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SYMMETRY, CHANGE, PERTURBATION, AND OBSERVING MODE IN NATURAL COMMUNITIES[1]

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Abstract. Like a kaleidoscope, nature presents continuously fleeting images of natural communities. It has been difficult to discern patterns of community structure in these elusive images. For both theoretical and applied considerations, however, holistic ecosystem properties need to be identified and quantified. An analogy of a kaleidoscope is used here to describe symmetry, change, and perturbation in the plankton community of Delaware Bay. Notions of symmetry are used extensively by physicists but much less so by biologists. For the ecological application given here, symmetry involves the notion of internal order and invariant pattern within the structure of natural communities. The concept of core structure is introduced to illustrate the inherent symmetry of plankton communities arising from consistent linkages and feedback relationships. The core is determined by using the most prevalent variables and links of a series of individual loop diagrams, each describing the community at a given point in time, to form a summary or composite model. Change refers to the seasonal alterations in community structure, whereas perturbation involves the source and entry location of environmental variation to the community network. Observing mode includes both the intrinsic (biological intuition) and extrinsic (loop analysis) models an observer uses to characterize symmetry, change, and perturbation.

Loop analysis was used to model the Delaware Bay plankton community at 12 dates in an annual cycle. Loop diagrams consist of qualitative network models based on positive, negative, or zero interactions between variables in a pair for all pairs of variables. The fit of models to the data using the directed change technique resulted in 95% agreement. The core structure contained 18 variables in a three-tiered configuration with distinct subsystems of predators and small-sized algae and their associated herbivores. There were 3 nutrient, 5 algae, and 10 zooplankton variables in the core structure. It is proving to be consistent for several other marine communities. Various network properties related to community structure and stability were computed for the networks. The mean loop length varied from 1.6 to 2.8 variables for the individual networks; a network consisted of 22–31 loops of various lengths. Connectance ranged from 14 to 18%. The individual networks were stable; however, the stability of the core structure was questionable. The uniqueness problem, or verification of the single best-fit model, is presented as a concern central to all types of ecosystem modelling. The notion of three different-sized loop universes (sets of loop models) is introduced to illustrate one approach to this problem.

Key words: community structure; connectivity; Delaware Bay; food-web models; loop analysis; marine plankton; qualitative modelling; stability; symmetry.

INTRODUCTION

In 1817, Sir David Brewster patented the kaleidoscope as we know it today. Since then it has fascinated several generations of pattern watchers. The name kaleidoscope comes from the Greek and can be roughly translated as an instrument for showing (scope) beautiful (kalos) forms (eidos). It works on the principle of multiple reflection using mirrors along the length of the tube. When an observer looks into the tube he sees a dazzling variety of circular patterns which are arranged into submultiples of four right angles.

Nature is analogous to a kaleidoscope in that it presents an endless variety of species combinations and interactions (Fig. 1). In the study reported here, this analogy is used to illustrate the structure and stability of a marine plankton community. No analogy is ever perfect or complete since there is not a one-to-one correspondence between the real system requiring explanation and the analogous model. Analogies can be useful, however, if the model-system correspondences are explicit. Four aspects of this analogy will be emphasized: symmetry, change, perturbation, and observing mode. These terms are used in specific ways as defined here.

The dictionary defines symmetry as "correspondence in size, shape and relative position of parts that are on opposite sides of a dividing line or median plane" (Webster's New International Dictionary 1961). This is geometric symmetry. It is illustrated in Fig. 1. A secondary definition involves the beauty of form arising from the harmony of balanced proportions. In science, however, the notion of symmetry implies much more than these dictionary definitions. Physicists use the concept of symmetry in several contexts, such as charge symmetry referring to an antiworld and mirror symmetry involving a temporal dimension (Weisskoff 1969). They describe a deep degree of symmetry among

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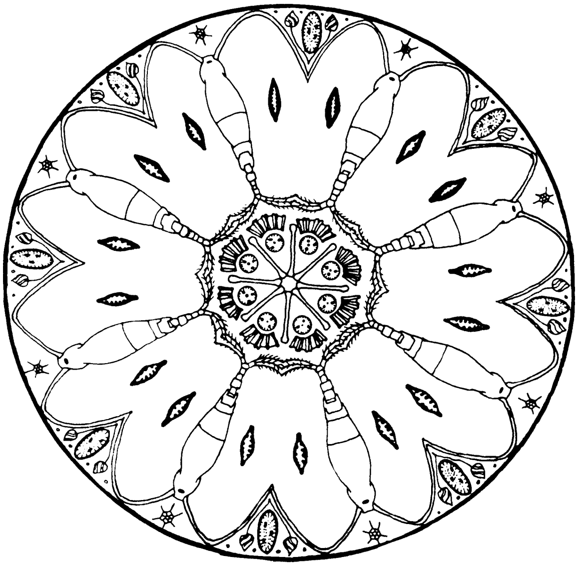

FIG. 1. A plankton kaleidoscope featuring *Acartia,* a dominant copepod genus, and several phytoplankton species found in Delaware Bay. The type of pattern illustrated here is termed geometric symmetry.

the forces of nature and often use the terms invariance and symmetry interchangeably (Weinberg 1977). In this context, symmetry means a type of internal order, a constancy or invariance in the state of a system in space, in time, and/or in abstraction. Symmetry is used in this paper as a partial synonym for community structure. It includes the general area of community descriptors but it adds a meaning of balance or internal order with some unspecified structural constraints on the interactions of the parts.

Nature's kaleidoscope does not hold still; it presents us with a continuous procession of images. Change is normal and ubiquitous in ecosystems and it encompasses a rich diversity of biological phenomena. A manufactured kaleidoscope has only so many bits of red, blue, and green glass, which form the patterns. Even though there is a bewildering array of images, the number of patterns is constrained. By analogy, some ecologists have expressed the intuitive notion that there must be constraints on ecosystem pattern and behavior. Despite these constraints, it is unlikely a single model can capture the essence of symmetry in a natural community. Thus, change is used here to emphasize that a set of models may be needed to represent differences in state description from one time to the next.

Environmental variation or perturbation affects the symmetry reflected in the various states of an ecosystem. Perturbation is related to change of state since it usually forces the change. When a kaleidoscope is turned, the perturbation results in a change in the symmetrical images. A perturbation or driving force to an ecological network can initially affect any variable and then feed through the system to affect all other variables. Unlike a manufactured kaleidoscope, which undergoes only one type of perturbation, ecosystems are subject to many different kinds of stresses, which may operate simultaneously.

To describe the pattern of a kaleidoscope image implies that there is an observer. Observers are not identical beings nor do they have identical perceptions. It is becoming increasingly apparent that all observers have and use intrinsic and extrinsic model systems that greatly affect their observations. Biological intuition can be considered equivalent to what is termed here the intrinsic model system. The extrinsic model system used for this study is loop analysis, a qualitative network technique. This methodology was developed by Levins (1973, 1975) and applied to aquatic communities by Lane and Levins (1977) and Lane (1982). Mason (1953) used a similar type of theory for problems in electrical engineering.

Purpose

The purpose of this study is to demonstrate how loop analysis can be used to characterize (1) community structure (symmetry), (2) shifts in community patterns over an annual cycle (change), (3) type and input location of environmental variation to the communities (perturbation), and (4) general features of applying the methodology and interpreting results (observing mode). An intuitive description of how loop analysis works is also given. Improved community descriptions through loop analysis may help to resolve many questions in theoretical ecology as well as to improve current methods of environmental impact assessment.

METHODS

Details of the theory of loop analysis are omitted here and only a brief summary is given. See Levins (1973, 1975) or Lane and Levins (1977) for the mathematical formalism.[2]

For a system with n components that are represented by the n system variables $x_1, x_2, \ldots, x_n$ or by the n graph nodes 1 to n, the community matrix is defined to be the n-order matrix of elements a_{ij} as follows:

$a_{ij} = +1$ if a positive link ($\rightarrow$) exists from node j to node i,

$a_{ij} = -1$ if a negative link ($-\!\circ$) exists from node j to node i,

$a_{ij} = 0$ if no link exists from j to i.

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[2] See also ESA Supplementary Publication Service Document No. 8525 for 55 pages of supplementary material on the theory of loop analysis and the preparation of data for loop modelling. Part A of this document consists of 28 pages of material by J. A. Wright and P. A. Lane on the theoretical underpinnings of loop analysis. For a copy of the document, contact the author or order from the Ecological Society of America, Cornell University, Ithaca, New York 14853-2701 USA.

The stability to perturbation of this system can be predicted by the feedback (F_k) at each level, k, from 1 to n. This is defined by the formula

$$F_k = (-1)^{m+1} L(m,k),$$

where $L(m,k)$ represents the product of the elements along any set of m disjunct loops (i.e., closed pathways that have no variables in common) that span or visit exactly k variables of the n possible. Each of the k variables will be included once and only once by one of the loops. The sum is over all such spanning sets of disjunct loops, and m refers to the number of loops in each set.

Stability criteria are as follows:

1) if the system is stable, the overall feedback, F_n, will be negative; note that $F_n = (-1)^n D_n$ where D_n is the determinant of the community matrix;
2) if all n feedbacks at levels 1 through n are not negative, the system may not be stable; and
3) if for the feedbacks at the first three levels the Routh-Hurwitz condition $F_1 F_2 + F_3 > 0$ does not hold, the system will be unstable.

When a positive parameter input at a given variable j causes that variable's growth function to increase, the direction of change in the level of each system variable i is the community effect E_{ij} and is given by the formula

$$E_{ij} = \Sigma\, P_{ij}^{(k)} \cdot F_{n-k}[\text{compl } P_{ij}^{(k)}]/F_n,$$

where $P_{ij}^{(k)}$ is the algebraic product of elements along a simple, open path from node j to node i; k refers to the length of the path, i.e., its number of variables. $F_{n-k}[\text{compl } P_{ij}^{(k)}]$ is the feedback of the order $n - k$ submatrix formed by omitting the variables on the path $P_{ij}^{(k)}$ from the system by removing corresponding rows and columns from the community matrix. The resultant submatrix is referred to as the path complement and the feedback term as the complement feedback. A complement must be nonzero for a given path to operate in the network. Nonzero feedbacks are termed valid complements, and paths with valid complements are termed valid paths. The summation is over all such valid paths from j to i and, as before, F_n refers to the overall system feedback. The community effect E_{ij} is also termed the model-directed change prediction.

Note that since it is assumed in parameter input analysis that the system is in steady state, it can be further assumed that F_n is negative. Also note that $F_0 = -1$ and $P_{ii}^{(1)} = 1$ by definition. This is to make certain special cases fit the formula as written.

Some examples

Four closely related sample systems are shown as loop diagrams in Fig. 2A–D. The associated community matrices and predictions of community effects are given in Table 1. These examples are discussed in detail to illustrate the underlying intuition of loop analysis and how the mathematics can be translated into ecology. Fig. 2A is a four-variable system structured as four trophic levels so that each variable except the first is a consumer of the one that precedes it, and each variable except the last is a resource of the one that follows it. Variable N represents the concentration of a nutrient pool. Its self-damping would be the result of (1) an independent rate of input that is not related to its current concentration and (2) a rate of consumption by algae that is proportional to nutrient concentration. Generally, the lowest trophic levels represented in loop diagrams are self-damped, as are all abiotic variables that are not self-reproducing (Lane and Levins 1977). In Fig. 2A, the nutrient is consumed by an edible algal group (AE). AE is eaten by herbivore H. Finally, the herbivore is consumed by a carnivore (C) that is also self-damped. For biotic, self-reproducing variables, self-damping can arise from any of a number of biological mechanisms, such as cannibalism for C in Fig. 2A or self-shading or self-poisoning of algal species.

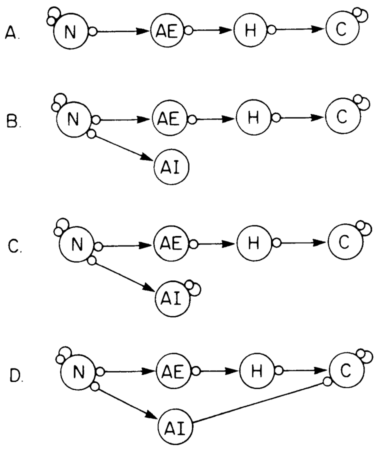


FIG. 2. Four sample aquatic ecosystems with four trophic levels. N is a nutrient pool, and AE and AI are populations of edible and inedible algae, respectively. H and C are herbivore and carnivore populations, respectively.

Each of these variables is modelled as an interacting component of a system. In reality, each component might include a single species or a group of similarly functioning species. Components may also represent nutrients or nutrient complexes. In the analysis, each of these components is represented by a variable that measures the total abundance of the given species group or total concentration for a nutrient variable.

Were this a real-world system, it would be necessary to justify the isolation of these components as a closed system. Thus, it is assumed that (1) nutrient (N) is the sole requirement of and consumed solely by algae (AE) or (2) any other consumers or resources are held at a constant level or (3) changes in any components of the ecosystem not included in the model occur at a rate so

Table 1. Community matrix and predictions of community effects for the four sample loop diagrams (A–D) shown in Fig. 2.* For community effects, predictions are read across rows for each parameter input.

	Community matrix†						Community effects‡				
	Variable					Input	Affected node				
A. Variable	N	AE	H	C		node	N	AE	H	C	
N	−1	−1	0	0		+N	+	+	+	+	
AE	1	0	−1	0		+AE	−	+	+	+	
H	0	1	0	−1		+H	+	−	+	+	
C	0	0	1	−1		+C	−	+	−	+	
B.	N	AE	H	C	AI		N	AE	H	C	AI
N	−1	−1	0	0	−1	+N	0	0	0	0	+
AE	1	0	−1	0	0	+AE	0	+	+	+	−
H	0	1	0	−1	0	+H	0	−	0	0	+
C	0	0	1	−1	0	+C	0	+	0	+	−
AI	1	0	0	0	0	+AI	−	−	−	−	+
C.	N	AE	H	C	AI		N	AE	H	C	AI
N	−1	−1	0	0	−1	+N	+	+	+	+	+
AE	1	0	−1	0	0	+AE	−	+	+	+	−
H	0	1	0	−1	0	+H	+	−	+	+	+
C	0	0	1	−1	0	+C	−	+	−	+	−
AI	1	0	0	0	−1	+AI	−	−	−	−	+
D.	N	AE	H	C	AI		N	AE	H	C	AI
N	−1	−1	0	0	−1	+N	0	−	0	−	+
AE	1	0	−1	0	0	+AE	0	+	?	+	−
H	0	1	0	−1	0	+H	0	−	0	−	+
C	0	0	1	−1	−1	+C	0	+	0	+	−
AI	1	0	0	0	0	+AI	?	−	?	−	+

* Abbreviations as in Fig. 2 legend.

† The community matrix is defined as the n-order matrix of elements a_{ij}, where a_{ij} equals +1 if a positive link (→) exists from node j to node i, −1 if a negative link (—o) exists from j to i, and zero if no link exists from j to i.

‡ Positive (+), negative (−), or zero; ? = ambiguous prediction.

slow compared to the time frame of the interactions depicted that they can be considered as system parameters.

The determinant of matrix A in Table 1 is 2 and since it is of even order, the feedback is −2. Thus, there is no immediate indication of instability. There are five loops (Fig. 2A) and they are all negative. Two are self-damped loops of length (=level) 1: from N to itself and from C to itself. (Loop level or length refers to the number of variables included in the loop.) The other three are the consumer-resource loops of length 2: between N and AE, AE and H, and H and C. The self-damping loops are obviously negative whereas the length-2 loops are all composed of a positive consumer link and a negative resource link, which have a negative product.

The feedback at level 1 is the sum of the self-damping terms. These are the only one-variable submatrices that have any loops; therefore $F_1 = -2$. The feedback at level two consists of three negative terms coming from the consumer-resource loops plus one more negative term that is the product of the two self-damping loops times −1 (because there were two of them; remember the $[-1]^{m+1}$ factor in the feedback formula, where m is the number of loops in the product). Thus, $F_2 = -4$. In total, there are four sets of disjunct loops contributing to feedback at level 3, and they are all negative. Each set includes a self-damping loop times one of the two consumer-resource loops in which the self-damped variable does not occur, multiplied by −1 because there are two loops in the set. $F_3 = -4$.

The feedback at level 4, which is the overall feedback, has two terms, both negative. One is the product of three negative loops (the two self-damping terms and the intermediate algae-herbivore loop) times +1 since the number of loops is odd. The other is the product of the N-AE loop and the H-C loop, times −1 for two loops. That the feedback at all levels is negative implies that at steady state the system is stable to any perturbations. Thus, any changes to a system variable will be absorbed and damped out by the rest of the system.

Negative loops, especially short ones, tend to improve the stability of a system. Self-damping terms naturally tend to absorb changes in variable levels, so long as the variable's intrinsic growth rate or rate of input to the system is not permanently changed. Resource-consumer loops are also damping. If a resource level temporarily increases, then its consumer will enjoy a brief period of prosperity during which its growth function will increase from its steady state or zero value and its level will increase. The increased numbers of consumers, however, will produce a decrease in the resource back to its original level or lower; this will make the growth function of the consumer negative so that the level of consumers returns to normal. Depending on the strength of the interactions and the time lags involved, this damping may be either asymptotic or oscillatory. Likewise, should the level of consumer temporarily rise, it will be stabilized by the resource.

When these resource-consumer loops are chained into a trophic series, they still form a stable unit, as in this example. For the system of Fig. 2A, an increase at a variable will cause temporary growth increases up the chain and decreases down the chain. The increased consumption from above and decreased resource levels from below, however, will quickly act to normalize the level of the variable and eventually the whole system. These effects may be weakened over long chains. In this example, stability is improved by the self-damping terms at either end. The feedback at various levels can be used to determine whether the system is stable in regard to short- or long-term mechanisms, and the terms of the feedback levels can be examined to determine which links are involved in the stabilizing loops.

In Fig. 2B the variable AI (inedible algae) has been added as a second algae group that consumes nutrient N. In Fig. 2C this variable is also self-damped. In both cases, feedbacks at all levels are augmented by negative terms resulting from extra negative loops. In the case of Fig. 2B the overall feedback is -1 (the determinant is also -1 since this is an odd-order system) while for Fig. 2C it is -3. The extra two terms in the case of Fig. 2C involve the self-damped AI demonstrating the ability of self-damping to improve system stability.

Parameter inputs and community effects

As opposed to perturbations, which are temporary changes in variable levels with no change in the intrinsic growth functions, a parameter change is a permanent change in the growth rate of one or more variables. Such a change may be caused by some external factor, such as an increased flow of nutrient or an increase of temperature or light favoring plant growth, or by another species group in the ecosystem that affects one or more of the system variables but is not directly affected by the community, at least in a commensurate time frame (e.g., increased hunting by humans). Such changes may cause the levels of some or all system variables to be permanently altered, that is, the steady state may move. The community effect formula from loop analysis indicates, for an increased growth rate of any one variable, in what direction the steady-state level of any other system variable, or of itself, is likely to move. Also, the number of pathways that lead to, respectively, an increase or a reduction in steady-state levels can be determined. The community effect from an input variable to an affected variable is the summed effect over all pathways from input to affected variables. The effect over a given pathway is the product of the links on the path times the ratio of the feedback of the path complement to the feedback of the whole system. The feedback ratio indicates how the system may absorb or reverse the effects of a given path.

In Fig. 2A a positive parameter input at variable N causes an increase in the levels of all system variables. An input to AE, perhaps because of increased light improving plant growth, increases levels of H and C, both of which directly or indirectly use AE as a resource. The levels of N, however, are reduced by increased consumption by AE. An input to H, perhaps because of a more favorable temperature, increases levels of C and decreases levels of resource AE. The reduced levels of AE, however, allow levels of N to increase. Finally, an input to carnivore C, perhaps because of reduced pressure from human hunters, reduces H and N but increases AE.

If there is an input to both AE and H, the combined effects are additive. Levels of H and C are clearly increased. The increased growth of AE, however, is offset by the increased consumption of H and the resultant community effect is ambiguous. That is, without measuring the interaction rates both ways, even the direction of the community effect cannot be predicted. Also since the level of N depends on AE, it also will be ambiguous.

In Fig. 2B, the links to variable AE cause some pathways to have no valid complement. In particular, for any path involving N but not AI, AI will be in an invalid complement causing the feedback to be zero. In effect, the negative loop between N and AI with AI undamped acts like a second self-damping loop on N. Thus, the level of N cannot be changed by parameter inputs except at AI, because the effects of changes in the growth rate of N are absorbed by changes in the level of AI.

An input at AE causes increased competition with AI for resource N. Levels of AI tend to decrease so that levels of N remain the same. Levels of AE, H, and C increase as before. An input at H reduces the level of AE, which allows the level of AI to increase to take up the excess N. Since H is damped by loops with C and AE, its level is unchanged, as is that of C. Similarly, input at C will not reduce the level of H, since the effects of increased consumption on H are offset by increased resource levels for AE. As with the other inputs, this increase of AE forces a reduced level of AI. Finally, an input at AI increases its own level, since it is not damped, and reduces N. This, in turn, reduces AE, H, and C.

In Fig. 2C, AI is self-damped. Since the level of AI is more controlled, the level of N is not as heavily damped. When AI is in a complement without N, it has its own self-damping loop to keep it stable. Thus, this system behaves more like the system in Fig. 2A. An input at N increases all levels in the system, as its simple pathways would imply. An input at H increases H itself and C, but reduces AE. This allows N and AI to increase. An input at C increases C itself, reduces H, increases AE, and reduces N and AI. Finally, an input at AI increases AI itself but reduces levels in the rest of the system, as in Fig. 2B.

In Fig. 2D, the algal species AI interferes in some way with the growth of carnivore C, perhaps by producing a toxic substance. The determinant of this community matrix is 0, implying at best a neutral stability. The graph for this community differs from that of Fig. 2B in having a positive loop of length 5 involving all variables in the system. This results in a positive feedback term at level 5, which balances the negative term that was present in the previous diagram. Basically, the destabilizing effects of the long positive loop involving AI tend to be counteracted by the negative or damping effects of the trophic chain from N to C involving AE and H. Depending on the actual interaction strengths, either condition may predominate. If they are exactly equal, the condition of neutral stability, as described above, exists.

Because of this ambiguity, the predicted effects of parameter changes are also ambiguous; however, that an affected variable will not change can be predicted with certainty. Ambiguous results, recorded as question marks in the prediction table, result from either multiple paths or complements having opposite signs for a particular calculation of E_{ij}. The sign of any directed changes, however, depends on whether the system is actually in the stable or unstable region. On the assumption that the system is stable, a parameter input at N causes no change at N, as in Fig. 2B, but rather causes an increase of AI, which is itself undamped. As before, pathways from N to itself or to other variables in the trophic chain leading to C are not valid because of the undamped AI, which absorbs any increased input of N. The increased level of AI, through its negative pathway to C, causes some differences with the system of Fig. 2B. Not surprisingly, the level of C decreases; however, its reduced pressure on H tends to be compensated for by a reduced level of AE, corresponding to the greater competition from AI for N. Thus, it is counterintuitively predicted that an input of N will actually reduce the level of its consumer AE. This prediction results from the negative pathway from N to AE through AI and the undampedness of AI, which results in a zero feedback for the direct path from N to AE.

In the case of an input to AE, the results are very much the same as for Fig. 2B. There are tendencies to increase for AE, H, and C, while any level change at N is prevented by its damping loop with AE. In this case, the level of AI decreases to balance the increase of competitor AE. This benefits C, which in turn tends to reduce the level of H. Whether there is an increase at H depends on (1) the balance of interaction strengths in the direct negative pathway from AE vs. the indirect negative pathway via AI and (2) the assumption that the system actually preserves its steady state.

The effects of a parameter input at H in Fig. 2B would be entirely absorbed by a decrease in AE, which would result in an increase for AI. In Fig. 2D the increased AI causes a decrease in the level at C, but the effects of this on H remain damped by the loop with AE. The effects of a parameter input at C in Fig. 2B are similarly damped by AE, which would increase, and AI, which would decrease. The direct path from AI to C in Fig. 2D only encourages further increase in C.

Finally, in Fig. 2B, an input at AI contributes to an increase in its own level and, not surprisingly, a decrease through the trophic chain from N to C. The extra pathway in Fig. 2D creates a further tendency to reduce the level of C. This in turn creates tendencies to increase H, decrease AE, and increase N, which causes the overall effects for N and H to be ambiguous, depending on the actual strengths of the links.

Network properties and stability measures

A set of loop models is summarized by variable, links, and parameter inputs to determine the dominant or core network of the ecosystem. The core diagram is a composite network formed from the most prevalent linkages in the individual models. In the example analyzed in Results, there were 12 model diagrams, each based on data collected on a single date of an annual cycle. The following criteria were used in constructing the core diagram: links had to be present in more than one diagram and pairs of variables in more than two diagrams to be included in the core structure. A link was drawn as a solid line if it occurred in >50% of the diagrams in which its connecting variables co-occurred. Dashed lines indicated interactions that occurred in 33.3–50% of the cases of variable co-occurrence. Although a loop diagram for a single date can appear to have missing links, the core structure for an annual cycle probably represents the bulk of important relationships among these variables fairly well.

Network properties are characterized and stability calculations are made on both the individual loop models and the core. They include the number of each type of link; distribution of loops by level, where level is equal to the number of variables (1 to n) in the loops; total number of loops per network; analysis of feedback of the whole network (F_n); percent connectance (%C); and connectivity (B). Several of these measures are apparent by inspection of the loop diagrams. The number of feedback terms at level k is equal to the number of subproducts of determinants of matrices of k variables. Percent connectance is calculated as:

$$\%C = I/V^2,$$

where V is the number of nodes or variables and I is the number of one-way interactions or links, including self-damping terms. A predator-prey relationship would have an L value of 2. Thus, $\%C$ is the percentage of nonzero elements in the community matrix. Connectivity $(B) = I/V$; it is the average number of inputs or outputs per node.

Loop universes

In any system of analysis where a model is developed and used to predict the behavior of a system, it is of interest to know how many different models could possibly fit the system, and how many of them would make the same predictions. This is called the uniqueness problem and is directly related to model validation and verification. It can then be asked which of the models best fits the system and makes the most accurate predictions.

Calculations of how many loop models are possible for a given size system (that is, a particular number of variables) with similar characteristics (patterns of links) can be made. These are referred to as the universes of the system model and can be considered as concentric subsets; the diameter of the subset depends upon how many constraints are applied (that is, how closely the possible systems must match the given ideal system). Three universes are described here: macro-, meso-, and micro-universes (MA, ME, and MI, respectively; see Fig. 3).

The largest possible number of signed digraphs of a given size is termed the macro-universe. All other universes are subsets of this. For a system of n nodes, there are $n(n - 1)/2$ pairs of nodes and since each pair can have either of two kinds of links (+ or −) or no link (0) in either direction, each pair has nine possibilities. In addition, each node can be linked to itself positively, negatively, or not at all, assuming we allow self-enhancing variables to exist. Allowing three possibilities for each node, there are $9^{n(n-1)/2}\cdot 3^n$ possibilities in all. Note that this is equivalent to the number of possible square matrices of order n where there are three possible values for each element: $3^{(n^2)}$.

It can be seen that even for relatively small orders, the number of possible systems in the macro-universe is staggering. A vast number of these, however, will be "biologically unreasonable" (Lawlor 1978). That is, they will contain links that could not exist in a real-world system. On mathematical grounds, the following could be excluded: (1) self-enhancing variables; (2) all unstable systems; (3) all systems that contain subsystems not linked to the rest of the system; and (4) all systems that contain variables that are identical to other variables or to a combination of other variables. Finally, if we characterized the system variables accurately, we would know which variable pairs could not possibly be linked and what links out of the nine potential ones were possible for a given pair. Different constraints and combinations of constraints create overlapping and/or concentric sets of possible networks, which are referred to as meso-universes. Their calculation is beyond the scope of this paper.

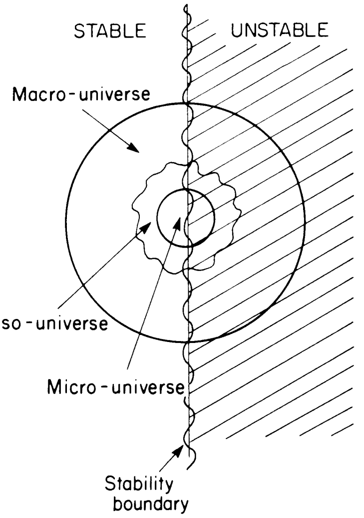


FIG. 3. Schematic representation of loop universes. The wavy line delineating the meso-universe indicates that its exact location is unknown. The location of the stability boundary is also unknown.

For a set of graphs constructed on a single ecosystem, the number of link types for each node pair is summed and these sums are multipled over all node pairs. The resultant value is termed the micro-universe. It represents the number of possible networks for the ecosystem given that each link type observed is independent of every other one. This essentially represents an exploration of the network space around the core structure. It can be expressed as

$$1^{(m_1+k_1)}\cdot 2^{(m_2+k_2)}\cdot 3^{m_3}\cdot \;\ldots\; \cdot 9^{m_9}$$

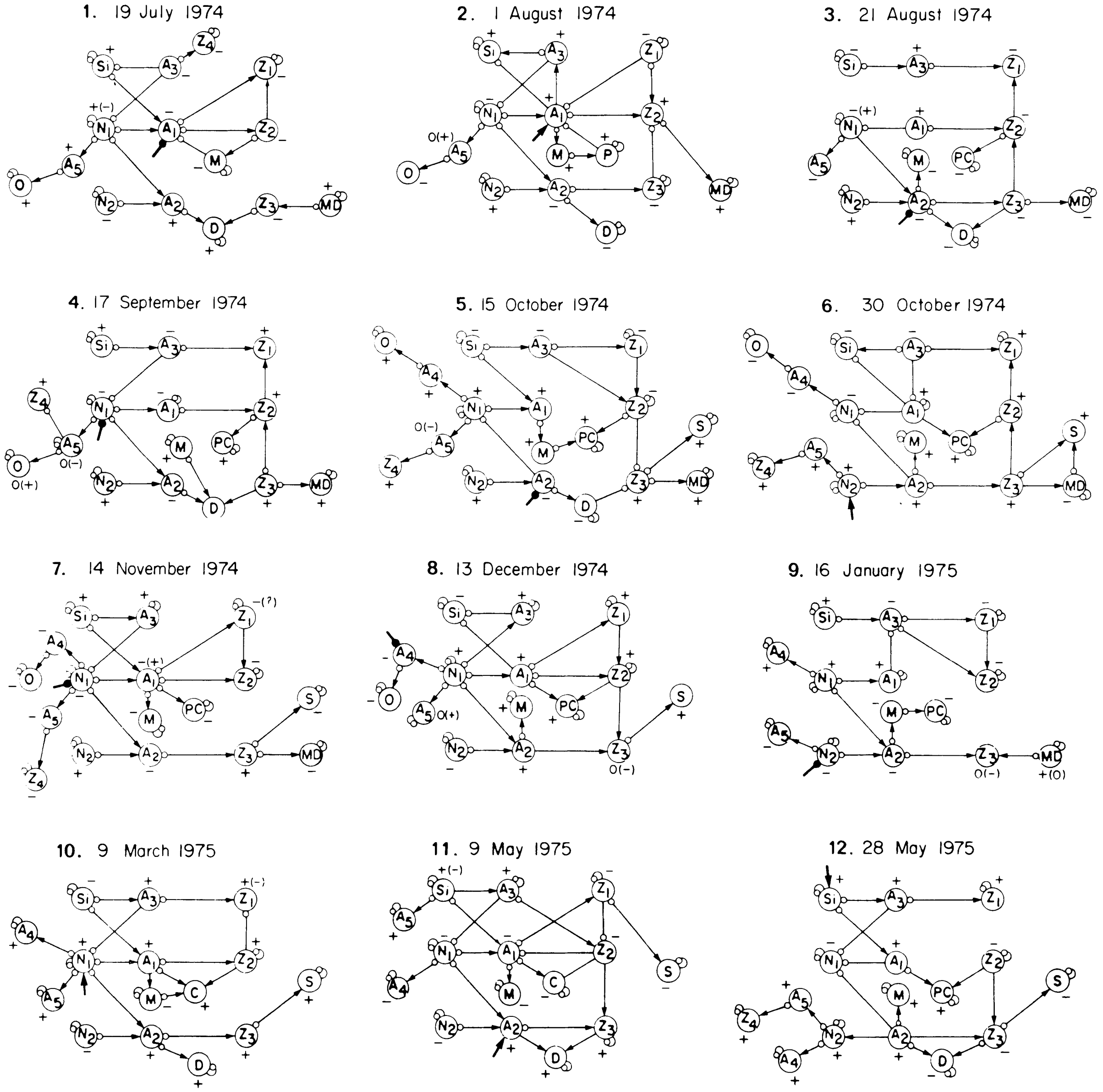
where m_k is the number of node pairs that had k different combinations of links in the given set of graphs. m_1 includes the number of node pairs that were unlinked in all graphs and n_1 is the number of variables that were either self-damped or self-reproducing in all graphs, whereas n_2 is the number that exhibited both conditions. Note that

$$\Sigma\, m_k = n(n - 1)/2 \text{ and } n_1 + n_2 = n.$$

Where there are nodes that appear in some but not all of the graphs, they are added to the remaining graphs as unlinked nodes. As more networks are included in the micro-universe calculation, its size will approach that of the meso-universe. MI*, ME*, and MA* indicate universes of stable networks.

Computation

Most of the computer software has been specially designed for this methodology; however, SPSS version 8.3 (Hull and Nie 1981) on Dalhousie University's mainframe CDC CYBER 170-730 was used for pre-



1. 19 July 1974
2. 1 August 1974
3. 21 August 1974
4. 17 September 1974
5. 15 October 1974
6. 30 October 1974
7. 14 November 1974
8. 13 December 1974
9. 16 January 1975
10. 9 March 1975
11. 9 May 1975
12. 28 May 1975

FIG. 4. Loop diagrams for 12 dates over the 1974–1975 annual cycle in Delaware Bay. SI = silicate, N_1 = N/P ratio, N_2 = organic nutrients, A_1 = diatoms, A_2 = dinoflagellates, A_3 = luxury-consuming diatoms, A_4 = small flagellates, A_5 = miscellaneous algal groups, Z_1 = copepod adults 1, Z_2 = immature copepods, Z_3 = copepod adults 2, Z_4 = cladocerans, O = *Oikopleura* sp., C = cirripeds, P = polychaete larvae, PC = P + C, M = mollusc larvae, MD = medusae, D = decapods, and S = *Sagitta* spp. Parameter inputs are represented by dark → (positive inputs) and —● (negative inputs) external to the networks. Parameter inputs are analogous to the driving functions commonly used in computer simulation models. The inputs represent the effect of the environment on a particular variable, which then causes other variables in the network to change. Model-directed change predictions or community effects appear next to each loop variable. Qualitative data-directed changes appear in parentheses when in conflict with model predictions.

liminary report listings and basic statistics. The qualitative statistics and directed change programs were written in FORTRAN V or 77 and they were also run on the CDC CYBER 170-730. The loop-correcting program and stability calculations were performed in Language C on a VAX-11 with a UNIX operating system (Berkeley version 4.1) (Joy et al. 1980). Compilation of loops, network properties, and micro-universe calculations were performed in BASIC on an Apple III microcomputer.

RESULTS

Loop models

Loop analysis was used to model the plankton community of Delaware Bay, one of the major coastal plain estuaries in the eastern United States. Data were collected approximately monthly over an annual cycle in 1974–1975.[3] Twelve loop diagrams are shown in Fig. 4; they are arranged in the chronological order of the field collections. The models depict a three-layered ecosystem structure with three major nutrient variables, five groups of phytoplankton, and four groups of meso-zooplankton (copepods and cladocerans) as well as several miscellaneous and macro-zooplankton variables. The linkages for the 12 models are summarized in Table 2. The interactions in the loop diagrams are mostly predator-prey and self-damping links; however, there are enough lateral links and one-way flows that these models cannot be considered to be simple food-chain or trophic-level models. There are nine possible types of linkages between any two variables (○—◯, ↔, ○→, ←○, ○—, —○, ←, →, or no link). On the average (in the row labelled Mean), there were 130 possible pairs of variables, of which 103 had no link with each other. The hypothetical average diagram would also have ≈13 predator-prey links, 10 self-damping links, and 5 one-way links. Parameter inputs are shown as darkened arrow- or circle-heads in Fig. 4. Predicted changes are given next to each variable.

In these models, there is a subcommunity of several types of small organisms, including A_4, A_5, O (*Oikopleura* sp.), and Z_4 (cladocerans). The algal groups are usually directly connected to N_1 (nitrogen-phosphate ratio). The frequent presence of self-damping on O and Z_4 indicates that predation is occurring by a predator omitted in the diagrams. Cannibalism could not account for these particular self-damping links. Unfortunately, many smaller zooplankton species were not adequately sampled so that these predators cannot be identified. The predation of O and Z_4 on small algal forms, especially naked flagellates, is well known. All attempts to place *Oikopleura* sp. (O) in other locations in the networks were unsuccessful. It appeared to feed upon A_4 whenever this algal group was present. If A_4 was absent, then O consumed A_5. On only one date did O and Z_4 feed on the same algal food. They may be potential competitors that alleviate competition through resource allocation.

Three nutrient pools were present in all diagrams and were always self-damped. N_2 is a complex organic nitrogen pool that meets some unique nutritional requirements of the dinoflagellates not shared by the diatoms. Numerous attempts to model inorganic nitrogen and phosphorus individually have not been successful. The phytoplankton species appear to be responding to the nitrogen-phosphate ratio (N_1) and not to the absolute amounts of these nutrients. Several species that occur in A_3 may be auxotrophic in that they require B_{12} or another vitamin for growth, whereas species in A_1 are probably autotrophic (Swift 1980). Although the relationship between luxury consumption and vitamin requirements is not well established, it may be that the species in A_3 luxury-consume nutrients, especially phosphorus, until vitamin concentrations are adequate to sustain a burst of growth, when they can use their stored nutrient supplies. During data preparation,[3] many phytoplankton species consistently separated into these categories (A_1 and A_3) for several marine environments (Lane and Collins 1985). This indicates some inherent physiological differences that are crucial for understanding the ecological dynamics of marine plankton communities.

TABLE 2. Summary of types of links* between each two variables in the 12 loop diagrams in Fig. 4. Mean values for the diagrams are compared to the core structure.

Model	Number of variable pairs	○—◯	—○	→	○→	↔	No link
1	120	9	3	2	13	0	93
2	120	8	2	4	12	0	94
3	153	12	1	1	16	0	123
4	120	8	5	1	13	0	93
5	105	9	1	4	10	0	81
6	171	10	3	2	15	0	141
7	120	9	2	2	14	0	93
8	153	10	4	4	12	0	123
9	120	11	0	4	13	0	92
10	136	9	2	1	14	0	110
11	136	11	3	3	12	0	107
12	105	9	1	1	12	0	82
Mean	130	10	3	2	13	0	103
Core	190	15	1	2	21	0	151
All	215	115	27	29	156	0	1232

* ○—◯ is a self-damping link, —○ and → are one-way links, and ○→ is a predator-prey link. There were no self-enhancing links (↔).

For the meso-zooplankton, Z_1 preferentially feeds on A_3, whereas Z_3 mostly consumes large flagellates. The interactions between the adult copepods (Z_1 and Z_3) and their immature forms (Z_2) change sign frequently; thus, links from Z_2 to the rest of the network are termed volatile. This volatility is undoubtedly related to the complicated life history of copepods, encompassing 12 developmental stages, and to the seasonal succession of dominant species. The links are almost always one-way flows but the direction of effect is largely dependent upon whether or not reproduction (including growth and development) predominates over predation. Z_3 is especially prone to macro-zooplankton predation by chaetognaths (*Sagitta* spp.), a variety of decapod larvae, and medusae. The self-damping of Z_2 and Z_1 are probably largely related to cannibalism, although Z_1 could be subject to predation from a predator, such as fish larvae, omitted from the loop diagrams. Z_3 was self-damped only once, when its predators were not present. Although each of the large predators was represented by a variable with more than

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[3] Part B of ESA Supplementary Publication Service Document No. 8525 consists of 27 pages of supplementary material by P. A. Lane on the collection and preparation of marine data for loop modelling. See footnote 2 for information about ordering this document.

TABLE 3. (A) Summary of agreement of data-directed changes and loop predictions.* Loop models are diagrammed in Fig. 4. (B) Summary of sign and location of parameter inputs (external environmental effects on the system) for the 12 models.

	Loop model											
	1	2	3	4	5	6	7	8	9	10	11	12
A. No. predictions	14	14	13	15	16	16	15	14	13	14	14	15
No. correct	13	13.5	12	14	15.5	16	14	13	12	13	13	15
No. incorrect	1	0.5	1	1	0.5	0	1	1	1	1	1	0
No. variables	15	15	14	16	18	17	17	15	14	15	15	16
B. Parameter input	$-A_1$	$+A_1$	$-A_2$	$-N_1$	$-A_2$	$+N_2$	$-N_1$	$-A_4$	$-N_2$	$+N_1$	$+A_2$	+SI

* Scoring of predictions explained in Results: Loop Models.

one species, the species within a variable appeared to have a functional coherence in their network relationships.

Two other miscellaneous groups, the mollusc (M) larvae and the polychaete-cirriped (PC) larvae, occurred frequently in the loop diagrams. Usually both variables were self-damped; it is possible that the polychaetes were preying upon the cirripeds. Occasionally PC appeared to consume M, and both variables were predators on A_1. PC also consumed immature copepods (Z_2). M ingested dinoflagellates (A_2) on five dates.

No two of the loop diagrams were identical to each other. This is expected because they were fitted to disparate sets of directed changes.[3] In several hundred loop diagrams, each of which involves a column of directed changes for each date, no two columns have been identical even over time scales much smaller than those used here. A simple calculation illustrates the reason: for 20 variables, each directed change can be +, −, or 0, or the variable can be absent. Therefore, there are 4^{20} or $\approx 1.1 \times 10^{12}$ possible patterns of directed change. Because of this large number, there is a very low probability that a particular column of signs would repeat itself, especially in a small sample size of 12 dates.

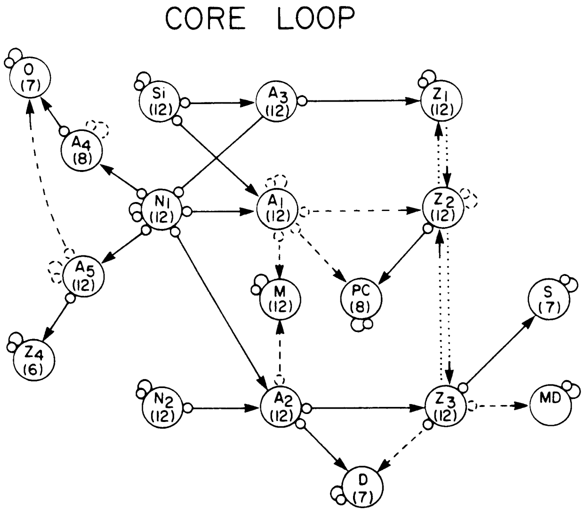

FIG. 5. Core network for Delaware Bay plankton community. Numbers in parentheses within each variable's circle indicate number, out of 12 dates, that the variable was present in individual networks. The key to the variables is given in the legend to Fig. 4 and the types of links are explained in the Table 2 legend. Volatile links are shown as dotted lines.

The results of comparing loop predictions to the qualitative data (directed changes) are given in Table 3. Usually there were one or two fewer predictions than variables in the diagram because of missing values for N_2 and sometimes Z_2. Of a total of 173 predictions that were possible for the 12 diagrams, 165 (94.8%) were correct. There were 9 incorrect predictions. There was not more than one wrong prediction per single loop diagram. A wrong prediction was recorded for complete disagreement in sign (+ vs. − or − vs. +) between predictions and data; a one-half wrong prediction was recorded for an ambiguous prediction when a prediction disagreed with the data and a zero was involved.

The sign and location of each parameter input are listed in Table 3B. Of the 12 inputs, six entered nutrient variables (three+, three−) and six affected algal variables (two+, four−). Generally, parameter inputs that enter above the nutrient level indicate that there is moderate enrichment in the environment. Algal parameter inputs occurred throughout the July–August period, at the end of October, once in December, and once in early May. At these times the nitrogen-phosphate ratio was low ($\approx$15–20). At the other times the higher nutrient ratios were coincident with parameter inputs to nutrient variables.

Community structure and stability

In Fig. 5, the core structure of the Delaware Bay plankton community is represented. This model is a summary network formed from the most prevalent linkages in the 12 individual models. Although a loop diagram for a single date can appear to have missing links, the core structure for an annual cycle represents the bulk of important relationships among the variables. The volatile nature of the immature copepod links is shown by using dotted lines. Each link drawn with a dotted line was equally probable among the interactions summarized in the individual diagrams. Cirripeds (C) only occurred on two dates as a variable distinct from PC; they were not included in the core. Significant seasonal phenomena are also incorporated into the core. For example, cladocerans occurred on only half the dates, but can be an important part of

TABLE 4. Summary of the distribution of loops by level in all individual networks and the core. Loop models are diagrammed in Fig. 4.

Level*	Loop model (network) 1	2	3	4	5	6	7	8	9	10	11	12	Total no. loops per level	Core
1	9	8	9	9	10	10	12	8	9	9	11	11	115	15
2	13	13	10	14	15	12	16	12	12	14	13	12	156	21
3	4	3	1	0	0	2	1	2	1	2	1	1	18	4
4	0	1	0	0	0	0	1	1	0	1	0	0	4	5
5	0	1	1	0	0	1	0	0	0	2	1	0	6	4
6	0	2	0	1	1	0	0	0	0	0	1	0	5	7
7	0	2	0	1	1	0	0	0	0	0	0	0	4	3
8	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Total no. loops per network	26	31	21	25	27	25	30	23	22	28	27	24		60
Mean loop length	1.8	2.8	1.8	2.0	2.0	1.8	1.7	1.8	1.6	2.0	1.9	1.6		3.0

* Loop level (=length) refers to the number of variables included in a loop.

the community when they are present. With the exception of April 1975, they were not present in the colder period from December 1974 to early May 1975.

In Table 4, the number of loops at each level up to level 8 is summarized for all of the loop diagrams as well as for the core network. No loops greater than level 8 occurred. The total number of loops and their weighted mean level are given. The average length of a loop ranged from 1.6 to 2.8 in the individual networks. Numbers of loops ranged from 21 to 31 per network. This preponderance of short negative loops partially suggests that the second stability criterion was satisfied. This criterion requires that there cannot be too much negative feedback at higher levels as compared to lower ones because longer loops represent longer time lags (Levins 1973).

A summary of the paths and loops in the diagrams appears in Table 5. The average model contained 368 paths, of which 317 were valid, and 26 loops. The absolute value of the matrix determinant ($|D|$) for the models had a mean of 53, while the mean feedback $F_n = -53$. F_n is the determinant of the matrix of all of the variables in a network. Usually this determinant will have many positive and negative subproducts. Most networks appeared stable. The only network of questionable stability was 2. Networks 3, 7, and 10 each had a small amount of positive feedback. All of the other models possessed only negative feedback, helping to satisfy the first stability criterion; this criterion requires that the feedback at each level be negative. Because of the additional variables and linkages in the core network, there were more longer positive and negative feedback loops for the core than for the individual networks. F_n of the core had 682 positive and 1178 negative terms; thus, the composite model cannot be assumed to be stable without additional analysis.

Measures of network properties are given in Table 6, including the number of variables (nodes; N), the number of links (L), connectivity (B), and the average connectance (%*C*). Connectivity values ranged from 2.43 to 3.16; percent connectance values ranged from 14 to 18% over the 12 networks, with a mean value of 17%.

The value of the macro-universe for the Delaware Bay networks, considering that there are 18 variables, is 3^{324} or 3.9×10^{154} possible networks. There were 3.7×10^{15} networks in the micro-universe. Many of these are undoubtedly not stable.

DISCUSSION

By reference to the four aspects of the analogy of nature's kaleidoscope, the results for Delaware Bay can be interpreted in a broader framework.

Symmetry

In nature's kaleidoscope, symmetry involves the concept of the internal order of natural communities with a peripheral notion of invariance. The identifi-

TABLE 5. Summary of the total number of paths, valid paths,* and valid complements,* and the absolute value of the determinant of the whole system (|D|). In each case the feedback of the whole system (F_n) equals − |D|. Loop models are diagrammed in Fig. 4.

Model	Total paths	Valid paths	Valid complements	|D|
1	407	385	2536	54
2	761	601	2341	34
3	192	189	852	19
4	393	277	884	15
5	455	373	3794	64
6	262	251	3224	64
7	413	413	5762	124
8	316	244	966	25
9	171	149	1511	44
10	481	360	2648	66
11	379	363	3279	79
12	183	183	2292	48
Mean	368	317	2507	53
Core	3208	2396	96 020	496

* A path complement is the community matrix minus the given path. It must be nonzero for the path to operate in the network. Nonzero feedbacks are termed valid complements; a path with a valid (i.e., nonzero) complement is termed a valid path.

TABLE 6. Measures of network properties. n = no. nodes or variables, $\%S$ = percent of self-damped variables, I = no interactions or links, B = connectivity, and $\%C$ = percent connectance. Loop models are diagrammed in Fig. 4.

Model	n	$\%S$	I	B	$\%C$
1	15	60	40	2.67	18
2	15	53	40	2.67	18
3	14	64	34	2.43	17
4	16	56	40	2.50	16
5	18	56	45	2.50	14
6	17	59	42	2.47	15
7	17	71	46	2.71	16
8	15	53	38	2.53	17
9	14	64	35	2.50	18
10	15	60	41	2.73	18
11	15	73	41	2.73	18
12	16	69	41	2.56	16
Mean	16	62	40	2.58	17
Core	19	15	60	3.16	17

cation of symmetry with associated invariants and changes involves questions that are fundamental to many areas of science (Weinberg 1977). What is a system? Why do some parts stay the same? Why do some parts change? Symmetry has not been systematically explored in biological systems. Monod (1969) stressed the overall importance of symmetry when he wrote, "For without invariants, without order, without symmetry, science would not only be dull; it would be impossible."

Many ecologists have been reluctant to recognize the symmetry or internal order of natural communities. Community structure, however, is a consequence of the interaction among the parts; it cannot be deduced from the mere compilation of those parts. Interconnection in ecological systems is often ignored, yet it is an integral part of the internal order of these systems. Proponents of the individualistic school of community ecology have sometimes denied the existence of community-level properties or invariants or even the need to look for them. At present, there are few rigorous community descriptors or whole-system properties for ecosystems and our whole-system methodologies are crude and undeveloped. Thus, it has been difficult to distinguish real patterns from reflections in nature's kaleidoscope and some observers may remain reluctant to do so.

The core.—The plankton kaleidoscope based on taxonomic forms (Fig. 1) has been transformed to one based on loop structures (Fig. 6). Annual parameter inputs turn the outside of the viewing tube, and it rotates with shifting linkages throughout the year. With close examination, there is a faint remnant of the original geometric symmetry of Fig. 1 shown in the alternating linkages around the outside of the kaleidoscope tube in Fig. 6. The original eight-part geometric symmetry has been mostly replaced, however, with internal order of a higher level, represented by the core loop structure in the center of the kaleidoscope.

Each individual loop model is based on the smallest number of links and variables that would explain the observed data patterns for directed changes. Thus, the most important pathways are represented in the networks. Other links causing ambiguity are not included. This does not mean that the excluded links are not present in nature but rather that their effects are probably much weaker than those of the included links. The core structure for the Delaware Bay plankton community can be considered a canonical form for the structure of marine plankton communities. The core essentially summarizes the individual loop diagrams that constitute a set of alternative descriptions for an ecosystem, and the core provides a framework for much associated biological and ecological theory.

Marine loop models have been made for experimental systems (Marine Ecosystem Research Laboratory [MERL] mesocosms at the University of Rhode Island and the tower tank, part of the Dalhousie Aquatron Facility) and field communities (in Canada: Bedford Basin, Nova Scotia; St. Margaret's Bay, Nova Scotia; in the USA: Narragansett Bay; Long Island Sound; Delaware Bay) (Lane 1982, 1985, Lane and Collins 1985; this study). All of these ecosystems possess similar core structures even though the data sets representing them are of different types and they were modelled independently. This indicates that the core is

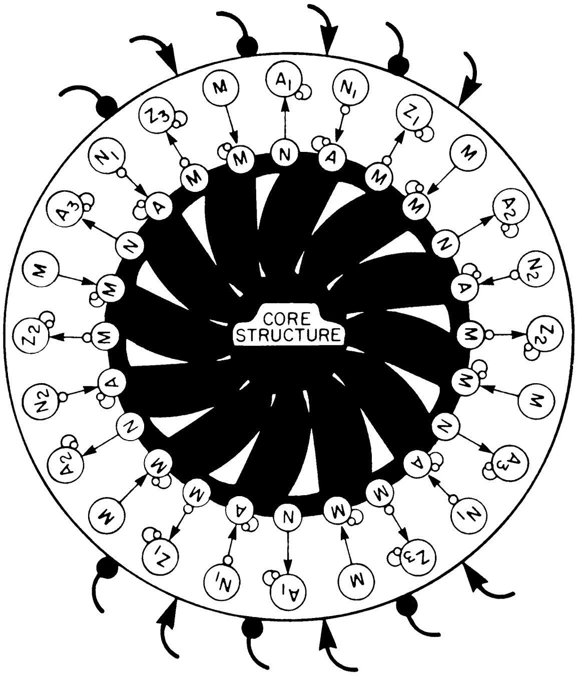

FIG. 6. Loop model kaleidoscope for a plankton community, with change incorporated into the symmetry depicting an annual cycle. Parameter inputs, which turn the viewing tube, are represented by dark ⌒ (positive inputs) and ⌒● (negative inputs). Most of the geometric symmetry of Fig. 1 has been replaced with temporal symmetry captured by loop analysis. Abbreviations are defined in Fig. 4 legend.

robust and in some sense represents invariant aspects of the internal order or symmetry of marine plankton communities. The core structure may not be observed in nature; but it is a theoretical construct about which the alternative states are continuously rearranged. Once a core structure has been delineated it can be used for analyzing subsequent data sets for the same environment. Usually only a few minor changes are needed in the core structure to explain most of these subsequent empirical observations. The core for Delaware Bay has ≈60 feedback loops and 3200 pathways among all combinations of connected variables. Not all of these pathways were operative because many would not have valid complements. The overall feedback, F_n, has many positive terms. With that degree of positive feedback, the core, if stable, is not strongly so. In addition, almost all of the predictions of changes in standing crops of core variables are ambiguous. There are simultaneous positive and negative community effects between each pair of variables.

Connectance.—Not all interactions of components are equally probable; but it is not obvious what the constraints on the type of interaction are or even the average level of variable connectivity. What is the total set of interactions and hence of patterns like? Is it large or small? Can it be handled by an abacus, a calculator, the human mind, a large computer, or no known computing machine?

The loop diagrams exhibited a mean level of connectance of ≈17% of the maximum number of possible interactions. Gardner and Ashby (1970), working with randomly generated networks, found connectance values in a similar range for stable networks. They concluded that the critical level of connectance was 13% between almost certainly stable and almost certainly unstable networks. These authors had all off-diagonal elements assume values +1 to −1 but did not include self-loops or diagonal elements in their calculation. Thus, their 13% value is close to the mean of 18% found here, for which all self terms were included.

If the core is unstable, the reason may not be that it represents so many alternative stable states; rather these stable states may exist because the ecosystem cannot exist in its unstable core form. When people design and build machines, they reduce and constrain interconnection. If there is too high a degree of interconnection among the parts, a machine will not work. Perhaps ecosystems have evolved bounds on interconnection or connectance so that only a constrained degree of strong interactions exists at a particular instant (May 1973).

The configuration of the loop models relates to the feedback relationships of the overall network structure. Each loop represents a time lag and thus embodies a temporal dimension. Loop diagrams essentially extract a set of temporal relationships (especially those of predator-prey pairs) from the myriad of potential ones operative in an aquatic ecosystem. Not all of these relationships, however, involve substantial energy flows. Symmetry or internal order arises from the interplay of these temporal relationships. Biomass is apportioned in the community by virtue of aggregating species and nutrients into loop variables. In one sense, connectance is a set of temporal relationships among a set of biomasses. Constraints on the symmetry of these ecosystems may result more from temporal patterns than through solely energetic restraints. Although inherent in the notion of energy transfer is a temporal dimension, these energetic restraints do not uniquely determine the temporal patterns in a community. It is interesting that the published range for ecological efficiency, which is defined as the ratio of assimilation values for two adjacent trophic levels, is close to the range of maximum connectance required by stability considerations. Perhaps this result has more significance than a happy coincidence. This similarity requires further examination, however, since connectance can be expressed by several formulations. J. A. Wright and P. A. Lane (*personal observation*) describe four basic types of connectance-connectivity measures with associated scaling factors.

In time, perhaps, it will be possible to express the internal order of natural communities in terms of symmetry principles with corresponding conservation laws like those used in physics. One of the current theories in aquatic ecology is the size-spectrum theory (Sheldon and Kerr 1972). It holds promise for identifying whole-system properties. The size spectrum has been determined to be a flat curve in a plot of particle concentration (biomass) vs. the logarithm of size over several trophic levels. Some curves have been empirically verified and are intimately related to predator-prey interactions. Biomass (and the energy it implies per size class) appears to be a conserved factor. Perhaps size spectrum theory incorporates a conservation principle for the symmetry found by using loop analysis.

Symmetry also relates to the notion of emergent properties and the choice of scale. There are emergent properties on all temporal-spatial scales. In a deterministic model with autonomous equations, a single variable can only give equilibrium or explosion. With two variables one can get limit cycles, and with three variables, chaos. Thus, it doesn't make sense to say that chaos was sitting in one variable and was only brought out when two more were added. If a predator that ate prey was not otherwise affected by the prey, the prey population might disappear. If prey increased the number of predators but were not affected by them, the predator population would increase indefinitely. It is the interrelationship between the predator and prey, represented by the negative feedback loop, that produces oscillation. There is always individual choice for a human observer as to the scale of the system to focus on, but each choice constrains other system properties because of consistency. The predator-prey oscillation can be represented by a simple equation, but if you look only at the prey, the predator becomes an external input, varying for reasons that are unknown. One can still track the response of prey to a varying predator and get a sufficient explanation of the subsystem; however, expanding to include the predator means that the input is less arbitrary.

Consider a large bay and a population of molluscs on a rock, or crustaceans in a tide pool. If we choose an individual rock or tide pool as a community, these animals are not self-reproducing; pelagic larvae enter from outside the system and the variable in question is self-damped, with the rate of input as an external parameter. If we now take the whole bay, the population is self-reproducing and the self-damping of the variable disappears. The makeup of the total population, which was an arbitrary parameter from the point of view of a local community, is now determined from within the system. So, yes, the observer has freedom of choice of the scope of the system, but must then model in a way consistent with that choice. The emergent properties related to autonomous oscillations arise only when both predator and prey are included, since there are no surprises about a variable oscillating in response to an oscillating input. In general, dynamic properties will be more accounted for as intrinsic in larger rather than smaller systems. In small systems, however, they are accepted as given and their consequences are traced.

Change

Change is ubiquitous in nature. As in nature, it is difficult to reconcile those things that change and those things that are constant in a set of loop networks. The core structure has a sort of robust reality over many coastal marine ecosystems that is not the result of sleight of hand or a trick of kaleidoscope mirrors. Yet the core is an abstraction. Since it is a compilation of several instants in the annual cycle of a plankton community, it integrates change into the symmetry. It captures fleeting images of community behavior throughout an annual cycle; however, the biology is constrained: historically, evolutionarily, behaviorally, physiologically, morphologically, and energetically. Now that the core has been identified, these constraints need to be elucidated. Some of the changes may even be selected for, for example, the volatile interactions between immature (Z_2, see Fig. 4) and adult (Z_1, Z_3) copepods. Whether by chance or design, these links serve to suppress many long loops in marine ecosystems, loops that could be destabilizing. Interpreting the biological nature of a particular link in relation to whole-system properties via loop diagrams offers some exciting research possibilities and gives a theoretical framework to assess the ecological ramifications of particular links and variables.

Change is intimately associated with stability but they are not mutually exclusive concepts. For example, the stable age distribution concept in population ecology involves changing numbers of individuals in each age class from one generation to another, yet the proportions of individuals per age class remain constant. Levins (1975) uses the metaphor of moving equilibrium for loop models; the system is always changing, but its parameters are moving slowly enough that the system returns to its steady-state trajectory after perturbation. Thus, the steady-state values are not constant. Stability is not so much a property of an ecosystem as a relative statement about its state in regard to its environment. It is still an open question whether or not marine plankton communities have a steady-state nature. In addition, loop analysis includes mathematical constraints (for example, feedback sign, complement formation) on the structure of its models, constraints that affect stability calculations. It is yet to be proven whether or not these mathematical constraints realistically represent biological ones. The possibility of mathematical artifacts always exists, especially with a new theoretical methodology.

Perturbation

Perturbation is related to the node of entry and the sign of the parameter inputs. These inputs were not selected arbitrarily in the Delaware Bay analysis. Large numbers of potential inputs did not work in fitting the networks to the data set. The patterns of directed changes are such that the choice of parameter input is greatly constrained. This is not to say that the parameter inputs selected here are unique, the most biologically realistic, or the optimal ones. At present, the models are fitted by hand and it is impossible to exhaust all possibilities.

I can, however, make some general observations about how perturbations affect marine ecosystems. In several marine and freshwater communities, 85% of all perturbations enter the bottom of the trophic hierarchy. This is interesting in that there has been longstanding controversy in aquatic ecology between proponents espousing nutrient limitation and those espousing predation control. The logic of their justifications is reminiscent of the limiting factor controversy (Likens 1972, Lane and Levins 1977). Actually both groups are right and both are wrong. Most perturbations enter through nutrients but most of the structure of the network comes from predator-prey interactions. The antagonists have been arguing about two different aspects (the driving forces and the links) of a single entity, the aquatic ecosystem. Both groups are wrong in that neither a driving force nor a link "controls" the total network. The manifestation of a parameter input arises because of interconnection within the total structure and its sensitivity to environmental variation.

When nitrogen/phosphorus ratios were high, there were more parameter inputs to nutrient variables with the exception of November 1974. For half of the annual cycle, these ratios were uncharacteristically high compared to other Atlantic coastal environments (Maurer et al. 1978). At lower N/P ratios, variables higher in the trophic hierarchy exhibited increased sensitivity to environmental variation. The biological mechanisms for input sensitivity are unknown. To date, most of the marine loop models have involved nutrient-enriched ecosystems in both field and laboratory. With strong enrichment, such as in the current experiment at MERL at the University of Rhode Island, parameters enter increasingly higher in the trophic hierarchy over an increasing trophic gradient; however, the N/P ratios remain characteristic at ≈ 10–20. I have not had an opportunity to study other types of marine perturbations (for example, oil pollution), which would probably exhibit different parameter inputs to the plankton network. Some inputs can lead to structural changes in the networks. For example, in lakes undergoing acid precipitation stresses, there is a definitive reduction in diversity, and there are other structural alterations (Lane 1985, Lane and Blouin 1985). The variables associated with nutrients are also more diverse and volatile in freshwater models than in marine ones.

In many sets of loop models, the signs and locations of parameter inputs often change from one date to the next without any clear pattern. My resolving power is not sufficiently developed to identify the underlying causes for these shifts. It may be simply the pattern of environmental variability or there may be inherent network consequences for particular variables that either buffer or sensitize them to environmental variation at different times of the year. The only network property firmly identified is associated with satellite variables. They have only one input and one output with another variable and they buffer that variable from environmental change. As more measures of network properties are developed, perhaps other structural features will help explain the shifts in parameter input. Patten et al. (1976) said that cause and effect arise everywhere in ecosystems. To solve many types of impact assessment problems, it will be necessary to develop a better theoretical understanding of the shifts in parameter inputs and their relation to cause and effect in network structure.

Observing mode

Observing mode includes not only the observer (intrinsic models or intuition) but whatever tools (extrinsic models) the observer uses to make observations. A brief comparison of Figs. 1 and 6 will emphasize the different observations that arise from different observing modes. The observer interacts with the systems he describes. Science is not the great objective activity we claim it is; and to some extent we all participate in this deceit. I have used loop analysis here as a tool for observing natural communities and making some statements about them. The way loop analysis is used is not automatic; it is not like pushing a button on an autoanalyzer and having nutrient concentrations read out on a microprocessor. I used biological intuition at several steps in the analysis. This is true of all types of ecosystem modelling and is not unique to loop analysis. My intuition consists of my set of intrinsic models about how nature works. These models are my own property; sometimes they change and some are shared with other investigators, but my set is not identical to anyone else's set. This applies to all observers and precludes the absolute objectivity of science.

There is always the possibility that my biological intuition has totally failed me, and that the kaleidoscope I am peering into is more like a random number generator than an instrument for discerning "beautiful forms" in natural communities. Other workers have commented on the large number of possible existing networks. For example, May (1973) conducted a computer study of stability and complexity in randomly-generated ecological networks; he found there were googols (10^{100}) of biologically reasonable systems. Lawlor (1978) demonstrated that for 40 species there would be 10^{764} networks of which 10^{500} would be biologically reasonable. They would be so sparse that random sampling would never find any of them. He further estimated that for a 20-species network, there is a 95% expectation of never encountering an actual ecological system in 10 yr if one million hypothetical networks per second were generated by computer. Thus, there is less than one chance in a googol of constructing an ecosystem with a random number generator. An aquatic environment can possess 1000 species. Thus, in the sense of Lawlor (1978) the networks in the water may exceed the number of sand grains on the beaches. Obviously, the number of possible networks is much greater than that which could be systematically studied and/or experimentally verified.

Loop analysis, as an observing mode, provides a convenient way for examining potential networks and discarding unstable ones. At present, however, a given loop diagram cannot be deemed the best or the only one to fit a set of predictions, since the sizes of the loop universes are also very large. I am not yet able to specify the meso-universe precisely. The meso-universe is reachable through working simultaneously from a revised micro-universe and a macro-universe. The micro-universe (MI) needs to be made smaller by weighting variables and linkages by their probability of occurrence. All of the networks in this new set (termed MI**) would need to be checked for data agreement with loop predictions. If the resulting number of agreeable networks is manageable, then the meso-universe can be reached by systematically improving MI** with biological intuition and testing for data agreement. Likewise, the macro-universe can be shrunk to include only those networks that are stable and for which biological linkages have been previously observed in nature. This gives an outer bound to the calculation. Undoubtedly, some other conditions, such as mean connectance, will have to be employed. For example, the Delaware Bay MI involves all 18 variables in the core structure even though there was a mean of only 15.6 variables per individual diagram. The addition of two or three variables can greatly expand a universe set.

In much of the modelling effort to date for all aquatic ecosystems, agreement of the model predictions with empirical observation has ranged between 85 and 97% (P. A. Lane, *personal observation*). Until the universe problem is systematically explored, however, one cannot be satisfied with even 97% agreement. It must be known whether or not other networks would give a similar or better agreement percentage. This is termed the uniqueness problem. In developing hundreds of loop models, I have found that as agreement reaches the 90% level, it is difficult to make major changes in the model and obtain a level of satisfactory agreement consistent with biological reality. Note that as the number of variables increases, the percentage of networks having a desired row of predictions decreases dramatically: with 2 variables, 11%; 3 variables, 4%; 4 variables, 0.01%; and 10 variables, 0.0017%.

Ecologists often complain of the great complexity at the ecosystem level, which they feel frustrates their efforts to identify patterns and interactions within the systems they observe. Rosen (1977), however, states that complexity is not an inherent property of a system, but rather a consequence of the number of ways observers can interact with it, producing multiple descriptions. Thus, an observer's recognition of symmetry, change of state, and stability under perturbation are contingent on the particular state description being used. Loop analysis provides a unique view of nature. A systems analyst using computer simulation or a biostatistician performing principal components analysis would undoubtedly see different community patterns by peering into nature's kaleidoscope. None of these descriptions is wrong, but each contains a different type of information.

When I was a child, kaleidoscopes were my favorite toys; I had a whole collection of them. I spent hours studying the patterns and alternately trying to find new and then repetitive ones. I was convinced that the complexity in the patterns must be related to the complexity of the machine. My curiosity so overcame me that I risked a parental reprimand and completely disassembled one of my precious possessions. I can remember being very disappointed at the collection of simple objects that fell onto the table as I took the instrument apart. How could a few bits of glass, some fragments of mirror, and a cardboard tube produce such a wondrous array of images? I was never able to fit the sorry pile of pieces together. Regardless of the observing mode employed, reductionism, which in the extreme is analogous to dismantling nature's kaleidoscope, precludes the delineation of symmetry, change, and perturbation at the community level. Meaningful theory cannot be developed if ecologists are equipped only with some bits of glass, mirror fragments, and a broken cardboard tube.

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LITERATURE CITED

Gardner, M. R., and W. R. Ashby. 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. Nature **228**:784.

Hull, C. H., and N. H. Nie. 1981. SPSS update 7-9. McGraw-Hill, New York, New York, USA.

Joy, W. N., R. S. Fabry, and K. Sklower. 1980. UNIX programmers manual. Computer Science Division, Department of Electrical Engineering and Computer Science, University of California, Berkeley, California, USA.

Lane, P. A. 1982. Using qualitative analysis to understand perturbations in marine ecosystems in the field and laboratory. Pages 94–122 *in* P. Archibald, editor. Environmental biology–state of the art seminar. EPA-600/9-82-007. Office of Exploratory Research, United States Environmental Protection Agency, Washington, D.C., USA.

———. 1985. Peering through nature's kaleidoscope at a marine plankton community. *In* R. Beyers, editor. Environmental biology–state of the art seminar. Office of Exploratory Research, United States Environmental Protection Agency, Washington, D.C., USA, *in press*.

Lane, P. A., and A. C. Blouin. 1985. Qualitative analysis of the pelagic food webs of three acid impacted lakes. Internationale Revue der Gesamten Hydrobiologie **70**:203–220.

Lane, P. A., and T. M. Collins. 1985. Food web models of a marine plankton community: an experimental approach. Journal of Experimental Marine Biology and Ecology, *in press.*

Lane, P., and R. Levins. 1977. Dynamics of aquatic systems. II. The effects of nutrient enrichment on model plankton communities. Limnology and Oceanography **21**:454–471.

Lawlor, L. R. 1978. A comment on randomly-constructed model ecosystems. American Naturalist **112**:445–447.

Levins, R. 1973. The qualitative analysis of partially-specified systems. Annals of the New York Academy of Sciences **231**:123–138.

———. 1975. Evolution in communities near equilibrium. Pages 16–50 *in* M. Cody and J. Diamond, editors. Ecology and evolution of communities. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Likens, G. E., editor. 1972. Nutrients and eutrophication: the limiting nutrient controversy. American Society of Limnology and Oceanography Special Symposium **1**.

Mason, S. J. 1953. Feedback theory—some properties of signal flow graphs. Proceedings of the Institute of Radio Engineers **41**:1144–1157.

Maurer, D., L. Watling, R. Lambert, and A. Pembroke. 1978. Seasonal fluctuations of water quality (nutrient and pigments) in Lower Delaware Bay. Hydrobiologia **61**:149–160.

May, R. M. 1973. Stability and complexity in model ecosystems. Monographs in population biology, number 6. Princeton University Press, Princeton, New Jersey, USA.

Monod, J. 1969. On symmetry and function in biological systems. Pages 15–28 *in* A. Engstrom and B. Strandberg, editors. Symmetry and function of biological systems at the macromolecular level. Wiley Interscience, New York, New York, USA.

Patten, B. C., R. W. Bosserman, J. T. Finn, and W. G. Cale. 1976. Propagation of cause in ecosystems. Pages 457–579 *in* B. C. Patten, editor. Systems analysis and simulation in ecology. Volume 4. Academic Press, New York, New York, USA.

Rosen, R. 1977. Complexity and system descriptions. Pages 169–175 *in* W. E. Hartnett, editor. Systems: approaches, theories, applications. D. Reidel, Dordrecht, The Netherlands.

Sheldon, R. W., and S. R. Kerr. 1972. The population density of monsters in Loch Ness. Limnology and Oceanography **17**:796–798.

Swift, D. G. 1980. Vitamins and phytoplankton growth. Pages 329–370 *in* I. Morris, editor. The physiological ecology of phytoplankton. Studies in ecology, Volume 7. University of California Press, Berkeley, California, USA.

Webster's New International Dictionary of the English Language. 1961. Allan, W. A., T. A. Knott, and P. W. Carhart, editors. G. and C. Merriam, Springfield, Massachusetts, USA.

Weinberg, S. 1977. The forces of nature. American Scientist **65**:171–176.

Weisskoff, V. F. 1969. The role of symmetry in nuclear atomic and complex structures. Pages 28–35 *in* A. Engstrom and B. Strandberg, editors. Symmetry and function of biological systems at the macromolecular level. Wiley Interscience, New York, New York, USA.