have been without the loop. The situation becomes only slightly more complex when the transmission from A to D is considered. The value of D can be obtained from the value of C in Equation (3) as:

$$D = eC = e \cdot \frac{abA}{1-bc}. \quad (6)$$

Or, making use of the known effect of a self-loop, it is possible to simply see by inspection of Figure 1(b) that:

$$D = (abe)A \cdot \frac{1}{1-bc} = e\,\frac{abA}{1-bc} \quad (7)$$

These simple principles and techniques are considered adequate for formulating some useful trophic graphs.

GRAPH OF A TROPHIC UNIT

Graph theory has been applied to the analysis of a variety of problems in engineering, operations research, and the social sciences (Berge, 1958; Busacker and Saaty, 1965; Kaufmann, 1967; Harary, 1969). Its use in biological sciences has been much more limited. However, Benzer (1959) and Maruyama and Yasuda (1970) have applied these concepts to genetics, and Landau (1955) and Trucco (1957) have used graph theory in describing animal behavioral problems. Menshutkin (1969) appears to have been the first to apply graph theory to the study of communities of aquatic organisms. He used graph theory to derive expressions to illustrate the relationship of the biomass of harvested organisms (fish) to primary production under

specific conditions. He graphed the relationship between a prey and a predator as shown in Figure 2(a). For simplicity, all the vertices (capital letters) can be standardized in energy units (or energy per unit time). The lower case coefficients are dimensionless constants or have a dimension of reciprocal time with values between zero and 1.0. Vertices and coefficients are listed in Table 1. Subscript 1 refers to the prey and subscript 2 refers to the predator. When another trophic level is added later, use of these subscripts can be easily extrapolated. For example, D_{12} in Figure 2(a) is the amount of Prey 1 accessible to Predator 2; D_{24} in a later graph is the amount of Prey 2 accessible to Predator 4.

The symbols used in Figure 2 are further defined in the following manner.

TABLE 1.—Description of the vertices and coefficients utilized in model development.

P	= (net) production	
Q	= loss by "respiration"	
q	= "respiration" coefficient	$Q = qB$
B	= biomass	
M	= loss by natural mortality	
m	= natural mortality coefficient	$M = mB$
F	= loss by exploitation (fishing)	
f	= exploitation coefficient	$F = fB$
U	= loss in undigested or unassimilated food	
R	= actual food ration	$U = (1 - k)R$
kR	= food assimilated (gross production)	
k	= digestion or assimilation coefficient	
P	= $kR - Q$	
D_{12}	= accessible food	
d_{12}	= accessibility coefficient	$D_{12} = d_{12}B_1$
H_{12}	= maximum ration (most a predator would ever consume)	
h_{12}	= maximum ration coefficient	$H_{12} = h_{12}B_2$
R_{12}	= $a_{12}H_{12} + b_{12}\delta_{12}$	
δ_{12}	= $D_{12} - H_{12}$	
$\left\{\begin{matrix} a_{12} \\ b_{12} \end{matrix}\right.$		feeding coefficient

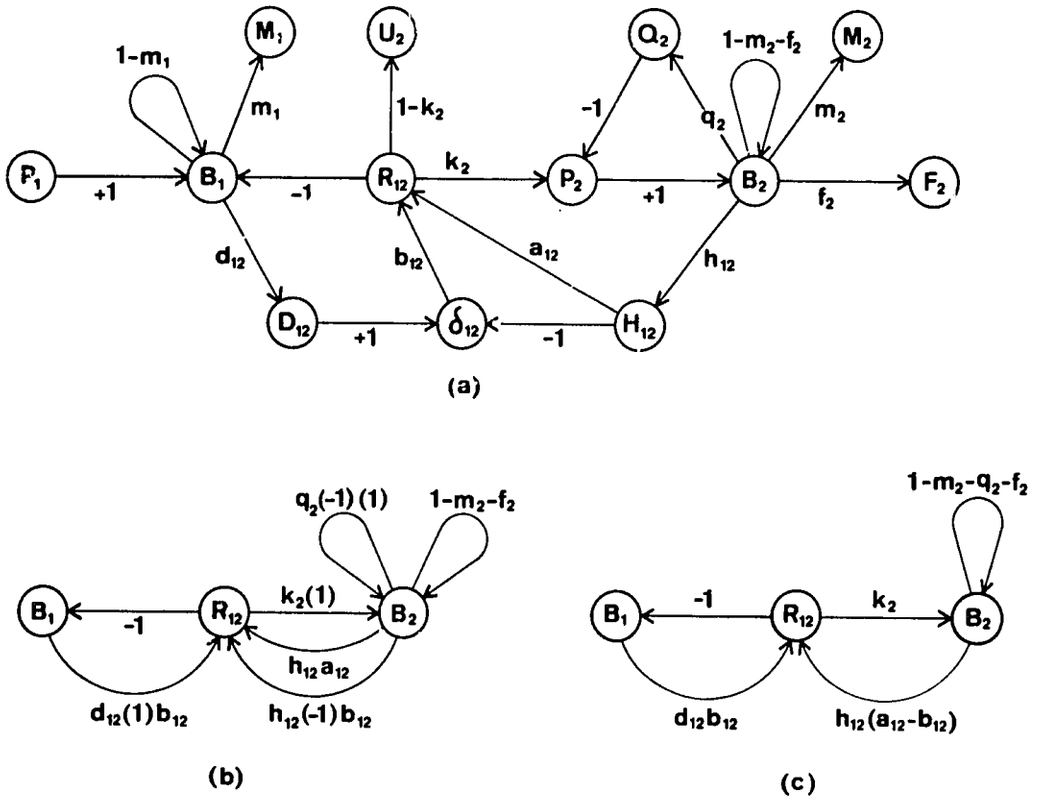


FIGURE 2.—Trophic graphs of Species 2 preying on Species 1. Part (a) illustrates Menshutkin's (1969) original formulation, and parts (b) and (c) represent the successive application of network analysis to obtain the basic trophic unit.

P in the graph is what is usually called net production (an energy rate). Net production P, is equal to gross production, i.e., assimilated food, kR, minus respiration, Q. Summing inputs at the graph vertex P_2, the value of P_2 is:

$$P_2 = k_2R_{12} - Q_2 . \qquad (8)$$

Respiration, Q, is expressed as the product of biomass and a "respiration coefficient," q:

$$Q = qB,$$

where B is the biomass (standing energy crop) of a species.

M is natural mortality, considered proportional to biomass;

$$M_1 = m_1B_1, \qquad M_2 = m_2B_2. \qquad (9)$$

Constancy of these coefficients is assumed.

F is fishing mortality which is used if an exploited population is considered. Death due to any other specific cause can be separately considered in a similar manner.

U is energy in the undigested (unassimilated) portion of food eaten, and k is the "digestion coefficient." The predator assimilates a fraction k of the ration R eaten, and the remaining energy, $U = (1 - k)R$, is lost.

Upon first inspection of the graph, it may be disconcerting to see vertices representing quantities such as biomass (energy) in the graph with vertices representing quantities such as production (energy per unit time). The confusion is resolved by realizing that the graph is not a pure flow network. It merely shows some assumed relationships, and at each vertex the same rules apply. For example, at vertex B_1 in Figure 2(a):

$$B_1 = (+1)P_1 + (-1)R_{12} + (1 - m_1)B_1, \qquad (10)$$

or,

$$P_1 - B_1 + B_1 - m_1B_1 = R_{12}. \qquad (11)$$

Net production — Natural mortality = Remainder eaten by predators.

Thus interpreted, the graph represents the relationships correctly.

An important feature of this formulation is the attempt to approximate the density dependence of feeding rate. Formulations for species interactions such as the classic equations of Lotka and Volterra express rates of change of the number or biomass of a species as products of coefficients and numbers or biomass of the interacting species. This approach has involved the assumption that feeding rate is independent of the abundance of prey and it is an oversimplification which results in an inherently unstable system. The experimental work of Ivlev (1961) provided a density-dependent feeding relation:

$$R = H\,(1 - e^{-\eta p}), \qquad (12)$$

where: H = the "maximum ration" of the predator, the most it would ever eat (or the maximum rate at which it would feed) no matter how much food were available;

R = the "actual ration" of the predator, the amount actually eaten (or the rate at which it feeds) under an actual condition of food availability;

p = the density or biomass of the prey population;

and η = a coefficient.

A linear approximation of this relationship, following Menshutkin (1969), can be used in the graph model. A parameter δ_{12} is defined as:

$$\delta_{12} = D_{12} - H_{12} , \qquad (13)$$

where: D_{12} = the amount of the prey biomass accessible to the predator $D_{12} = d_{12}B_1$. A constant of proportionality to prey biomass is assumed.

H_{12} = as defined above. Since H_{12} is obtained as a fraction of predator biomass ($H_{12} = h_{12}B_2$), the assumption is introduced that all predator individuals feed at the same rate.

The "actual ration" of the predator is then defined as:

$$R_{12} = a_{12}H_{12} + b_{12}\delta_{12} , \qquad (14)$$

where a_{12} and b_{12} are fractional coefficients.

This linear expression is used to approximate the following modification of Ivlev's exponential relation:

$$R = H(1 - e^{-\frac{\xi D}{H}}), \qquad (15)$$

where D and H are defined as before.

The implementation of Equation (14) in the graph of Figure 2(a) is seen by summing inputs at vertex δ_{12}:

$$\delta_{12} = (+1)D_{12} + (-1)H_{12} = D_{12} - H_{12}, \qquad (16)$$

and at vertex R_{12}:

$$R_{12} = a_{12}H_{12} + b_{12}\,\delta_{12}\,. \qquad (17)$$

Although lacking in mathematical rigor, this linear approximation can be made to give reasonably accurate results over a limited range of prey density, and it is considered to be an improvement over the simple density-independent assumption. Figure 3 provides a sample comparison of an Ivlev exponential relationship according to Equation (15) with the linear approximation of Equation (14). The coefficients a and b should, of course, be chosen in any real case to approximate either a desired analytic function of known utility or a set of data on feeding observations.

The "network analysis" techniques described previously were applied to the graph of Figure 2(a) to produce the simplified graphs shown as Figure 2(b) and Figure 2(c). The derivations

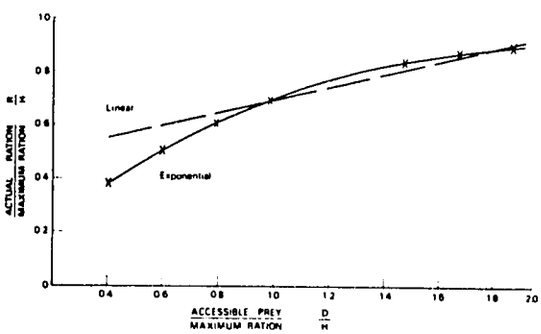


FIGURE 3.—Linear and exponential approximations of feeding behavior.

used do not require P_1 or m_1. Furthermore, M_1, M_2, and U_2 cannot give "inputs" at any vertex since they are all directed outward. Therefore, the above parameters were eliminated with no effect on the solutions. Vertices P_2 and Q_2 were absorbed using graph theory network techniques to produce Figure 2(b). The same figure shows the similar absorption of vertices D_{12}, δ_{12}, and H_{12}. Parallel inputs to a vertex can be combined. In this case, the two self-loops at vertex B_2 were combined, and the two edges from B_2 to R_{12} were combined. The resulting simplified graph, Figure 2(c), is the most basic graph that expresses the assumed relationships.

The above formulation describes a two-species predation model where Species 2 preys on Species 1. At this trophic level, and for the formulations to be used, the term "predation" is applied in its broadest sense. Since the formulation does not make use of production, mortality or any other vital property of Species 1, Species 1 is really just a resource. It could be vegetation, or with some reinterpretation of coefficients, even living space. Clearly, the above graph is a building block from which a variety of more complex food webs can be constructed. Only limited applications of this concept are made in the following material, and its validity awaits the test of further applications.

SOME MODELS AND THEIR INTERPRETATION

Since relatively little observational information is available concerning the important problem of community interactions, it was believed that a model study such as this might assist in a further understanding when additional observational data are taken.

Competitive and predatory interactions, with and without exploitation, were examined using trophic graphs made from the building block developed previously. Figure 4 shows Species 2 and Species 3 competing in their utilization of resource B_1. A relation was derived for the ratio of the biomass of each of the competitors to that of the resource: B_2/B_1 and B_3/B_1. In either case this was done by writing the very simple linear equations for each of two vertices

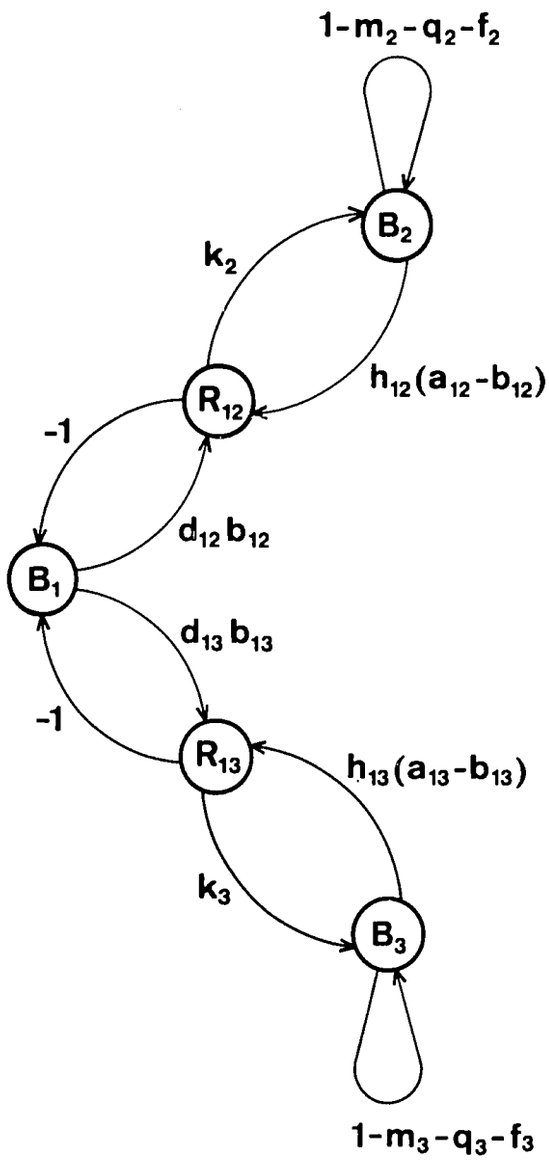


FIGURE 4.—Trophic graph of Species 2 and Species 3 preying on Species 1.

and solving them simultaneously in the classical manner. For competitor Species 2, R_{12} was written as the sum of its inputs in the graph, and B_2 was written as the sum of its own inputs. In this case there are two equations in the three variables B_2, B_1, and R_{12}. R_{12} was eliminated to give B_2/B_1 in terms of coefficients. B_3/B_1 was derived in a similar manner, and division gave the ratio of the biomass of the two competing species B_2/B_3 as follows:

$$\frac{B_2}{B_3} = \frac{k_2 d_{12} b_{12} V}{k_3 d_{13} b_{13} V'} \qquad (18)$$

where: $V = m_3 + q_3 + f_3 - k_3 h_{13}(a_{13} - b_{13})$
$V' = m_2 + q_2 + f_2 - k_2 h_{12}(a_{12} - b_{12})$

Inspection of Equation (18) reveals that if the two species compete exactly equally, or are exploited equally, the ratio is unity. This is entirely the expected result. By giving one species or the other a competitive edge in one or another of the coefficients, it is apparent that the B_2/B_3 ratio can be changed.

The simplest subweb involving predation on two competing species is shown in Figure 5. In this subweb Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1. The procedure for deriving the ratios B_2/B_1 and B_3/B_1 was exactly as described above. That is, an equation was written for each

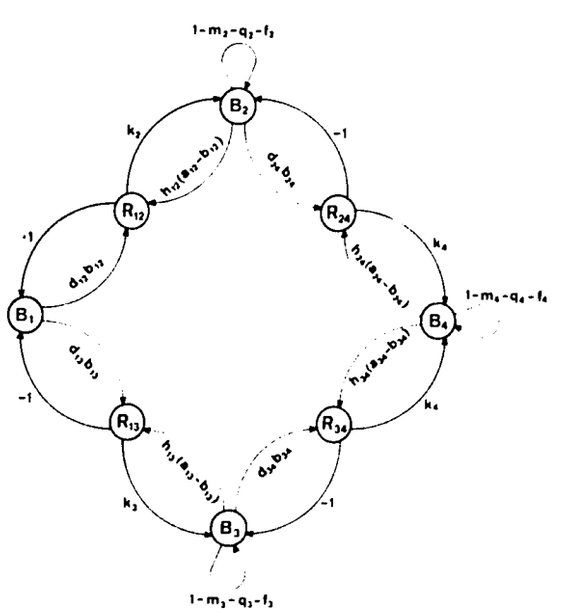


FIGURE 5.—Trophic graph of a 4-species subweb. In this case Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1.

vertex except B_1, and the equations were solved simultaneously. In this case there are seven equations, and the work of classical solution was not excessive. The result was found to be:

$$\frac{B_2}{B_3} = \frac{W - k_2 d_{12} b_{12} (XY + Z)}{W' - k_3 d_{13} b_{13} (XY' + Z')} \quad (19)$$

where:

$$\begin{aligned}
W &= k_3 k_4 d_{13} b_{13} d_{34} b_{34} h_{34} (a_{24} - b_{24}) \\
W' &= k_2 k_4 d_{12} b_{12} d_{24} b_{24} h_{34} (a_{34} - b_{34}) \\
X &= k_4 h_{24} (a_{24} - b_{24}) + k_4 h_{34} (a_{34} - b_{34}) \\
&\quad - n_4 - q_4 - f_4 \\
Y &= k_3 h_{13} (a_{13} - b_{13}) - d_{34} b_{34} - m_3 - q_3 - f_3 \\
Y' &= k_2 h_{12} (a_{12} - b_{12}) - d_{24} b_{24} - m_2 - q_2 - f_2 \\
Z &= k_4 d_{34} b_{34} h_{34} (a_{34} - b_{34}) \\
Z' &= k_4 d_{24} b_{24} h_{24} (a_{24} - b_{24})
\end{aligned}$$

Questions of interest here were the effects on biomass ratios of the competitors as a function of various competitive coefficients and exploitation, and the difference in these effects with and without predation on the competitors. "Coefficient" values from Menshutkin (1969) were introduced for the coefficients for predation by Species 4 on Species 2 and Species 3 (the same coefficients for both—equal predation). Basically the same coefficients were used for the competition of Species 2 and Species 3 as well. Coefficients were held constant except for the one whose effect was being considered. Using such values, the equations were simplified, and in most cases Species 3 was then given the nominal value of the competitive variable of interest while the value of that variable for Species 2 was made to vary above and below the nominal. This range of variation of Species 2 was expressed as the ratio coefficient 2/coefficient 3. The same process was performed for the earlier formulation without predation (Equation 18). Thus ratios B_2/B_3 were obtained from both cases—with and without predation.

A brief examination was made of the effect of various exploitation strategies on the relative stability of two model ecosystems, one with predation and one without predation. These systems are described by Equations (18) and (19), and stability was measured by the change in biomass. Figure 6 illustrates the results of various types of exploitation on the two systems. It is

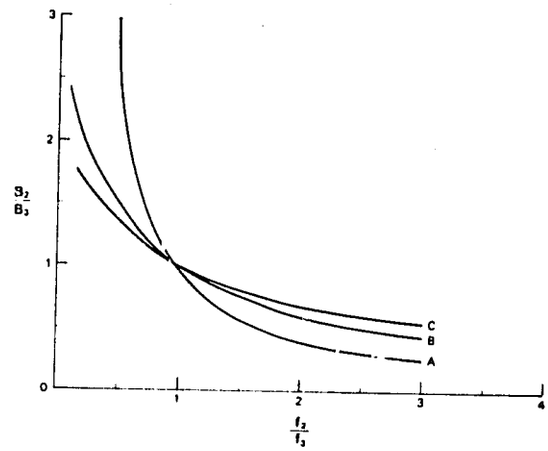


FIGURE 6.—Effects of predation and exploitation on model ecosystem stability as measured by biomass ratios. Curve A illustrates a 4-species subweb in which there is no exploitation of the top predator. Curve B illustrates a 3-species subweb with no top predator. Curve C illustrates a 4-species subweb with exploitation of the top predator as well as prey species 2 and 3. All numerical values of coefficients are from Menshutkin (1969). The nominal value of f_3 was taken as 0.3.

apparent from an examination of this figure that the most stable conditions examined involved predation as well as exploitation of the predator and the prey species. However, the system involving no top predator seemed to be more stable under exploitation of both prey species than the system involving predation, but with no exploitation of the top predator.

For different types of competitive advantage of one species over the other, the effect of predation on biomass ratios may be very different. Figure 7 demonstrates the effect of unequal competition in the coefficient d, which relates to the availability of the resource to Species 2 and Species 3. Without predation, the ratio B_2/B_3 of biomasses of the competitors is always the same as their d ratio. With predation, the ratio takes the much different form indicated. The values used for the d_{12}/d_{13} ratio ranged from 2.7 to 0.37. This range of values produces a full range of B_2/B_3 ratios, from the point where Species 3 becomes extinct, to the point where Species 2 becomes extinct. For the coefficient d, the results are not dependent upon the absolute value of d.

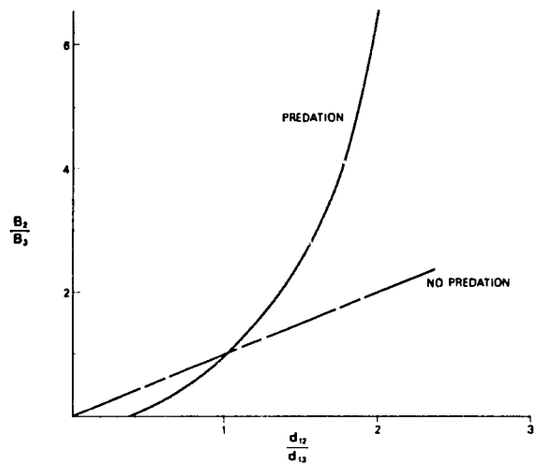
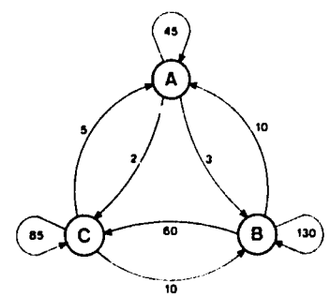


FIGURE 7.—An illustration of the effect of predation (as measured by biomass ratios) on competition as measured by changes in the ratio of the resource accessibility coefficient d for the two species.

The results shown in Figure 7 clearly indicate that some of the competitive coefficients have a very large influence on the relative stability of interacting systems. They suggest that if the stress of exploitation or other environmental stresses interact with other model coefficients as, for example, in a simple predator-prey interaction, the system may respond very violently, with the rapid extinction of one or the other of the competing species.

In some instances it may be desirable to have some rough empirical measure of the stability of exploited ecosystems consisting of interacting species. As Margalef (1969) has indicated, an adequate measure of community stability must include a measure of diversity as well as a measure of persistence. Furthermore, Margalef attempted to formulate a generalized mathematical model for their interdependence. It is suggested that an additional application of graph theory may also be utilized to provide some empirical indication of stability and persistence of communities subjected to either environmental or exploitive stresses, assuming certain types of background information are available.

Consider the following hypothetical example. Three communities of fishes (A, B, C) are subjected to various levels of exploitation. Assume that some crude index of diversity or community structure has been established which permits identification of the three communities as mutually exclusive groups. Assume that the three communities are sampled again during the course of a year, and that the frequency of samples which resemble the previously defined community as well as the frequency of samples which resemble the other two communities are listed. These frequencies can be displayed in the form of a network as shown in Figure 8. The data



$$F_0 = \begin{bmatrix} 45 & 3 & 2 \\ 10 & 130 & 60 \\ 5 & 10 & 85 \end{bmatrix} \begin{matrix} 50 \\ 200 \\ 100 \end{matrix} \qquad M = \begin{bmatrix} .90 & .06 & .04 \\ .05 & .65 & 30 \\ .05 & .10 & .85 \end{bmatrix}$$

$$M^2 = \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} \qquad P_0 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix}$$

$$P_0 M^2 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix} \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} = \begin{bmatrix} 68.50 & 111.25 & 170.25 \end{bmatrix}$$

FIGURE 8.—Example of a hypothetical network showing the frequencies of samples resembling their initial structure as well as those of the other two community structures. In this example F_0 is the matrix of frequencies at the end of the first sampling period, M is the corresponding probability matrix, M^2 is the square of the probability matrix and P_0 is the vector of frequencies by community type. P_0M^2 is the matrix-vector product expressing the expected new frequencies by community type at the end of the second sampling period under the assumption that the probability matrix remains constant during the time interval.

from the network is presented as a matrix (F_0 of Figure 8) of frequencies which was normalized to form a probability matrix (M of Figure 8). This probability matrix M is one in which the i, j entry gives the proportion of the samples from community v_i which resembled community v_j during the sampling period. An important theorem concerning probability matrices states that if B and C are probability matrices, so is their product BC. A corollary to this theorem states that if M is a probability matrix, then so is every power M^n, for any positive integer n. If the assumption is made that the probability matrix M remains constant over time, then if one knows the initial frequency matrix F_0 and the probability matrix M, it is possible to find the sample frequency distribution at a subsequent time t_n by finding the nth power of M and then forming the product P_0M^n where P_0 is the vector of row sums equal to the initial vector of frequencies by community type. In our case the frequency in year 2 is $F_2 = P_0M^2$. This matrix-vector multiplication is illustrated in the lower part of Figure 8. It is suggested that this derived frequency might be useful as the expected value basis for comparison with the sample observations made during subsequent years, if it is assumed the probability matrix remains constant over time.

CONCLUSIONS

The examples provided in this study are given primarily to illustrate the wide range of possibilities for the use of graph theory in studying the stability of interacting competitive and predatory relationships. The tentative results of this model study suggest that a nonselective exploitation strategy, which includes both predator and prey organisms, may be "best" from the point of view of maintaining community stability in complex ecosystems. The high desirability of obtaining experimental values for certain coefficients was also pointed out.

The limitations of a linear, steady-state model are many and obvious. However, if such a model can sometimes be utilized to provide approximate results suitable for use in practical management at the early stages of marine ecosystem management, then the model is a worthwhile tool, and the method utilized has some merit. If the method (graph theory) can be used not only to obtain some basic insight into system behavior but can also be used as an empirical tool, then it seems particularly worthwhile. Both these possibilities seem to await the results of future imaginative development.

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