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A CRITICAL EVALUATION AND EXPERIMENTAL TEST OF THE CONSERVATIVE ASSEMBLY HYPOTHESIS

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

David A. Kenny

May 1990

ABSTRACT

There are two basic approaches to community ecology. The first examines the role that processes occurring *in situ* have on maintaining structure. The second, on the other hand, explores the "rules" responsible for creating structure, i.e. assembly mechanics. Recently, an assembly rule, the conservative assembly rule (Sugihara, 1982), was proposed to explain certain topological regularities in community structure. The rule states that species invading a community will invade more readily when they overlap competitively with single guilds rather than multiple guilds.

As a test of this hypothesis, two sets experimental microcosm communities were invaded with an identical species set, which included *Hydra littoralis*, *Cyclops vernalis*, *Moina sp.*, and *Cypris sp*. However, these microcosms received the species with two different invasion orders, one conservative, one non-conservative. The conservative assembly hypothesis would predict that species invading non-conservatively should be less persistent.

The results of this experiment indicate that, in this case, conservatively invading species were no more persistent than those invading non-conservatively. Apparently, the impact of predation in these systems was so strong that the competitive effects upon which conservative

assembly is dependent were overridden. These results should be viewed as a thought provoking counter example which will help us to refine the conservative assembly concept, rather than an outright refutation of the hypothesis.

TABLE OF CONTENTS

CHAPTER I

INTRODUCTION

From the beginning of its conceptualization, the food web has been recognized as an important level of community organization in which researchers have attempted to elucidate common patterns which may convey some insight into the mechanisms responsible for pattern. Most recently, food web theorists have examined the assembly of food webs and its relationship to important community properties such as stability and persistence. In addition to the search for general trends in food webs, researchers have also sought underlying mechanisms which would fully explain the observed patterns. However, the quest for a unifying theory of food webs has to date yielded frustratingly little.

Nature's Network

What is it about food webs that makes them a singularly interesting, yet perplexing avenue of ecological inquiry? Perhaps it is the fact that the food web, or our conception of it, is the epitome of the continuity of nature, an idea which is the very basis of ecology. Indeed, the food web could arguably be viewed as the conceptual foundation from which all other approaches to characterizing community pattern and process have emerged. Since the early days of

Elton (1927), whose energy flow paradigm went unchallenged for until relatively recently, food webs and their constituent food chains have been thought of as basic to our understanding of ecology in general. Important processes such as predation, competition, nutrient cycling, and energy flow are either explicitly or implicitly present in every food web graph, and it is thus a natural starting point for our foray into the complex world of species interdependence. However, despite the fact that the food web has been recognized as a dynamic structure and that our understanding of pertinent variables has increased, our method of illustrating this complex entity, namely as a 2-dimensional graph, has received very little refinement.

This is no doubt due in part to continuing efforts to transform ecology into a "hard science." Hard sciences require data which can be analyzed mathematically, and characterizing complex systems as graphs meets this requirement. Additionally, graphs are a succinct way of conveying information that would take quite some time to describe verbally, i.e. the flow of some commodity, such as carbon or energy, from primary producer to top consumer, as well as the structure of species interactions such as predation and competition.

It is clear that the simplicity of the graph, and its efficiency as a communicative tool, makes it an ideal format in which to search for interesting patterns. Furthermore,

an increasing number of researchers are taking a graph theoretical approach to food webs and using the information this yields to make generalizations about community structure and assembly. The usefulness of these recent efforts, however, is dependent upon how well the graphs we use actually represent "real" food webs. Precision is desirable, and graphs are precise. The question is, are they accurate? In order to answer this question, we must first examine the concept of a food web, as well as the ecologist's concept of a graph as it applies to food webs. Only then will we be able comment thoughtfully on the validity of the graph theoretical approach.

What is a food web? Defining a food web is difficult not only because it is a set which incorporates a large number of elements operating at disparate levels of scale, but because it is virtually impossible to come up with a definition which is independent of a symbolic representation. The very word "web" implies a 2-dimensional structure composed of intersecting lines. While such an illustration is useful heuristically, the conceptual boundaries it creates may leave us vulnerable to the omission of important patterns that are outside the realm of that which is depictable by such an object. Furthermore, the possibility exists that some of the observed patterns to which we have attributed significance are mere artefacts of a graphical characterization. We must keep in mind that the abstrac-

tion which theorists term a food web, which may be defined mathematically and verbally, is distinctly different from the "food webs" which have been documented by empiricists. To be sure, something approximating our concept of what a food web should be exists in nature. Our capacity to accurately measure it, however, is a different matter entirely. I would like to consider three components of the food web definition, the empirical, the abstract/theoretical, and the graphical.

The Empirical Concept

The empirical definition of food web involves little more than a census of "all" the species in a community and the trophic interactions among them. This information is be most often represented in matrix form, which allows the application of formal mathematics to examine its structure. Additionally, the matrix is intermediate step in the conversion of the empirical data into graphical form, which is the preferred mode of depiction. To evaluate this approach, we should ask ourselves two questions. First, are we collecting data in a such a manner that the graphs thus produced have real meaning, and second, is the compression of a multidimensional system into a two dimensional representation acceptable.

Unfortunately, the level of resolution necessary to truly document all of the species and their feeding interac-

tions in most communities is nearly unattainable. Thus, many of the species and interactions in a given web are potentially missed. This would be less of a problem if there were a universal standard for what constituted an adequate sampling effort where food webs are concerned. While the census of species populations is fairly straightforward, determining what level of trophic interaction justifies a depicting link between two species populations is not. One could set an arbitrary percentage composition of the diet, and include only ingested items which exceed this value as prey. This is a common approach, but it is doubtful such a value could be standardized because of the vastly different ways in which resources are utilized by different organisms. For example, grass may account less than a fraction of a percent of a given carnivore's diet, but the vitamins provided may be essential to its existence. Additionally, dietary analysis of all of a food web's constituent species would be impossible.

Ideally, since distinct species populations have distinct dynamical behavior, all entries in food webs should be reported as biological species. Unfortunately, many webs, in addition to having entries at the species level, have entries presented at the level of Class, Order and even Kingdom. Such skews in distinction could be tolerated if they were randomly distributed among trophic levels; unfortunately, they are not. Certain kinds of organisms tend to

be classified much more broadly than others. Also, entries at lower trophic levels are typically placed in more general categories than those at higher trophic levels, being often lumped into broad functionally defined groups such as "grazer" or "producer." Thus, when we speak of the species in a web we are referring not to a biological species, but to sets of organisms which share similar prey and predators, and which may be comprised of categories reported separately by the original researchers (Cohen and Newman, 1986). Such sets are referred to as "functional" or "trophospecies" species (Yodzis, 1989). Some researchers (Cohen, Sugihara) claim this sort of lumping is justified because it does not change graphical properties. These are major drawbacks, as they could potentially affect a number of important food web properties.

The Graphical Concept

Camerano (1897) was among the first to represent a community as a set of compartments representing groups of functionally similar animals and plants, which were connected by a line segment to other compartments with which they interacted trophically. These compartments and line segments comprise a mathematical object known as a graph. Typically, the compartments are called vertices and the line segments edges. Trudeau (1976) offers the following formal definitions:

Definition 1. (Definition 5 of Trudeau) A graph is an object consisting of two sets called its vertex set and its edge set. The vertex set is a finite non-empty set. The edge set may be empty, but otherwise its elements are two-element subsets of the vertex set.
Definition 2. (Definition 6 of Trudeau) The elements of the vertex set of a graph are called vertices and the elements of the edge set are called edges.

An example of a graph is given in fig. 1. This graph is comprised of a vertex set v = { A,B,C }, and an edge set e = { {A,B}, {B,C} }. An edge is said to be incident to a vertex if that vertex defines one of its endpoints. Two vertices are adjacent if they are joined by an edge. A vertex on which k edges are incident is said to be of degree k. A vertex which is not incident to an edge is said to be isolated.

Graphs can be described in terms of the number of vertices and edges. A graph with n vertices and k edges is said to be of order n and size k. The connectance of a graph is the number of edges observed in the graph over the total number possible. Since a true graph cannot have vertices adjacent to themselves (loops) or more than one edge incident to the same vertex pair, the maximum number of edges possible is n(n-1)/2, where n is the number of vertices. The connectance values for several graphs of order 8 are given in fig. 2. Graphs which have loops and multiple edges are properly termed multigraphs and are useful for illustrating Lotka-volterra models of food webs.

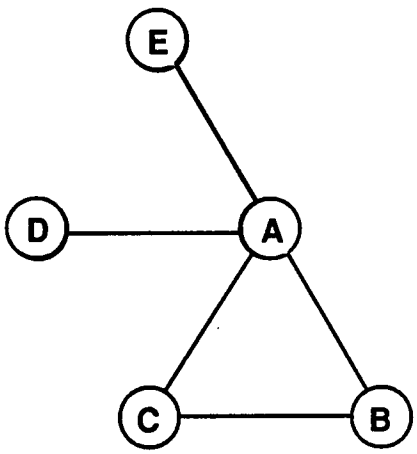
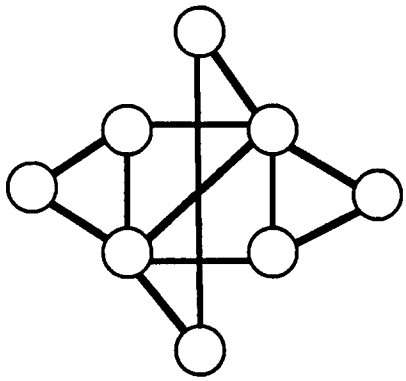
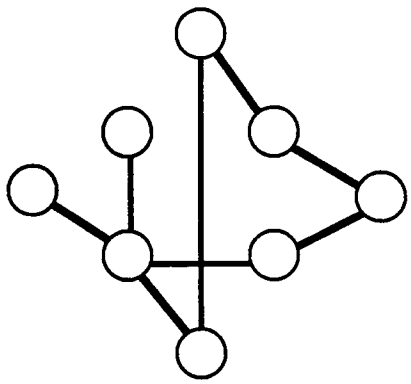


Fig. 1

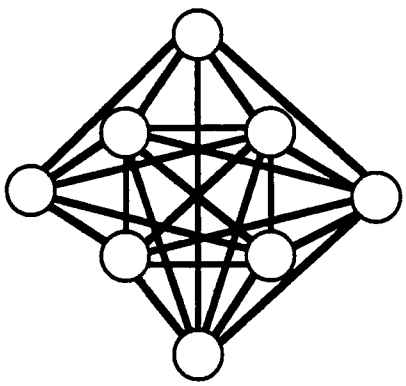
Graph with vertex set V = {A, B, C, D, E} and edge set E = {(A,B), (B,C), (C,A), (A,D), (A,E)}.



C = .429



C = .286



C = .857

Fig. 2

Connectance values for 3 graphs of order 8. Connectance C = (n(n - 1)/2)/k, where n is the number of vertices and k the number of edges.

Multigraphs are rarely used, however, to represent food webs themselves.

While all food webs may be represented by a graph, not all graphs are qualified to represent food webs. A food web must be represented by a special type of graph known as a connected graph. A connected graph is a graph that has no isolated vertices. The only exception is a graph containing one vertex, which is by convention considered to be connected to itself. The qualification is intuitive. Every member of a food web must interact with at least one other member of that web.

Aside from being connected, graphs of food webs are r-partite. Bollobas (1979) defines an r-partite graph as a graph with vertex classes V_1, V_2, ... , V_r, where each vertex in the graph belongs to only one class, and no edge joins vertices in the same class. In the case of food web graphs, r has a direct correspondence with the number of trophic levels in the web. One might argue that it is possible for a species in a particular trophic level to feed on another species in the same level. However, while such cases exist in the current compendium (Briand and Cohen, 1984), they are rare, and such graphs can always be redrawn as r-partite graphs. For simplicity's sake, all graphs referred to in this paper are assumed to be r-partite.

While the connected graph provides a basic framework for illustrating food webs, there are some additional

embellishments that are commonly employed. For instance, it may be useful to give an edge joining two vertices direction. Graphs that have directed edges are known as digraphs. The direction of the edge can be either from predator to prey or vice versa. The former is more common and is favored by those interested in representing dynamical effects, whereas the latter is often used to represent energy flow. It should be noted that, because of their partite nature, food web graphs are always implicitly directed even when they are not illustrated as such. Additionally, while multiple edges are prohibited in connected graphs, each edge is understood to represent both the effect of predator on prey and vice versa. Additionally, it may be helpful to think of edges as having magnitudes, especially for dynamical questions. Unfortunately the information required to assign a magnitude to a particular edge is not typically included in food web data. It is important to remember that graphs (and food webs) exist independently of illustration.

The Theoretical Concept

Consumption of resources and the resultant transfer of nutrients and energy are essential to ecosystem function. It is therefore no surprise that food webs have become, as Paine (1988) puts it, "grist for theoretical development." As mentioned earlier, a food web is nothing more than the

trophic interactions among all of the species of a given community. The real problem, however, is not defining what a web is, but rather, how it works. The discovery of pattern in food webs has led to the birth of food web theory, whose proponents search for the causes of these patterns and their relevance to ecology as a whole. Generalizations have been made regarding such food web properties as predator/prey ratios (Cohen 1977, Jeffries and Lawton 1985), the maximum length of food chains (Pimm, 1980; Yodzis, 1984), the distribution of species among trophic levels, the proportion of trophic links at different trophic heights, and the ratio of trophic links to species (Briand and Cohen 1984; Cohen and Briand 1984; Rejmanek and Stary 1979), and the number of species which feed on more than one trophic level (Pimm and Lawton 1978). Explanations for these patterns have typically fallen into two categories based on whether such patterns are ascribed to dynamical (May, Pimm, et al.) or energetic (Elton 1927, Yodzis, et al.) causes. Additionally, a third area based on graph theoretical formalisms (Cohen, Sugihara, et al.) has emerged. It appears that what is needed at this point is a concerted effort to synthesize the common elements of these approaches into a single unified theory.

Historically, the food web has been the conceptual infrastructure on which the superstructure of community theory rests. Recent theories on assembly and niche packing

are particularly dependent on the assumption that the mechanisms that govern pattern in food webs are the same ones that govern whole community patterns. Therefore, determining which variables should be studied and at what level of resolution is of the utmost importance to the future of food web theory. It is clear that for reasons previously discussed, the current data are inadequate for the purposes to which it has been applied. As Yodzis (1989) points out, however, we must work with what we have until such time as better data become available. In the meantime, we should establish a general protocol for collecting food web data so that future analyses will carry more weight. Pimm and Kitching (1988), in answering Paine's (1988) criticism of the current data, offered a number of suggestions on this issue. Of particular importance is their suggestion that researchers concentrate on discrete habitats with manageable numbers of species and interactions, such as phytotelmata. Such habitats allow a previously unattainable level of accuracy in dealing with such things as dietary variability within species populations and changes in food web structure through time. More importantly, experimental manipulations become possible.

Another way in which to deal with the onerous task of analyzing whole community structure and assembly is through the use of microcosms, which are essentially laboratory

tree-holes. Unlike field sites, microcosms have a defined invasion history, which is of supreme importance because the keys to structure are to be found in assembly.

CHAPTER II

RIGID CIRCUITRY AND CONSERVATIVE ASSEMBLY

Niche Overlap Graphs

While it is possible to use basic properties of food web graphs such as order and connectance to characterize structural regularities of whole communities, information about specific assembly processes is more difficult to obtain from such a graph because of its generality. The graph of a community food web involves a number of very different components, operating at different spatial and temporal scales. However, these differences are not apparent from the graph because the "species" are represented by a vertex set whose members are differentiated by the number and direction of incident edges, and their position relative to other vertices. Thus, the food web graph is designed to show the trophic relationship of a vertex to all the other vertices at a given point in time, and nothing more. If additional information is to be obtained from the data which we use to create such a graph, the meanings we attach to vertex and edge must change. One way to do this is to construct a niche overlap graph, also referred to as a consumer overlap graph. In this graph, vertices represent consumers, and are joined by an edge if they share at least one resource. (Sugihara, 1982b) It is

not necessary, however, to collect new data for this graph if one assumes that the data which was collected for the purpose of constructing food web graphs is complete. If this is the case, the niche overlap graph is easily derived from the food web graph. One simply constructs an adjacency matrix for the consumers in which the existence of shared resources is denoted by a "1", and the lack of shared resources is denoted by a "0." In graphical terms, two consumers share a resource if the set of vertices to which both are adjacent is non-empty. Figure 3 shows the adjacency matrix for a California tidal flat taken from an early food web compilation (Briand and Cohen, 1984). This produces the web given in fig. 4, which in turn produces the niche overlap graph in fig. 5. What does this new type of graph tell us and how is it useful? As is apparent from the name, the niche overlap graph divides the community into components containing species which share part of the trophic dimension of their niche with the other species in the component. When each species in a component shares a resource with <u>every</u> other species in that component, then these species comprise a clique. According to Sugihara (1982b), a clique may be thought of in ecological terms as roughly equivalent to a guild (sensu Root, 1967). However, Root originally defined a <u>guild</u> as "a group of species that exploit the <u>same</u> class of environmental resources in a

	CDEFGH IJKLMNOPQRSTUVWXY
A	11001010000000000000000
B	10111111000000000000000
C	01000000000000000000000
D	00000000010000000000000
E	00000000010000000000000
F	00000000000100000001110
H	00000000010100000000000
I	00000000001100000000011
J	00000000001101000000000
L	00000000000000110000000
N	00000000000000000000001
O	00000000100000000110000
P	00000000000000000000011
Q	00000000100000000011100
R	00000000100000000010001
S	00000000000000000000001

A. primary producers
B. detritus
C. protozoa
D. crustacea
E. *Caliannassa*
F. shore crabs
G. phoronophis
H. *Urechis*
I. clams
J. *Lumbrenereis, Notomastus*
K. heron
L. *Clevelandia*
M. wading birds
N. stingray
O. *Nereis, Glycera*
P. nemerteans
Q. terns, shorebirds
R. *Cabezon*
S. flounder
T. *Cerebratulus*
U. loon, cormorant
V. striped bass
W. scoter
X. gulls
Y. man

Fig. 3

Adjacency matrix for a california tidal flat.

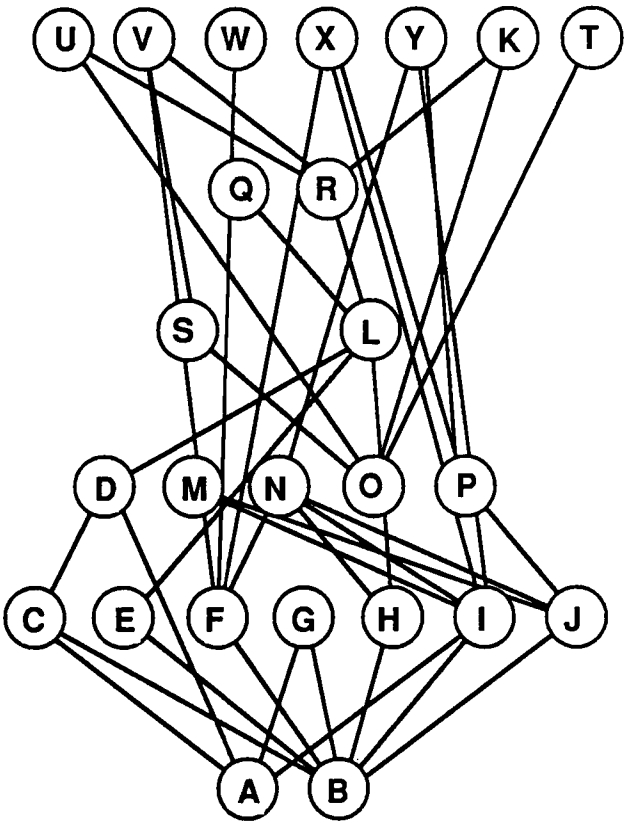


Fig. 4

Food web derived from matrix in fig. 3.

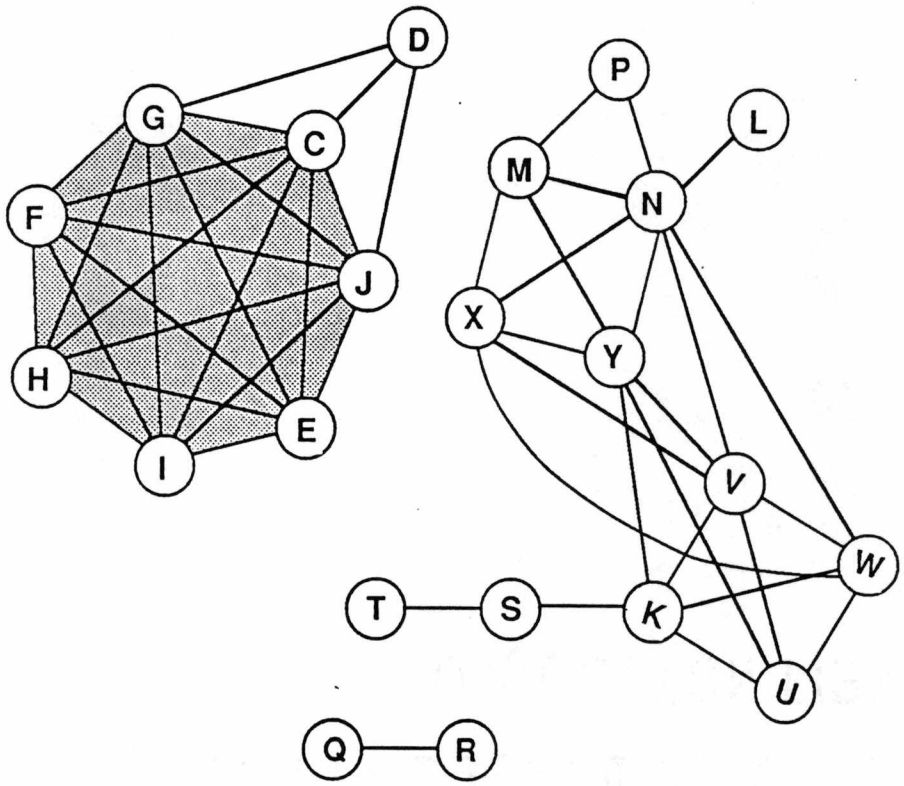


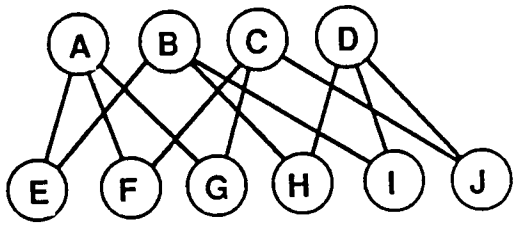
Fig. 5

Niche overlap graph of food web in fig. 4.

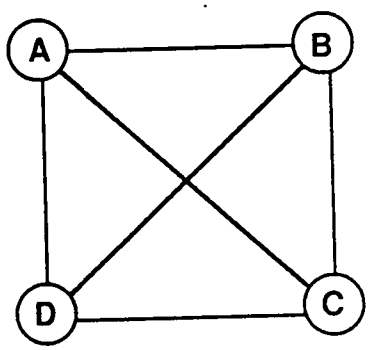
similar way.", thus members of a guild all have at least one resource in common. This is not necessarily true of cliques as is illustrated by figs. 6 - 8, which show three hypothetical food webs and their corresponding niche overlap graphs. In fig. 6 species A, B, C, and D define a maximal clique, but do not share a common resource. In fig. 7, species A, B, C, and D again define a clique, but in this case the sub-maximal clique A,B,C all share resource "J" and may thus be considered a guild under Root's criteria. In fig. 8, the entire maximal clique is also a guild. Sugihara (1982a) attempts to circumvent this difficulty by extending the definition of guild to allow for differing degrees of functional relatedness among the constituent species, claiming that this approach is more "realistic." While future references to clique and guild should be assumed to follow this more flexible definition, I cannot justify abandoning a rigid, biologically derived definition (Root, 1967) in favor of one which is limited by a mathematical abstraction which is used to represent the object in question.

Intervality and Rigid Circuitry

Cohen (1977) was the first person to realize the ecological significance of niche overlap graphs, noting that a majority of the niche overlap graphs of available food webs could be represented in one dimension as overlapping



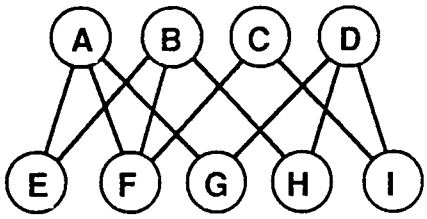
A



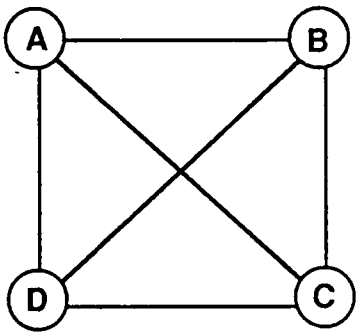
B

Fig. 6

Food web and niche overlap graph where consumers do not all share a common resource.



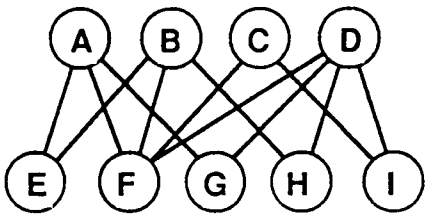
A



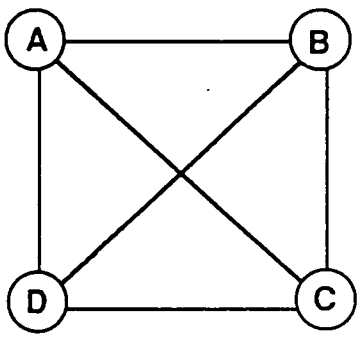
B

Fig. 7

Food web and niche overlap graph with a submaximal clique defined by consumers A, B, and C, which share a common resource F.



A



B

Fig. 8

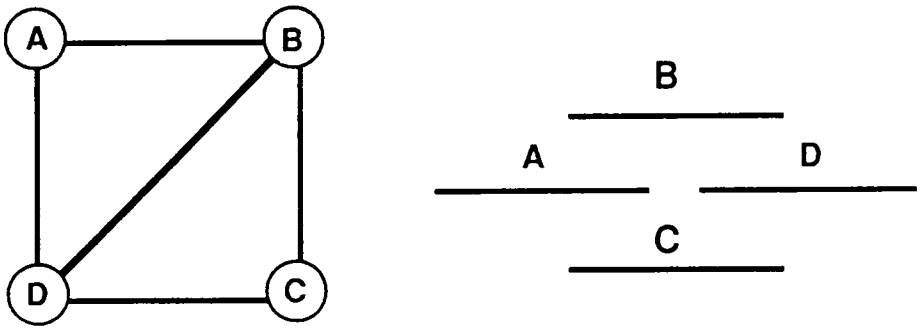
Food web and niche overlap graph where all members share a common resource F.

line segments. These diagrams are known as interval graphs. Fig. 9 shows two niche overlap graphs, one interval, one non-interval.

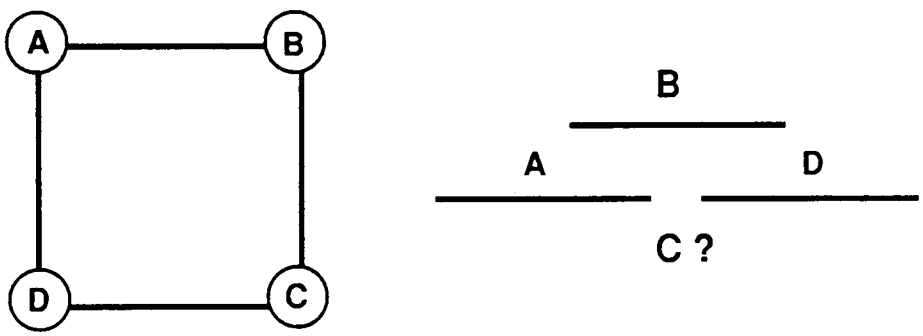
Cohen asserted that intervality was not a property of random connected graphs, but offered no biological explanation for the pattern. Sugihara (1982a), on the other hand, discovered another property of the niche overlap graphs produced by the data which explained the high incidence of intervality. This property is called rigid circuitry. Graphs possessing this property are defined as having no circuits of path length ≥ 4 that are not bisected by a chord (Dirac, 1961). Some examples of rigid and non-rigid circuit graphs are given in fig. 10. There are two conditions that are necessary and sufficient for a graph G to be interval (Lekerkerker and Boland, 1962; Sugihara, 1982):

1. G must be rigid circuit.
2. G must not be asteroidal.

Sugihara argues that food web graphs which yield asteroidal niche overlap graphs are unlikely, thus the nonasteroidal condition is superfluous, and the high incidence of rigid circuitry adequately explains the high incidence of intervality. This observation, however, merely creates a different question, i.e. "what causes rigid circuitry?" Sugihara (1982b) provides a possible explanation in the form of the conservative assembly rule.



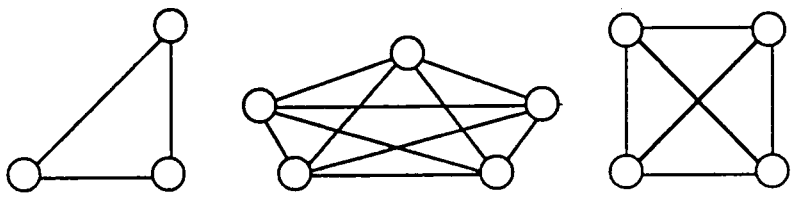
INTERVAL



NON-INTERVAL

Fig. 9

Examples of interval and non-interval niche overlap graphs.



RIGID CIRCUIT

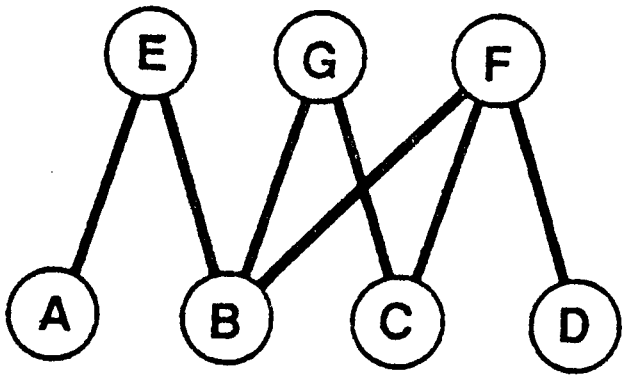
NON-RIGID CIRCUIT

Fig. 10

Examples of rigid circuit and non-rigid circuit graphs.

Conservative Assembly

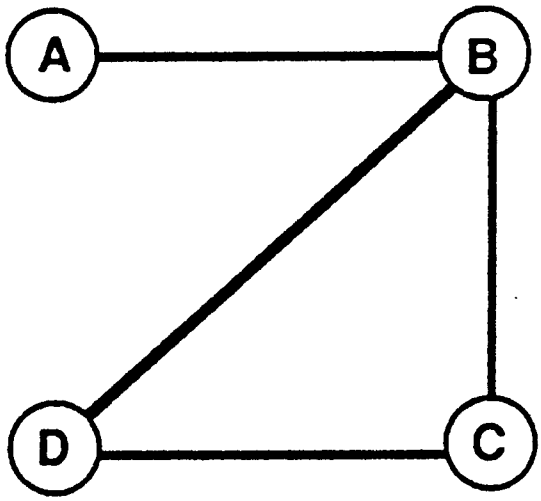
Sugihara (1982b) found that while the niche overlap graph provided information about community structure that is not apparent in the food web graphs from which they are derived, another type of graph, the resource overlap graph, is even more useful. The resource overlap graph is a formal conjugate of the niche overlap graph, meaning that the denotations of vertex and edge are reversed. In this graph vertices denote resources and edges shared consumers. For this reason, it is also referred to as the common enemy graph (Lundgren and Maybee, 1982). Recall that a clique in the niche overlap graph was equated to a guild. Similarly, in the resource overlap graph, the clique supposedly corresponds to a mapping of a particular species niche. An example is given in fig. 11. As was the case with the niche overlap graph, the definition of niche used by Sugihara deviates somewhat from that of the Hutchinson-Whittaker model he cites. In the Hutchinson-Whittaker model, which views a species niche as n-sided hypervolume existing in an n-dimensional hyperspace (Hutchinson, 1959). The dimensions of this space includes both biotic and abiotic axes, and the edges of hypervolumes within this space could be roughly viewed as the tolerance limits of the particular organism whose niche it represents (Whittaker, 1970). Sugihara states that a species n-dimensional niche "consists of n resource points all mutually connected." This is not



A

Fig. 11

Hypothetical food web and resource overlap graph.



B

Figure 11 (continued)

exactly the case. The dimensions of the n-dimensional hypervolume of the Hutchinson-Whittaker model include everything that delimits where and when a species could exist, not just resources, and it should be clear that such an object could not possibly be adequately represented by a two-dimensional graph. Sugihara's "niche" is actually a mapping of only one of the n components of the entire niche, i.e., the trophic niche. As such, we should not expect a resource overlap graph to tell us any more about community geometry than a single letter of a given word reveals about the solution to a crossword puzzle. Furthermore, as with the niche overlap graph, it is possible for a set of resources to define a clique without sharing a common consumer (fig. 12). In this case it is not clear what, if anything, the clique represents. For the purpose of examining the theory, however, I will assume that Sugihara's claims are valid in most circumstances.

With the resource overlap graph, we can begin to characterize food web structure in terms of niche packing. The graph can be modified by viewing it in three dimensional terms as a section of a polyhedron. Each clique or section is now termed a simplex, and the surface that results from fitting them together, the simplicial complex (Sugihara, 1982b). Sugihara states that with this model, "a community hypervolume may be broadly visualized as a multidimensional crystal having clusters of crystal faces which correspond to

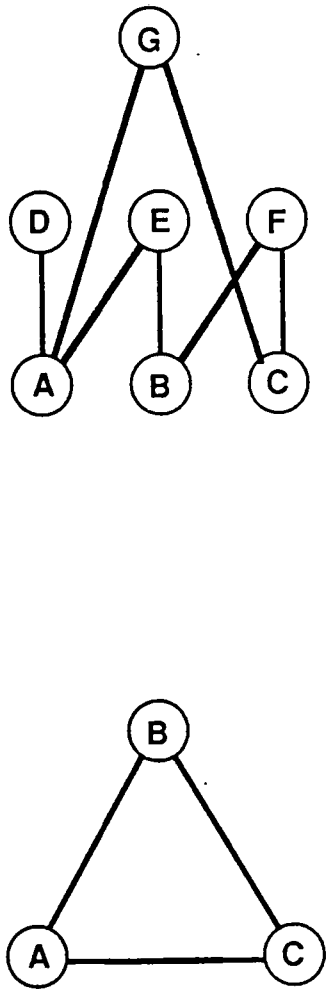
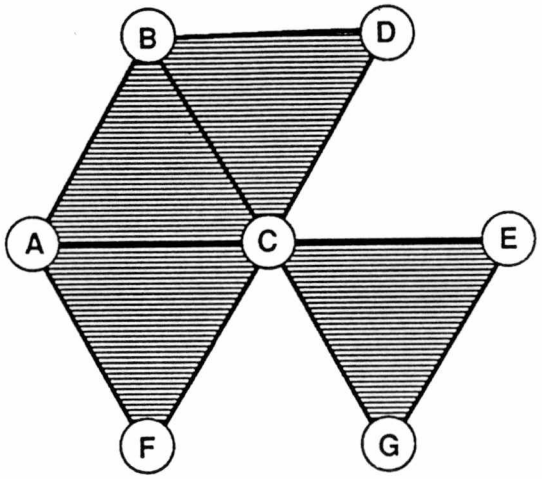


Fig. 12

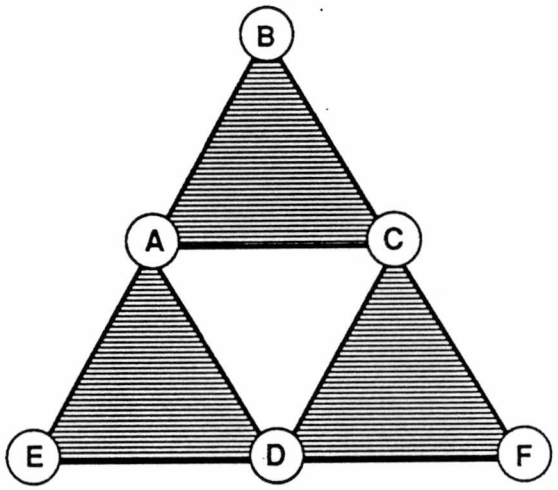
Food web and resource overlap graph where the prey species defining a clique (A, B, C) do not all share a common predator.

individual species niches." Using this characterization, Sugihara tried to determine whether natural communities are packed densely to form a solid, or loosely so that they contain holes (fig. 13). An analysis of Briand's (1983) data set, which contained 73 communities, revealed only two communities with holes. Furthermore, these holes were one-dimensional (a hollow sphere contains a 2-dimensional hole). This was somewhat unexpected, because a model based on randomly assembled simplicial complexes predicted that 22 of the 73 would contain holes. It appeared then, that the absence of holes was an important characteristic of real communities.

In ecological terms, this fundamental topology implied that "resources in the environment are ordered or correlated with each other by various means (e.g. spatially, taxonomically, by size) and that this ordering is perceived similarly by all of the species involved." (Sugihara 1982b). As an example, Sugihara offers a case where the members of a lizard "community" group prey according to size. A "hole" would be created if a species of lizard which fed on only the smallest and largest prey items, but not middle-sized prey were to be incorporated into the community. A clearer picture of what this means in terms of food web structure may be obtained by observing a food web in which prey are not ordered, and the resultant niche overlap graph (fig. 14). Note that the niche overlap graph is non-rigid. How



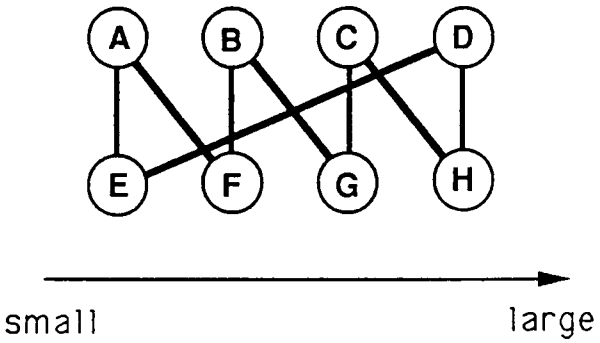
DENSELY PACKED



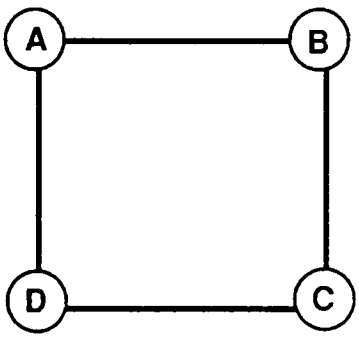
LOOSELY PACKED

Fig. 13

Simplicial complexes



A



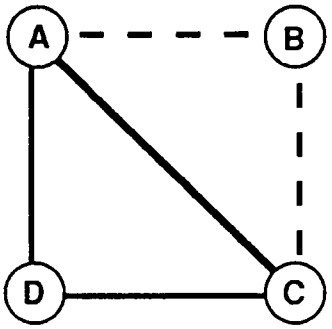
B

Fig. 14

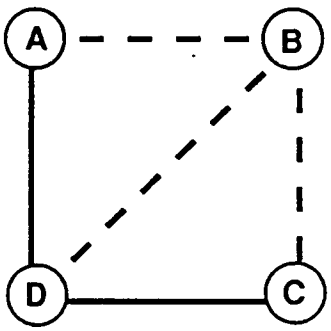
Non-rigid niche overlap graph of web where prey ordering is not followed.

could this topology be arrived at in terms of community assembly? Sugihara proposed the conservative assembly rule, which states that species are incorporated into the community by attachment to a single guild/clique in the niche overlap graph, rather than "bridging" multiple guilds (fig. 15). This rule is dependent upon two factors: 1) The observation that all of the niche overlap graphs in Briand's collection were rigid circuit, and 2) That the degree of relative specialization of invading species increases as assembly proceeds (invading species overlap with fewer species than their predecessors). The second condition is supported by Drake (1985). In terms of graph theory, this means that invading species must form an extreme vertex.

The conservative assembly rule is important in that it could explain both the ubiquity of the rigid circuitry property and the lack of holes in community niche space. While there is no necessary mathematical connection between rigid circuitry and a lack of holes in simplicial complexes, a statistical correlation exists between the two, indicating the possible existence of some factor which ties the two together. (Sugihara, 1982a) Since conservative assembly is sufficient to guarantee rigid circuitry and a lack of holes, it seems reasonable to invoke it as an explanation for these properties. However, neither rigid circuitry or the lack of holes in simplicial complexes requires conservative assembly. Additionally, conservative assembly explicitly



ALLOWED



VERBOTEN

Fig. 15

Example of conservative (allowed) and non-conservative (verboten) assembly.

requires a sequential increase in specialization, a generalization which though somewhat intuitive, has not yet been demonstrated with adequate scientific vigor. There may be a number of possible explanations for these properties.

It is clear that in order to evaluate the conservative assembly rule, we must critically examine both the implicit and explicit assumptions it requires. These include:

1) That the rigid circuit property is indeed robust.

2) That the trophic dimension of a species niche provides an adequate portrait of the entire n-dimensional niche.

3) That both rigid circuitry and a lack of holes in niche space are not properties of randomly generated graphs.

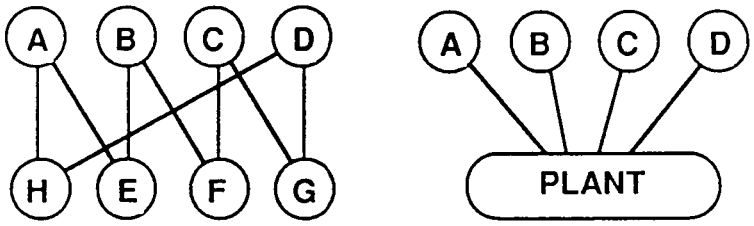
4) That communities assembled conservatively are more persistent than those assembled non-conservatively, and

5) that the data generated food webs meet the demands of statistical rigor.

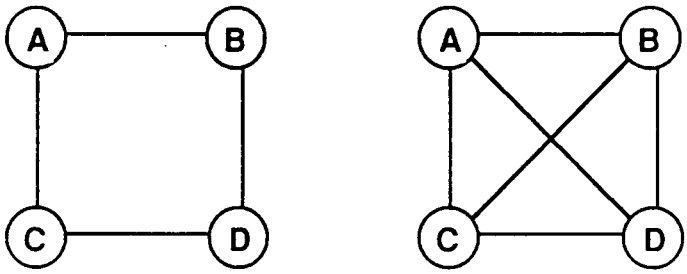
The Data: Is It Adequate?

The point of assumption (5) is that in order for the structural regularities observed in these webs to have any meaning, the webs have to be comparable in terms of scale, i.e. a vertex should not represent the sum total of individuals belonging to a kingdom in one sample and a species in another. Some degree of lumping is permissible,

but just how much may be a difficult question to answer. It has been established that the lumping of functionally identical groups of organisms into trophospecies has no effect on topological properties like intervality and rigid circuitry. This type of aggregation is performed after the fact, and thus the investigator may always test for differences in pattern before and after lumping. Far more troubling, however, is the lumping of species into broad before trophic relationships are noted. In these cases, the initial reasons for lumping are known only to those who collected the data and may amount to a lack of familiarity with the taxonomy of the groups involved. Very few individuals have the expertise to properly document most food webs. An example of the problems lumping could cause is given in fig. 16, where four species, H, E, F, and G, are collapsed into a single category called "plants." In this case, the lumping has changed the topological status of the web's niche overlap graph from non-rigid to rigid. An alteration in the food web given in fig. 4 has a similar result. Recall that organisms which feed on identical resources, in this case, shore crabs and protozoans, may be collapsed into a single vertex without affecting the topological properties of such graphs (Sugihara, 1982a). The assertion that crabs and protozoa are trophically identical is of course absurd, and it is perhaps for this reason that they are presented as separately in the matrix.



A



B

Fig. 16

Food web and niche overlap graph before and after lumping.

If one were to divide primary producers into unicellular algae and macrophytes, a reasonable distinction, and detritus into particulate and macroscopic categories, then the food web could be represented by the matrix and web in fig. 17. This food web contains a non-rigid circuit. Of course, further refinements and/or corrections of this matrix could result in a return to rigid circuitry, but this in no way weakens the point that topological properties may vary according to the degree of taxonomic refinement.

Null Models

As mentioned earlier, an important requirement of the conservative assembly hypothesis is that both rigid circuitry and the lack of holes in simplicial complexes are properties that emerge as the result of a specific assembly rule, i.e., they are <u>not</u> properties of random connected graphs. It appears that Sugihara (1982a) has adequately shown that randomly assemble simplicial complexes have a higher frequency of holes than those generated by the data. However, Sugihara's null model test for the significance of rigid circuitry appears to be inadequate.

The test involved the random addition of edges to randomly generated spanning trees. A "tree" is a connected graph with no circuits. Thus, Sugihara's test involved randomly connecting the terminal vertices of the trees "branches" in order to form circuits of varying lengths.

	EFGH
A	1100
B	0011
C	1100
D	0101
E	0000
F	0000
H	0000

A. particulate detritus
B. macroscopic detritus
C. phytoplankton
D. macrophytes
E. protozoa
F. crustacea
G. *Callianassa*
H. shore crabs

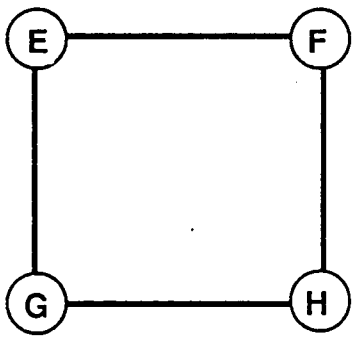


Fig. 17

Matrix and niche overlap graph of California tidal flat data, which has been altered to reflect a higher degree of resolution.

The resultant graphs showed that rigid circuitry is not a property of random connected graphs. The problem with this analysis, is that it tests for significance at the wrong level. Since the niche and resource overlap graphs Sugihara analyzed were dependent upon data used to generate food web graphs, the question of interest is not whether rigid circuitry is a property of random connected graphs, but whether it is a property of the niche and resource overlap graphs they produce. Additionally, food web graphs are always labelled, directed, and bipartite. Thus, any null model testing for structural regularity in these graphs must consider the number of vertices (species), edges (links), and the relative proportion of vertices in a given vertex class (predator-prey ratio). As an example, consider the case of an eight species web with eight links, and a 1:1 predator-prey ratio. Given these conditions, there are nine possible configurations, only one of these produces a non-rigid niche or resource overlap graph. One can easily see the importance that the predator-prey ratio plays in this case, for any change in the ratio makes the construction of a non-rigid overlap graph impossible. Similarly, an increase or decrease in the number of edges produces the same effect. In fact, the graph highlighted in fig. 18 is the only one out of over 250 million possible graphs with eight vertices that gives a non-rigid circuit overlap graph. Of course this single example does not prove that the rigid

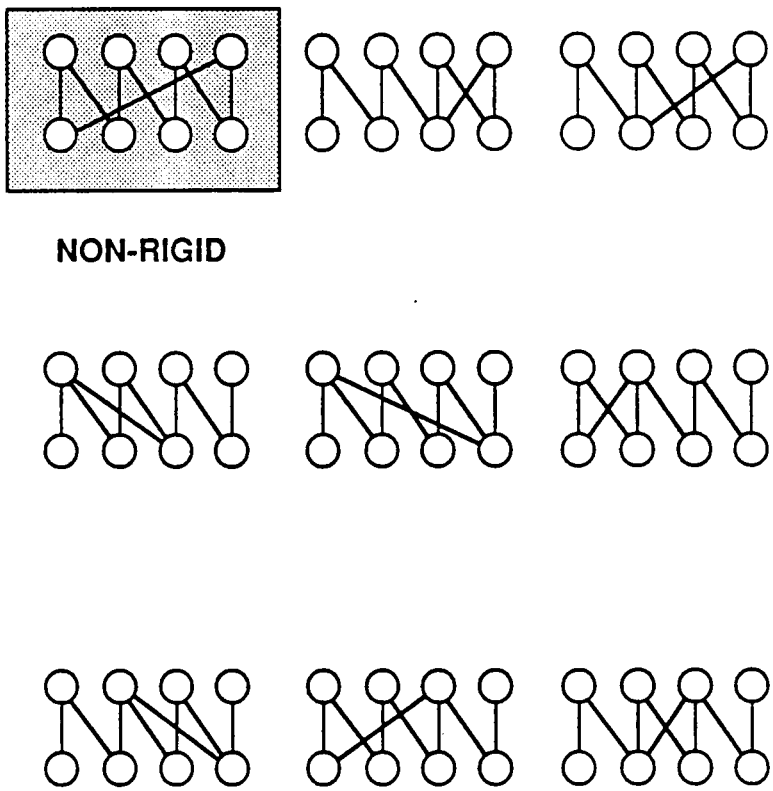


Fig. 18

Nine possible webs with 4 predators, 4 prey, and 8 edges.

circuit property is an artefact. It does, however, illustrate the need for a more thorough understanding of the graphs themselves.

The problem of finding the appropriate level at which to test structural properties of data generated graphs against random models is confounded by the unclear relationship between the elements of graph topology. To alleviate this problem, it may be necessary to establish a hierarchy of graphical properties based on the constraints that one property places on another. To do this, we must first identify the topological elements which are germane to our characterization. The two most obvious elements to include are order (number of vertices) and size (number of edges). In this case, the former constrains the latter. The order of the graph not only determines the minimum and maximum number of edges possible, but the distribution of possible configurations among size classes. For example, there are 4 possible labelled connected graphs (food web graphs) of order 3. Of these, 3 have the minimum 2 edges and 1 has the maximum 3 edges (fig 19). With the possible graphs of order 4, on the other hand, 16 have the minimum 3 edges, 15 have 4, 6 have 5, and 1 has the maximum 6 edges. Some examples of the distribution of configurations within the size (edge) classes of graphs of a given order are given in figure 20.

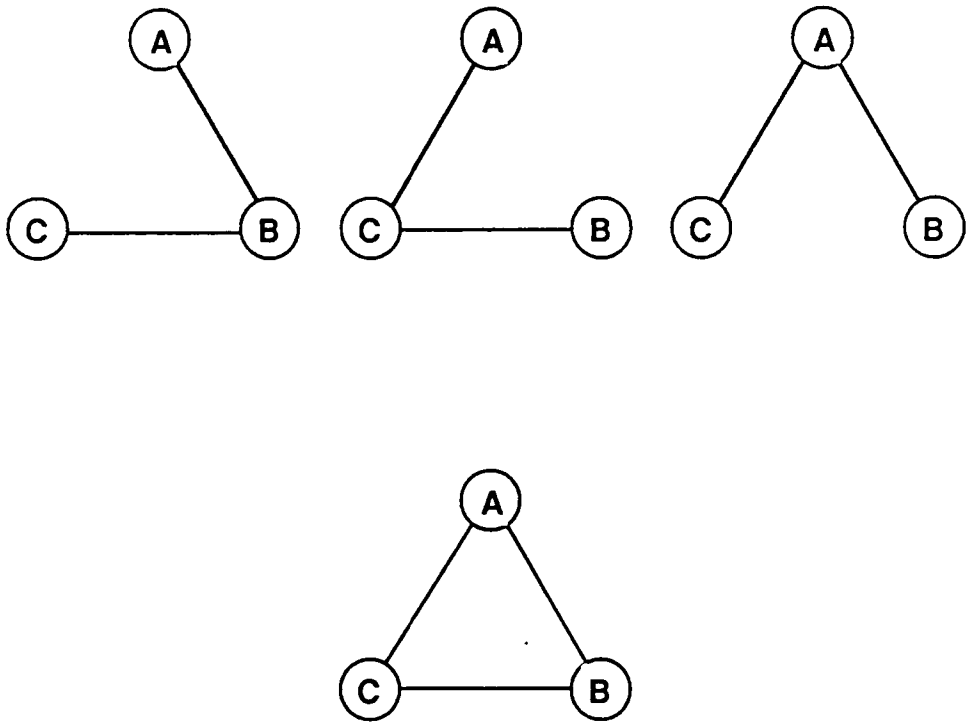


Fig. 19

The set of all possible webs with 3 species.

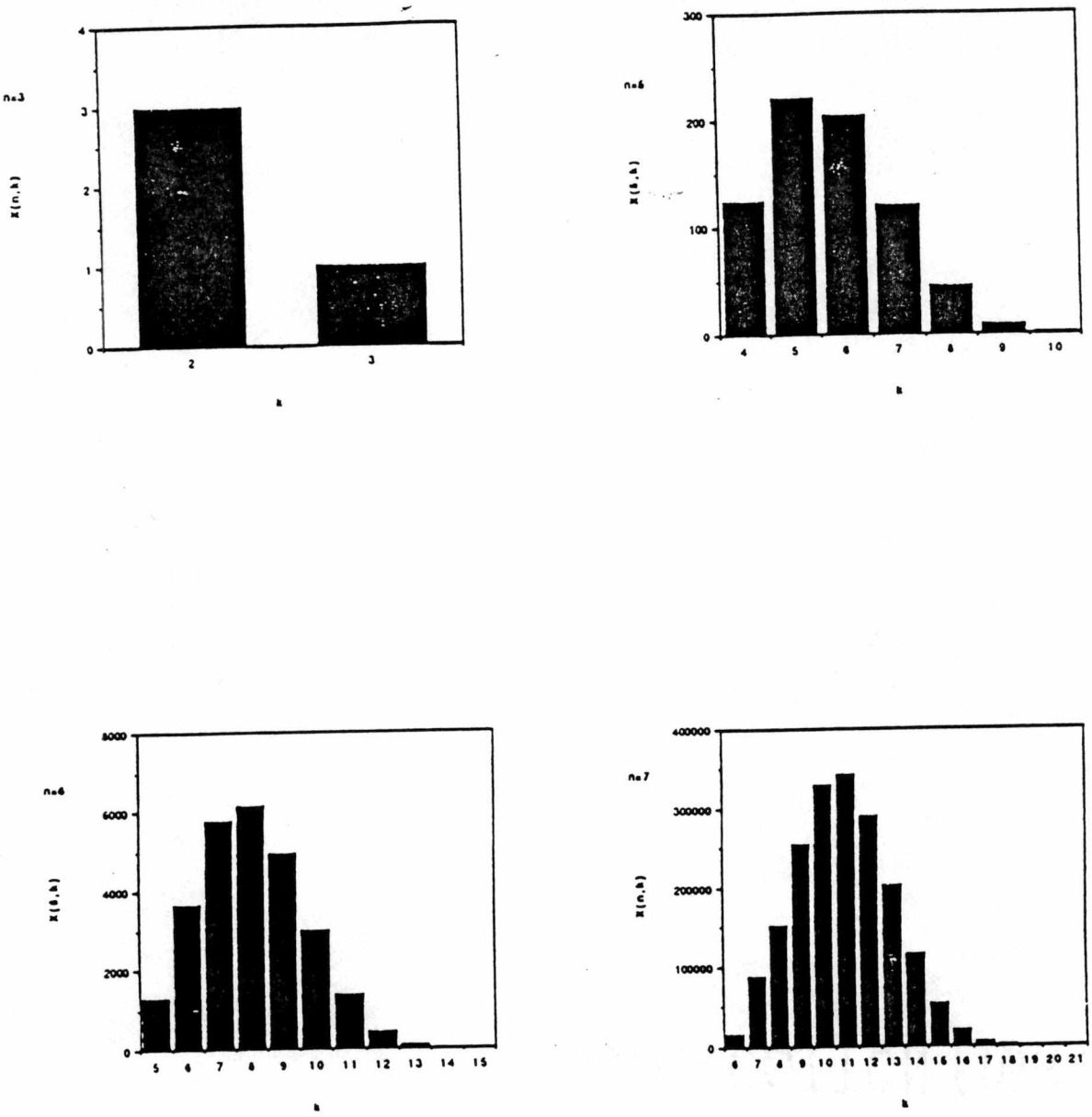


Fig. 20

Sample distributions of possible connected graphs with n vertices and k edges.

How are these distributions obtained? Though it is possible to draw all of the possible graphs when a very small number of species is involved, such a task quickly becomes daunting as the graphs increase in order. Fortunately, in many cases there is an enumeration function which will give us the number of potential configurations of a given class of graph. The enumerating function for labelled connected graphs is given in fig. 21.

The role of the null model in testing graph theoretical generalizations of food web structure has received little attention. This is a major shortcoming of current food web theory, and is primarily due to the sheer complexity of both ecology and graph theory. Specifically, the ecologist has not yet been able to determine what consequences arise when n-dimensional dynamic systems are represented as discrete, unvarying mathematical objects. In view of this, it would seem appropriate for ecologists to increase the number of conceptual tools available for characterizing systems of interest. This does not mean that the connected graph and associated analytical techniques should be abandoned as a characterization of communities. On the contrary, the connected graph has been instrumental in eliciting an interest in discrete mathematics among ecologists. However, it is imperative that we broaden our conceptual base to include other tools within this powerful discipline if we

$$C_n^k = \binom{\binom{n}{2}}{k} \sum_{i=1}^{n-1} \binom{n-1}{i-1} \sum_{j=i-1}^{\min\left(k,\binom{i}{2}\right)} C_j^i \binom{\binom{n-i}{2}}{k-j}$$

i = size of connected component containing the distinguished element.

j = number of edges in the component in the distinguished element.

Fig. 21

Equation which gives the number of possible labelled, connected graphs with n vertices and k edges.

are to elucidate process and pattern in food webs and understand the relationship between them.

Is Conservative Assembly Intuitive?

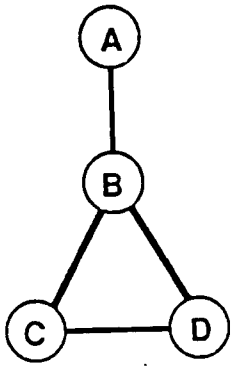
On the surface, the conservative assembly rule is a succinct and ecologically reasonable explanation for some of the patterns observed in community food webs. However, pattern at the level of food webs is not the only variable pertinent to community assembly and structure, there are larger patterns among communities that need to be dealt with (e.g. alternative states). Furthermore, there are also a number of processes operating at various levels within a community, such as intransitivity and historical effects, which may not be accommodated by a hypothesis as inflexible as the conservative assembly rule. One might ask, then, whether the conservative assembly rule is reconcilable with these patterns and processes. In other words, is conservative assembly "ecologically intuitive."

In many ways, the conservative assembly rule is similar in spirit to MacArthurian view of community structure, in that competition is seen as the primary structuring force. Sugihara comments that in framing his ideas on assembly, he "concentrated on the competitive structure of niche overlap graphs, for the idiosyncratic reason that it is at this level where interesting regularities seem to find coherent expression." Keep in mind that cliques in the niche overlap

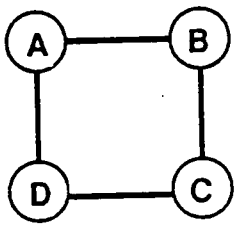
graph were said to be the graphical equivalent of guilds. Thus, the niche overlap graph may be thought of as reflecting the effect that competition has had on the number and orientation of species belonging to a particular functional group. If this is the case, then should food webs that have rigid circuit niche overlap graphs be more stable dynamically than those that do not?

Sugihara attempted to answer this question by determining the stability properties of two systems with the same number of species and the same number of edges, that differed with respect to topology, i.e. one was rigid circuit, one was not. The graphs of these systems is given in fig. 22. Of the two, the rigid circuit system (model A) had the larger stable parameter space ($-0.80 < a < 0$, vs. $-0.50 < 0$), a result which would seem to support the conservative assembly rule. Though Sugihara admitted that this result was "limited but promising," the logic behind the test itself is questionable on two points.

First, as with the null test for the significance of the rigid circuit property, the test appears to be at the wrong level. Though competition certainly occurs in food webs, such relationships are only implicit in the graphs from which Sugihara obtained his data. Thus, a more meaningful test would involve comparing the stability of two food web graphs which were identical in every respect (i.e. connectance, number of species, and predator-prey ratio)



Model A

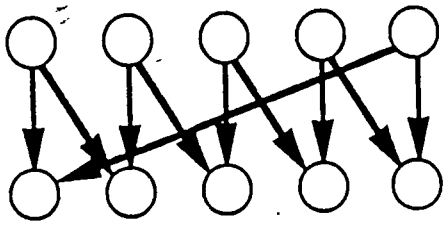


Model B

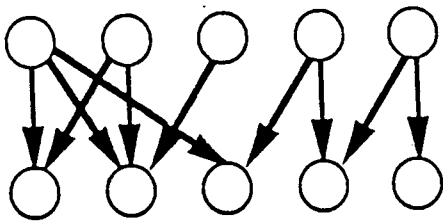
Fig. 22

Two hypothetical niche overlap graphs having the same number of species and edges.

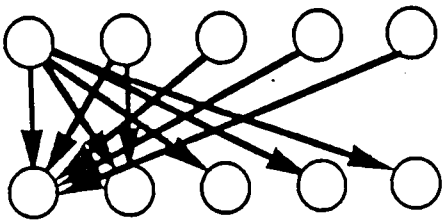
except for the produced niche overlap topologies, i.e. one would produce rigid-circuit overlap graphs, the other non-rigid. The difficulty of course, is that determining a food web's stability is difficult if not impossible when realistic numbers of species are involved. In light of this, it may be more useful to approach this question not in terms of mathematical stability, but in terms of persistence. Logically, when one documents a community food web, persistent species are more likely to be included than non-persistent ones. Therefore, one would expect rigid circuit webs to be on average more persistent than non-rigid webs. To test this a three food webs were simulated differing only with respect to the rigidity of their niche overlap graphs, i.e., the predator-prey ratios, number of species, connectance, initial conditions, growth parameters, and interaction strengths were identical. These webs and their niche overlap graphs are given in figures 23 and 24, respectively. The results of the simulation show that the persistence of web A was greater than both B or C over a wide range of interaction strengths (fig. 25). Clearly, the difference in topology has an effect, but one which is quite different than what we might expect. Web A is non-rigid, and yet has the highest persistence. This result is less mysterious when we draw these webs so that no edge crosses another (fig 26). These uncluttered diagrams allow us to isolate vertices/species that are at particular risk for



Web 1



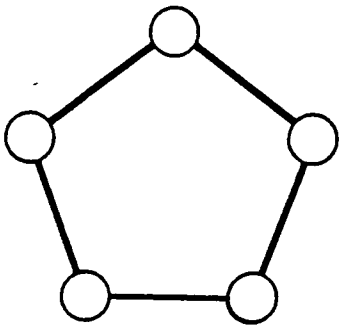
Web 2



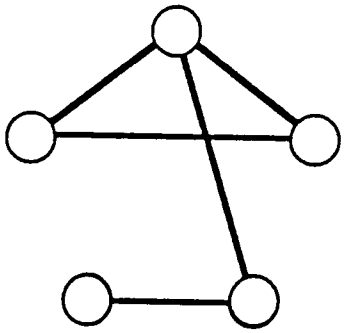
Web 3

Fig. 23

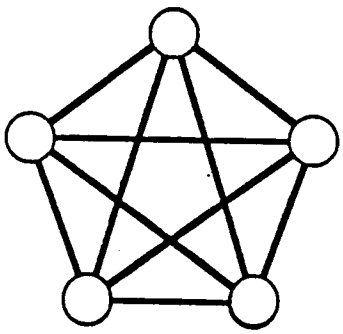
Three hypothetical food webs having the same number of predators, prey, and edges.



Web 1



Web 2



Web 3

Fig. 24

Niche overlap graphs of webs in fig. 23.

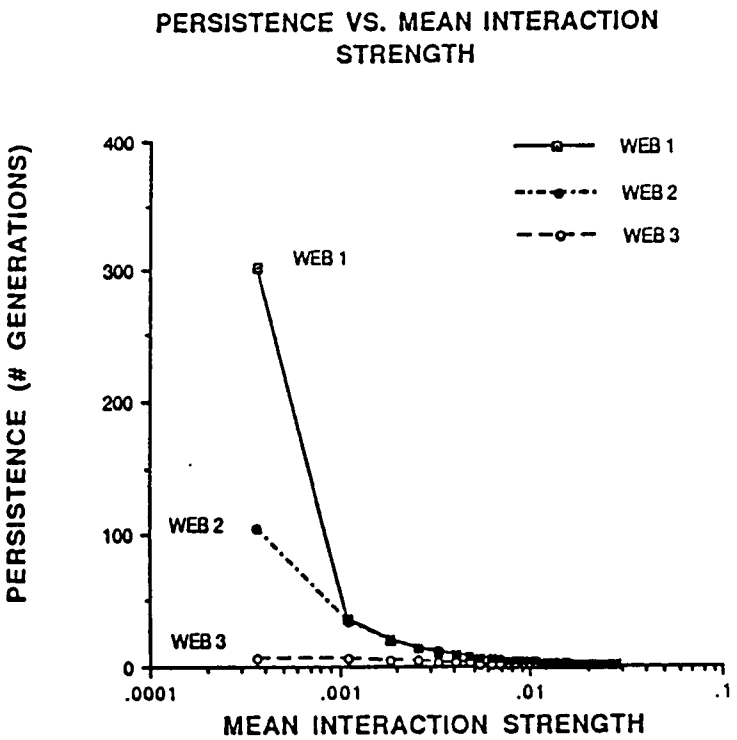
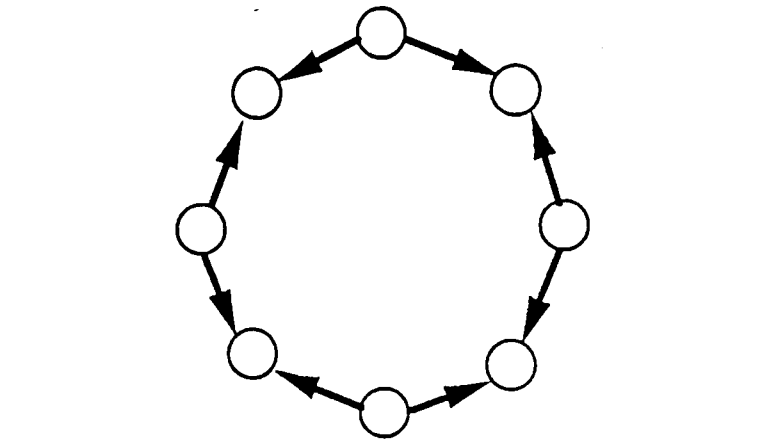
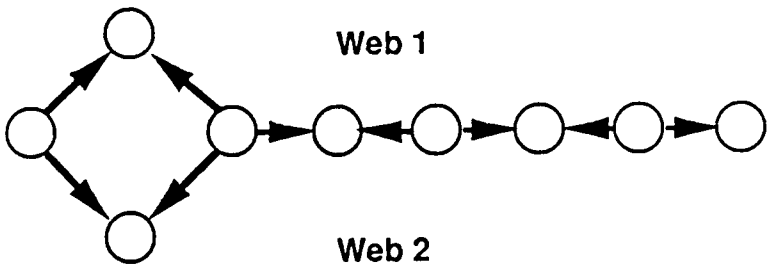


Fig. 25

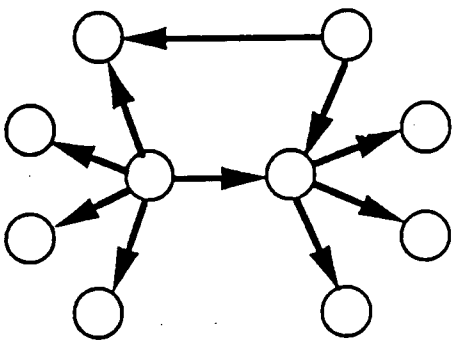
Persistence vs. interaction strength of the webs in fig. 23.



Web 1



Web 2



Web 3

Fig. 26

Webs from fig. 23 redrawn to clarify species interactions.

extinction. Quite simply, given an equal effect for all edges, the greater number of edges incident to prey vertex, the more likely it is to go extinct. Notice that of the three, web A is the only web in which we can not differentiate a susceptible species population because the degree of all the constituent vertices is the same. Additionally, while not all persistent systems are necessarily stable, all stable systems are persistent.

The second problem with the stability test of the niche overlap graphs lies in the assumption that overlap in resource utilization necessarily results in competition. It does not. Resources must be limiting for competition to occur, and, while it is likely that some members of a particular guild (clique) are competitors, this is by no means guaranteed. Even if one were to argue that resource overlap implies competition in most cases, the degree to which the niche overlap graph would reflect the influence of competition on structure is questionable because of the uncertain relationship between graphical definition of guild (clique) and the biological definition.

Another difficulty with the conservative assembly rule is that it does not apparently allow the situation where the successful attachment of a non-conservative invader to a stable community results in the extinction of an "established" community member. One possible way to account for this would be to adopt the view that species which go

extinct during the process of assembly are transient elements which are not considered to have "assembled," i.e. assembly is the process of putting together the species which will be present in the final configuration or climax of a given community. This explanation unsatisfactory for several reasons. First, the likelihood of an attempted invasion is independent of community structure. In the above example, if the species which attached non-conservatively had never attempted to invade, then we might have referred to situation A as the climax community. Additionally, while transient species are not apparent in depictions of the "final" community structure, they play a very important role in succession. Additionally, it is not wise to assume that the food web data we have collected represents communities that are completely assembled or at least at a discrete "stopping point" in assembly. As you can see, such an assumption is required for the conservative assembly rule because the inclusion of transient species could result in spurious regularities.

Perhaps the most important weakness of the conservative assembly rule is the fact that while it allows for a type of sequence effect, it does not allow for the effect that temporal distance between invasions can have on the course of assembly within a given sequence. The conservative assembly rule implies that the same sequence will always result in the same structural endpoint. This result was not

obtained by Drake (in press), who noted the existence of alternative states in microcosms into which identical sets of zooplankton and phytoplankton were introduced. Drake found that community states varied both within a given introduction sequence and among different introduction sequences of the same species. This could be explained by variability among the physiological condition of propagules or by alternative orderings between sets of species that manifest themselves when a given species is presented with different initial conditions upon invasion. The latter phenomenon is referred to as intransitivity.

Intransitivity and Alternative States

In the broad sense, intransitive systems are those which have no definite endpoint. A classic example of this would be the endless staircases popularized in the drawings of Escher, where one could apparently ascend several flights of stairs only to return to the starting point. In the ecological sense, intransitivity refers to sets of species whose unique relationships allow different configurations in environments that appear to be "identical." In such systems, stochastic effects, such as differing invasion orders, abiotically induced changes in population densities, and the chance absence of a particular species from a suitable habitat due to unsuccessful dispersal, are extremely important in determining eventual community

structure. As with Escher's staircases, their is no definite endpoint, rather, a number of alternative states exist. One might argue that this is trivial, because with any given set of species, different communities will result even in very similar environments. While this is true, intransitive systems differ from "normal" systems in the degree of difference among the possible endpoint communities. For example, while grasses, shrubs, conifers, and hardwoods may all be present in climax communities, it is unlikely that grasses would dominate one climax community and hardwoods another, given similar environmental conditions.

Empirical data suggest two basic types of intransitivity. With the first type, outcomes vary according to presence or absence of species from a set of competitors. Sets of competing species are often thought of as having a hierarchial relationship, that is, species A > species B, species B > species C, and species A > species C. Connell (1961) found that this situation existed among certain intertidal species. Competitive abilities, however, may also be arranged in a network, e.g., species A > species B, species B > species C, and species C > species A. This apparently occurs in some coral reef communities (Buss and Jackson, 1979). In these systems, spatially competing cryptofauna from a study area near Jamaica formed three and four species networks in artificial system, and outcomes

varied according to the relative position of competing neighbors. It should be noted that all but one of the 51 networks observed occurred among species belonging to different major taxonomic groups. In addition to competitive networks, second order effects may also lead to a type of intransitivity. Hairston et al (1968), found that a certain species of paramecium's competitive superiority to two other species was severely reduced when it encountered them together, rather than separately. Sequence effects also appear to be important. Competition among larvae of toads (Bufo) and frogs (Rana) was significantly less when the toad larvae were introduced to ponds before the frog larvae, than when the situation was reversed, or when the two were introduced simultaneously.

The community states resulting from the second type of intransitive effect are dependent on the relative abundances of the species involved. A striking example of this was observed by Barkai and McQuaid (1988), who noted that rock lobsters occurred in the benthos of only one of two suitable islands off the coast of Africa. This was surprising in view of the fact that the lobsters had occurred in both places initially, and that the benthos of the lobster-free island had an extremely high density of whelks, the lobster's main prey. They subsequently found that the role of predator and prey at the lobster-free island had been reversed. Lobsters that Barkai and McQuaid

reintroduced to this island were overwhelmed by a host of whelks and consumed in less than an hour. Apparently, some previous environmental occurrence had a disproportionately negative effect on lobster density. The whelks subsequently increased in density and diversity to the point where exclusion of the lobsters by predation was possible.
Though conditions are presently suitable for lobster recolonization (caged lobsters thrived at the whelk island), the intransitivity allowed for the persistence of two very different community states.

Conclusions

It is clear that minute differences in initial conditions during assembly may have a major effect on extant community structure. In light of this, and our typical characterization of nature as unpredictable, it is difficult to imagine what role an assembly "rule," especially one as rigid as conservative assembly, could have in our concept of community ontogeny. The conservative assembly rule is special, however, in that it allows for a number of alternative interpretations itself. This is due in large part to the inherent ambiguity of the terminology in which it is framed. Few ecologists can agree on the exact meaning of words such as "community," "niche," or "assembly," to name but a few. However, there are some general expectations generated by the conservative assembly rule

which deserve examination, in particular, the idea that conservative assembly should confer stability. Additionally, the discovery of both rigid circuitry and the absence of holes in niche space have provided a much needed impetus towards a search for patterns which are common to all communities. Such research promises to be an integral part of the quest for a unifying theory of communities.

CHAPTER III

AN EXPERIMENTAL TEST OF THE CONSERVATIVE ASSEMBLY HYPOTHESIS

Introduction

Traditionally, there have been two fundamental perspectives in community ecology. The first involves interactive processes, such as competition, predation, and mutualism; properties which have a major effect on community stability and presumably structure. According to theory, these processes may either maintain or disrupt the delicate "balance of nature." The second area of study involves the analysis of the history of community assembly, usually referred to as succession. Here, more importance is attributed to the context in which the aforementioned processes operate, and how this affects community structure.

Recently, attempts have been made to reconcile these approaches through demonstrating the effect that particular invasion orders have on community structure and how these effects are the result of rules governing the operation of ecological processes in time and space. One of these rules, the conservative assembly rule, appears to explain a good deal of the structural pattern in community food web data. Sugihara (1982) noticed that the most of the food webs in the data possessed a property known as rigid circuitry.

This means that when the resource overlap of predators is displayed as a graph, there will be no circuits of more than 4 edges that are not bisected by a chord, i.e. the graphs are triangulated (Sugihara, 1982a). This property was important because it was a necessary an sufficient condition for intervality, a property noted earlier by Cohen (1977). According to Sugihara, this topology could only be assured if invading species attached to single cliques rather than bridge multiple cliques. Recall, that in graph theory, a "clique" is defined as a maximally connected sub graph. Conservative assembly is a goal oriented process. The goal being a community topology that eliminates the possibility of holes in niche space. Why should there be no holes in niche space? Sugihara implies that a lack of holes confers stability to a community by showing that dynamical models that are rigid have a larger stable parameter space than those that are not (Sugihara, 1982a).

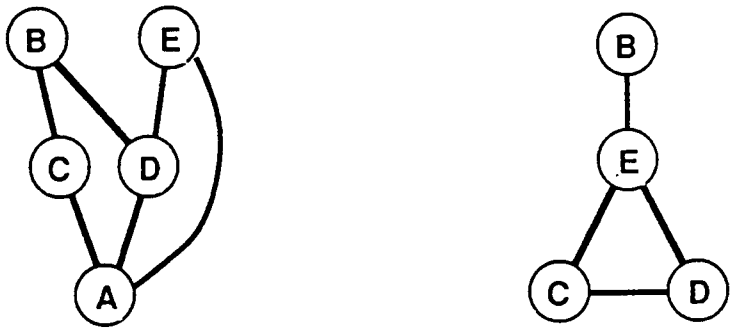
While conservative assembly explains how a rigid circuit niche topology is produced, it does not explain why. Obviously, if conservative assembly insures rigid circuitry, which in turn promotes stability, we should expect that there is an immediate advantage conferred to species that assemble conservatively. I will argue that species that assemble conservatively should have relatively more "stable" populations than those that do not, where "assembly" is understood to mean long-term incorporation into a community.

One problem with testing this hypothesis as stated is that while the word "stable" has an intuitive meaning, it must be defined in very precise terms for experimental purposes. Although there are objective criteria for determining the stability of the mathematical models used to represent food webs, obtaining the same information for real interacting populations in the field or laboratory is exceedingly difficult because of the tremendous number of variables involved and the difficulty of measuring them. However, several other properties which may be subsumed under the general heading of stability exist including resistance, resilience, and persistence (Pimm, 1982, 1984). Of these, persistence is the most easily measured when defined as the time a particular assemblage remains in a given configuration. In other words, a food web persists as long as there are no invasions or extinctions, and as long as the trophic relationships among constituent species remains unchanged. Additionally, since the likelihood of observing a species or interaction increases with increasing persistence, persistent food webs or subsets thereof are likely to be more common in the data. Thus, persistence may be correlated with the topological regularities of these webs. Though this in itself does not imply a causal relationship between the topology produced by conservative assembly and persistence, it is clear that persistence is a fundamental component of a given invader's success.

Presumably, non-conservative invaders would be unsuccessful during an assembly sequence, and therefore persist for a shorter period than conservatively assembling species. From this, one can readily extrapolate to the community level. Communities whose constituent species are persistent are themselves more likely to be persistent.

The Experimental Design

As a test of the conservative assembly rule, I designed an experiment which targets the assembly process itself independently of the topological status of the communities such assembly produces. Consider the set of organisms whose trophic relationships and niche overlap graph are given in fig. 27. From this set of species two sequences can be chosen, one conservative, one non-conservative. In the conservative sequence, hereafter referred to as sequence B, the third species, is an omnivore and thus overlaps with two separate guilds. However, only one of these guilds is present when species C invades, thus the sequence obeys conservative assembly (fig. 28). In sequence A, on the other hand, where species E is the last to invade, the conservative assembly rule is violated because species E attaches to both guilds simultaneously. This situation is depicted in fig. 29. Obviously, species E is "special" in that its position in the invasion order determines the status of the assembly. It is the relative success of this



A. *Scenedesmus quadricauda*
B. *Hydra littoralis*
C. *Moina sp.*
D. *Cypris sp.*
E. *Cyclops vernalis*

Fig. 27

Food web and niche overlap graph of experimental organisms.

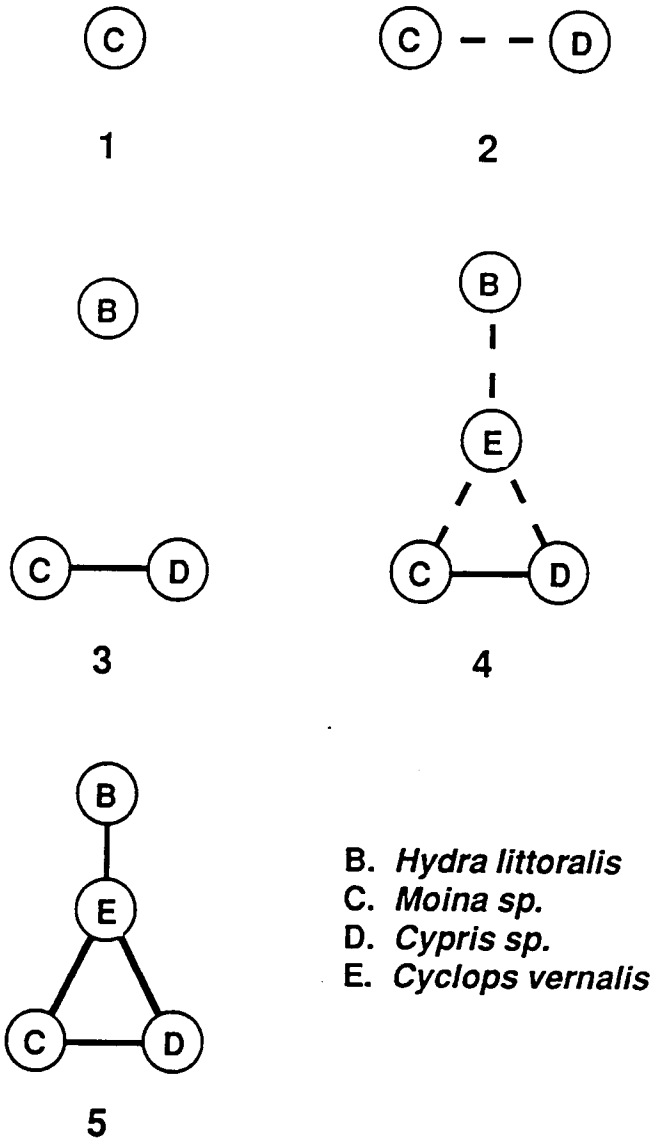


Fig. 28

Conservative assembly sequence of experimental organisms.

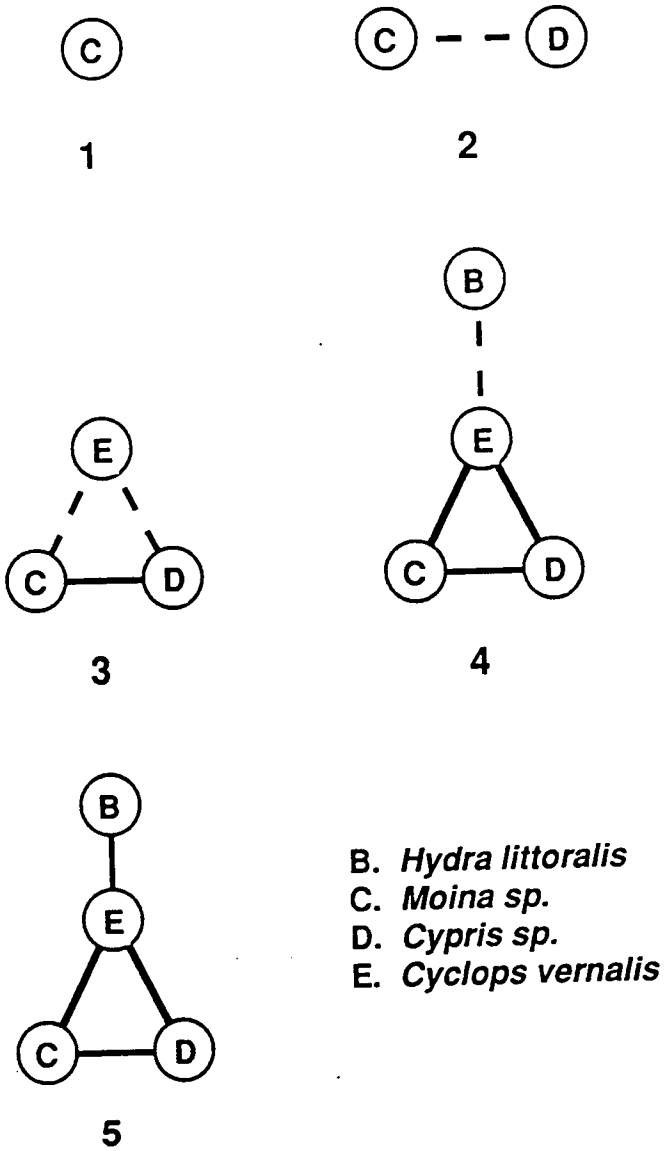


Fig. 29

Non-conservative assembly sequence of experimental organisms.

species that we are interested in. The "success" of this species would be measured in terms of persistence. In addition, the persistence of the entire food web would also be measured. Higher persistence values for the species E and the entire food web in the conservative treatment would support the conservative assembly hypothesis. It should be clear that this is superior to testing the respective persistence of rigid and non-rigid communities, because the rigidity or non-rigidity of the community depends on the assembly, not vice-versa.

Ideally, the experiment described above would be conducted with species which could be maintained in a controlled environment, and whose trophic relationships could be known with certainty. Zooplankton meet these requirements, and are also desirable because of their short generation times and the ease of maintaining pure cultures. The species chosen were Moina sp., a cladoceran; Cypris sp., an ostracod; Cyclops vernalis, a copepod; and Hydra littoralis, a cnidarian. In addition, Scenedesmus quadricauda, a green algae, was chosen as the producer species. Preliminary observation of the feeding habits of these species established that their trophic relationships followed the scheme given in figure 27. Both Cypris and Moina filter algae and bacteria. They differed, however, in there positions in the microcosms. Cypris fed exclusively on algae which had accumulated in visible clumps on the

sides and bottom of the beakers. Moina, however, in addition to feeding on the bottom, also filtered algae suspended in the water column. Hydra preyed primarily on cladocera, but would on occasion ingest an ostracod. Cyclops' diet was the most complex, preferring algae in the immature copepodid stage, but later switching to cladocerans and even larval Cyclops. Zdenek (1972) observed that such cannibalism increased with decreasing cladoceran densities in laboratory cultures of cyclopoid copepods.

Materials and Methods

The choice of appropriate vessels to serve as microcosms was the result of the careful consideration of a number of pertinent factors, as well as results from a good deal of trial and error experimentation involving both conventional and custom-built containers. In the end, 1 litre beakers were chosen because of their durability, uniformity, economy, and the ease with which they could be sterilized. A beaker was chosen over a flask because previous experiments indicated that the narrow openings of flasks might inhibit gas exchange.

Prior to sterilization, each microcosm was filled with 750 mls. of a Zooplankton micromedium, a defined growth medium which has proven to be favorable for both algae and zooplankton. The recipe for this medium is given in table 1. The microcosms were then covered with plastic lids,

Compound	WC Medium (g/L)	ZP MICRO (g/L)
NaNO3	36.8	7.50
CaCl2 2H2O	36.8	36.00
MgSO4 7H2O	37	4.00
K2HPO4	8.7	2.00
NaOH	-	2.00
NaCl	-	30.00
NaHCO3	-	5.00
KHCO3	15.0	-
Na2SiO3 9H2O	28.40	28.40
FeCl3 6H2O	1.08	0.0625
EDTA	5.0	0.5
H2BO3	1.14	0.01
MnCl2 4H2O	0.51	0.01
CoCl2 6H2O	0.16	0.006
CuSO4 5H2O	0.16	0.005
(NH4)6Mo7O24 4H2O	0.11	0.01
ZnSO4 7H2O	2.20	0.001
NaMoO4 2H2O	-	0.48

Table 1

Microcosm medium

sterilized in an autoclave, and allowed to cool overnight before any introductions were made. There were 10 replicate microcosms in each treatment (sequence). An identification code was given to each which consisted of the replicate number followed by the sequence identifier, e.g. 1A, 3B, etc.

All microcosms were maintained in an EGC environmental growth chamber, with a 12 hour diel period, and a temperature that cycled from a minimum of 18 C to a maximum of 22 C during each 24 hr period. The humidity was maintained at a constant 60% to minimize evaporation. However, fluid levels within the beakers were adjusted periodically with sterile distilled water. In order to minimize the impact of edge effect error, the beakers were placed randomly in a 5 X 4 grid pattern within the chamber, and moved randomly within the grid every day.

Introductions were made every five days according to the following schedule: sequence A - algae, Moina, Cypris, Hydra, Cyclops; sequence B - algae, Moina, Cypris, Cyclops, Hydra. The algae, ostracods, hydra, and cladocerans were introduced with disposable pipettes. The copepods, on the other hand, were introduced with a fine mesh net because of the difficulty of capturing them in pipettes. Care was taken to avoid contamination during these introductions.

Counting of the zooplankton was conducted on every other experiment day by inspection. Although only

presence/absence data were required, the population densities of the organisms were estimated at each sampling event. Algae were not sampled since previous work had shown that the homogenization required to take accurate samples was often disruptive to zooplankton growth. Additionally, every effort was made to minimize the disturbance caused by introductions and adjustment of fluid levels. All microcosms were sampled until every one had experienced an extinction of at least one zooplankton population, at which point the experiment was terminated.

Results

The microcosms showed a great deal of variability with respect to community ontogeny and to terminal community structure. This is not surprising, given that there are 16 possible species combinations with a set of four species. Additionally previous work by Drake (1985) has shown that such variability is characteristic in assembly experiments. Despite the variability, however, a few general patterns emerge for both treatments.

No microcosm contained <u>all</u> of the heterotrophic species at the termination of the experiment. On the other hand, all microcosms had at least one species present in addition to the algae by the end of the experiment. However, 4 microcosms (1B,6B,7B,8B) were essentially "dead" by the end of the experiment because they contained only algae and

hydra, which would eventually die out in the absence of prey species. The two treatments did not differ significantly in terms of the number of species present at the termination of the experiment. Population trajectory data for the four zooplankton species in each of the twenty microcosms are given in the Appendix.

Moina were the most prodigious reproducers of the group, reaching densities of 50 or more in 16 out of 20 microcosms. Of these, 12 contained 100 or more individuals at some point in the experiment. In addition, three non-conservative (4A, 5A, 7A) and one conservative microcosm (10B) had moina populations which had appeared to stabilize at 100 individuals.

Hydra also proliferated in a number of microcosms, especially where Moina were abundant. This apparent interdependence of the dynamics of Hydra and Moina resulted in the most obvious differences among extant community structure in the microcosms. With the exception of two treatments where both species coexisted for the duration of the experiment (7A, 9B), either Hydra or Moina went extinct. The trajectories of their respective populations could be divided into to broad categories. In the first, which I will refer to as pattern one, the Moina show rapid growth after an initial period of slow growth or moderate decline. In these microcosms, Hydra are introduced when Moina densities are relatively high, and subsequently increase in

number, although there is somewhat of a lag time in their response. The increase in Hydra numbers results in increased predation which in turn leads to greater mortality and the eventual extinction of the Moina population. In some cases, it appeared that an extinction "cascade" may have occurred. This situation is exemplified by microcosm 7B, where the absence of Moina may have led to increased Cyclops mortality. Additionally, the high abundance of Hydra in these microcosms may also have resulted in increased Cypris and Cyclops mortality. Predation by hydra appears to be the major source of mortality in the Moina populations, since no extinctions of Moina occurred in microcosms where there were no hydra, even when the other predator, C. vernalis was present. Microcosm 3B (fig. 30) is a typical "pattern 1" microcosm.

In pattern two (e.g. 5A, fig. 31), Moina "peak" later in community assembly, and are usually at a relatively low density when hydra are introduced. In these microcosms, Hydra numbers dwindle to extinction, and Moina numbers either level off or show a moderate decline. One possible explanation for this is that the Hydra simply starve to death. The success of Hydra feeding is largely dependent upon encounter rate, and it seems reasonable to assume that there could exist some critical density of Moina for any given population size of Hydra, below which an invading population would be unsuccessful. However, since this

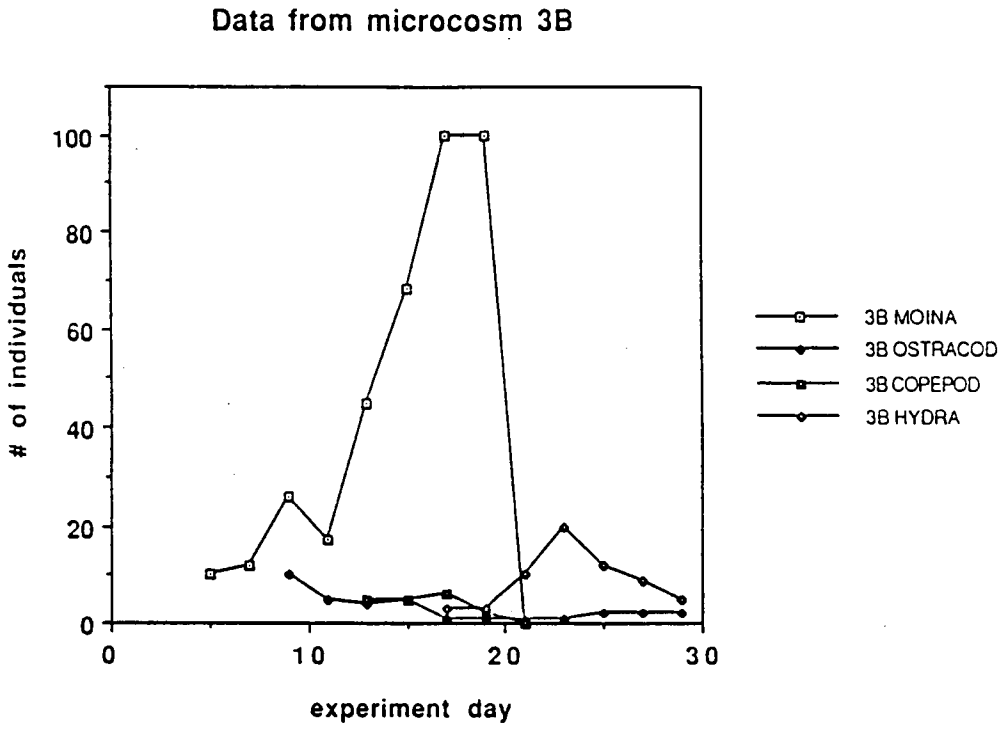


Fig. 30

Microcosm 3B, a pattern 1 microcosm.

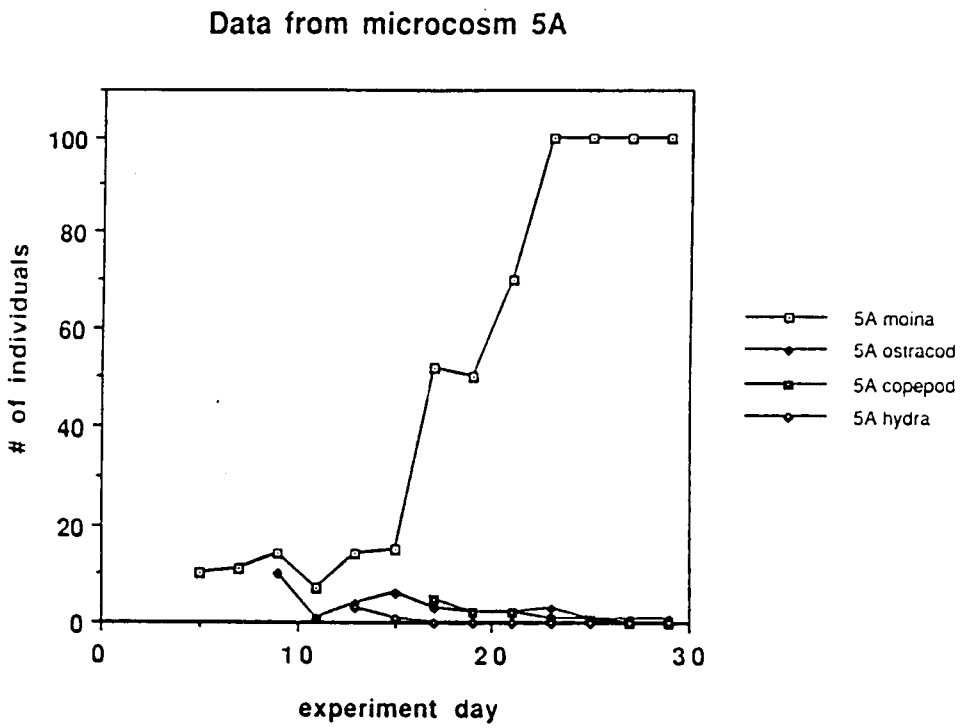


Fig. 31

Microcosm 5A, a pattern 2 microcosm.

experiment was not designed to test this, the exact mechanism of Hydra extinction in these systems will require further experimentation.

The success of C. vernalis varied. Their number increased in only 8 of 20 microcosms. Of these, 6 were in the non-conservative treatment. In general, Cyclops numbers were highest in microcosms where Moina, their preferred prey, were abundant (7A). Only two Cyclops populations persisted until the end of the experiment (7A, 6B). Both of these had relatively high numbers of copepods. However, the extant community structure in these microcosms was quite different.

A fixed factor one-way ANOVA was used to test for differences in persistence between the conservative and non-conservative treatment. The average persistence of cyclops populations was slightly higher in the non-conservative treatment, but the difference was not significant ($p = .1046$, table 2). This result does not support the conservative assembly rule, which would predict higher persistence values in the conservatively assembled treatment. The difference in the persistence of the entire species ensemble/food web between treatments was not significant either ($p=.238$, alpha $=.05$, table 3). Indicating that the effect of sequence had no effect on community persistence.

Analysis of Variance

Source of Variation	Sum of Squares	Mean square	d. f.	F-ratio	Sig. level
Between groups	11.25	11.25	1	2.922	.1046
Within groups	69.30	3.85	18		
Total (corrected)	80.55				

alpha = .05

0 missing values have been excluded.

Table 2

ANOVA for copepod persistence.

Analysis of Variance

Source of Variation	Sum of Squares	Mean square	d. f.	F-ratio	Sig. level
Between groups	16.20	16.20	1	1.491	.2378
Within groups	195.60	10.86	18		
Total (corrected)	211.80				

alpha = .05

0 missing values have been excluded.

Table 3

ANOVA for community persistence.

Cypris was the most commonly occurring species at termination, being present in all but three microcosms. However, Cypris showed no substantial growth in either treatment. This was probably due to the fact that the experiment was conducted in the late autumn, which is somewhat later than the peak of most ostracod reproduction, which occurs in the summer months (Pennak, 1978). Additionally, it is likely that some of the smaller nauplii were missed when counts were made.

Discussion

The results of this experiment seem to indicate that, in this case at least, conservative assembly did not promote the success of the key species or the community as a whole. However, these results have a very limited application, especially since the environment and invasion process were artificial. As with most ecological phenomena, conservative assembly is likely to be very scale sensitive, and the benefits it should have conveyed may not have had adequate time to manifest themselves. The results do, however, raise important questions about assembly rules in general and the expectations they generate.

Given the inherent idiosyncratic nature of communities, it would be interesting to know if there were some "types" of community that one would expect to adhere more strongly to conservative assembly. The answer to this question is

strongly dependent upon the perspective of the rule. The conservative assembly rule was derived to explain topological patterns in low resolution, snapshot data. In light of this, we might expect detailed examination of any particular case of assembly on a relatively small temporal scale to reveal occasional "violations" of this rule. In essence, the conservative assembly rule attempts to say something about the construction of a structure by examining the final product. This is analogous to deducing the way a house was built by looking only at the house. To be sure, there are certain generalizations that can be made about house building, foundations are always laid before frames are erected. But, sometimes tasks may be performed out of sequence without affecting the appearance or structural integrity of the final product. Additionally, experience tells us that things are more readily done out of sequence when things are held together loosely. In the case of communities, the "glue" holding everything together is the interaction among constituent species, and the magnitude of these determines its strength. Given this, it would be fair to say that conservative assembly should occur in communities where the "glue" sets quickly, i.e. in communities where interactions among species are strong and vary little over time.

As mentioned earlier, stable communities are guaranteed to be persistent and thus would show up frequently in the

data. The conservative assembly rule is thus a very reasonable explanation for the observed high incidence of rigid circuitry if we assume that communities in the data are at or near stable equilibria. However,communities with non-equilibrium population dynamics need not assemble conservatively since a stable equilibrium is not an possibility in these systems to begin with, regardless of topology. Consequently, while such systems might persist for some time, their persistence could not be directly linked to stability or any rule that would promote such stability. Such systems might be characterized by weak or fluctuating interaction strengths, stochastically variable environmental conditions, and/or intransitivity. It is not immediately clear whether these properties represent causes or effects of non-equilibrium dynamics. Nonetheless, the rules governing the topology of these communities are likely to be quite different from those governing systems at equilibrium. Given this, it is somewhat surprising that in the relatively stable and homogenous environment of the microcosms the conservative assembly rule did not apply. Again, however, it is not clear what effect the artificial spatial and temporal conditions would have on this result.

It appears from available data that the conservative assembly rule is a reasonable if not intuitive explanation for the high incidence of rigid circuit topologies in "real" food webs. This is further supported by results from

modelling, which indicate that, in general, invading species tend to become more specialized (Drake, 1982; Sugihara, 1982). However, as with any rule there are many possible exceptions and only a few of which have been discussed here. Furthermore, if we adopt a chiefly non-equilibrium view of nature, then conservative assembly would become more of an exception than a rule.

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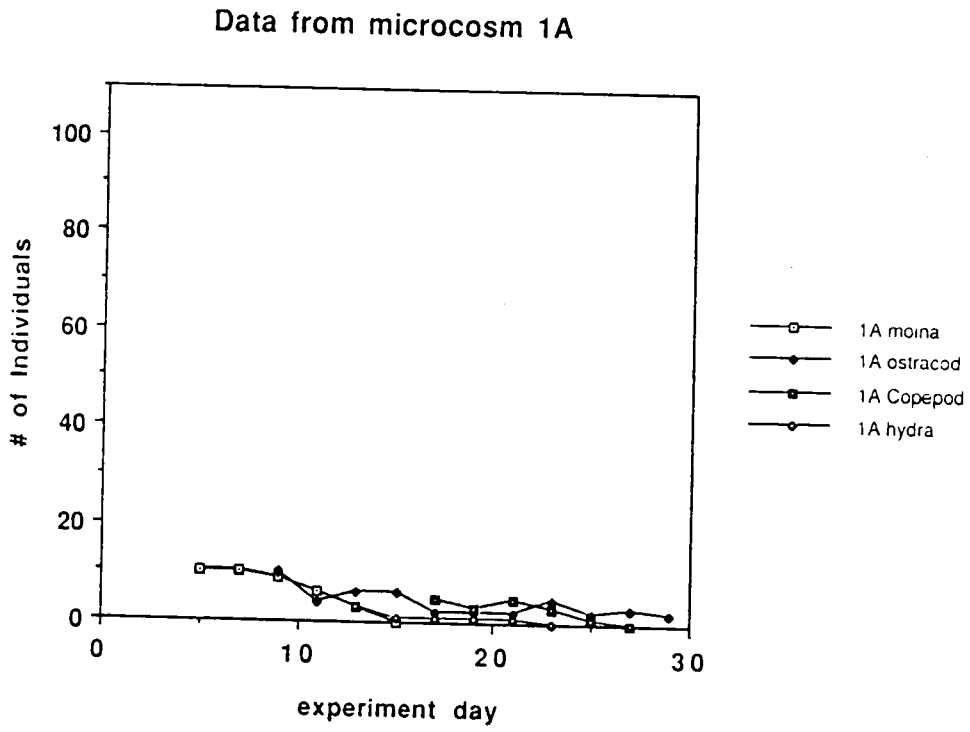
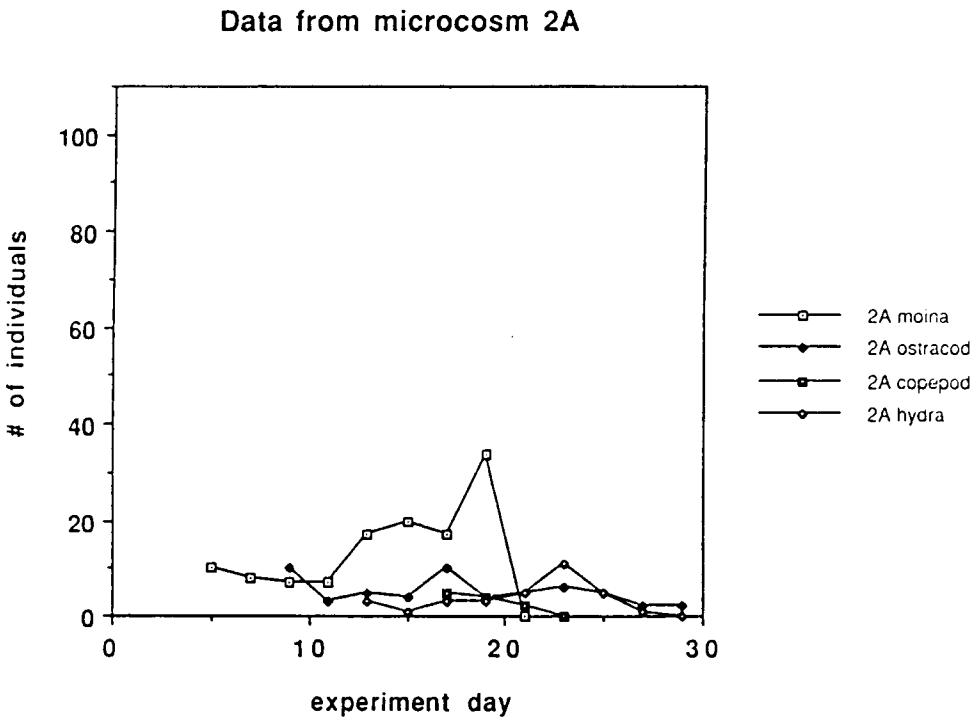
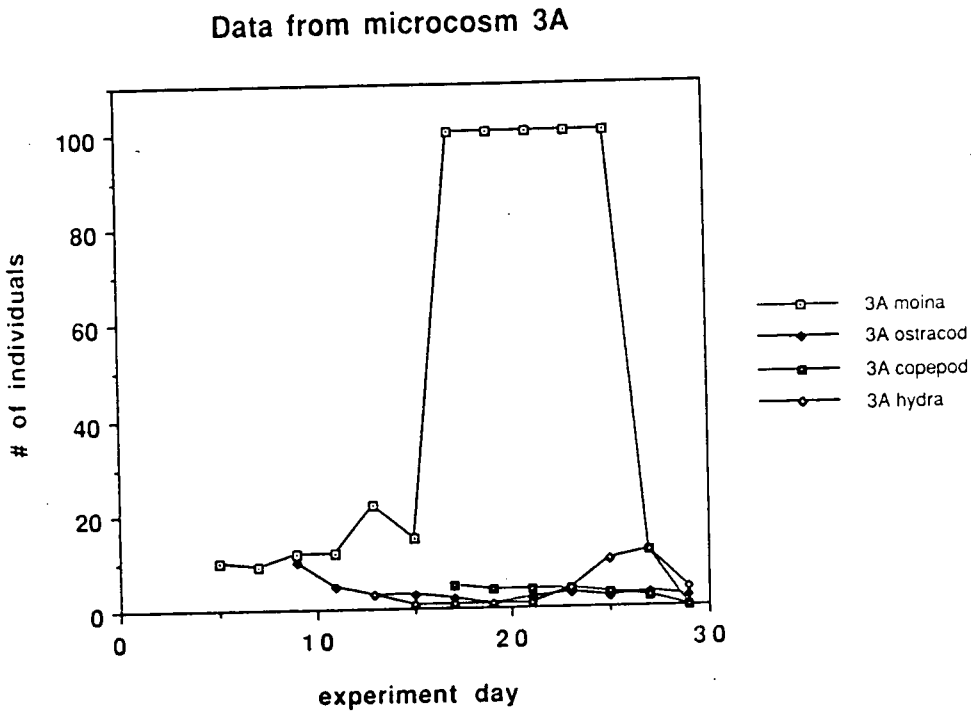
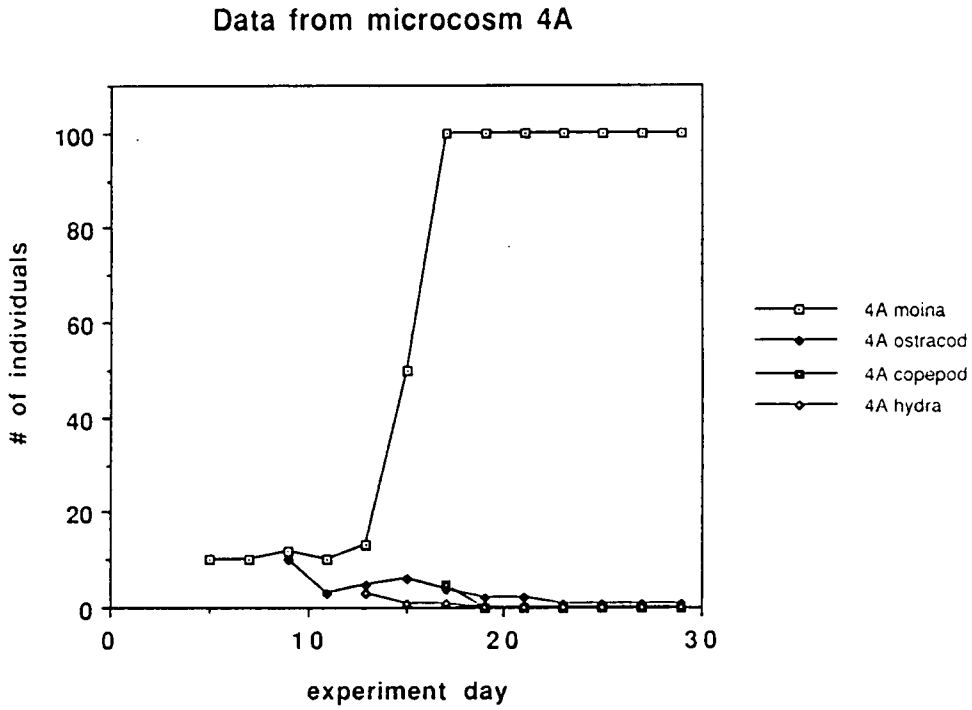
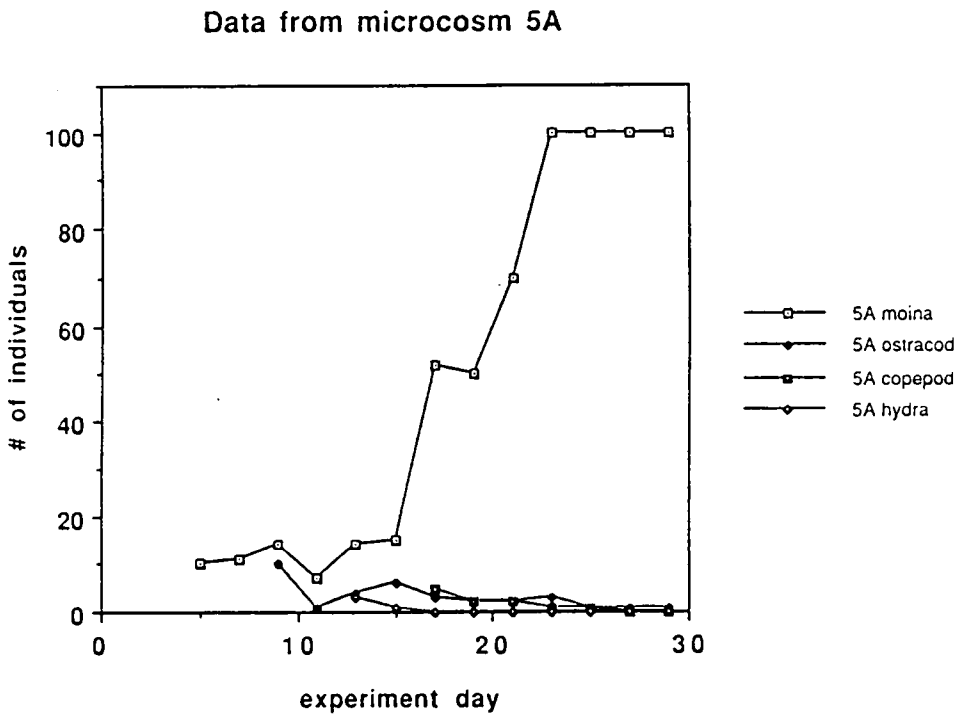
APPENDIX

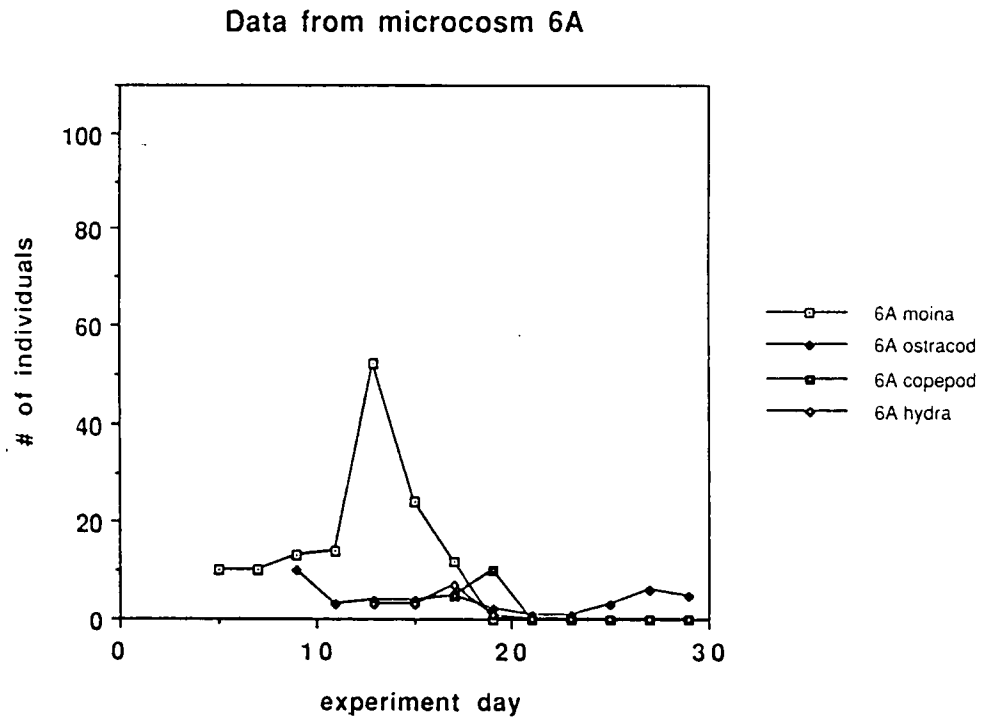

Data from microcosm 1A
100
80
60
40
20
0
# of Individuals
0
10
20
30
experiment day
1A moina
1A ostracod
1A Copepod
1A hydra

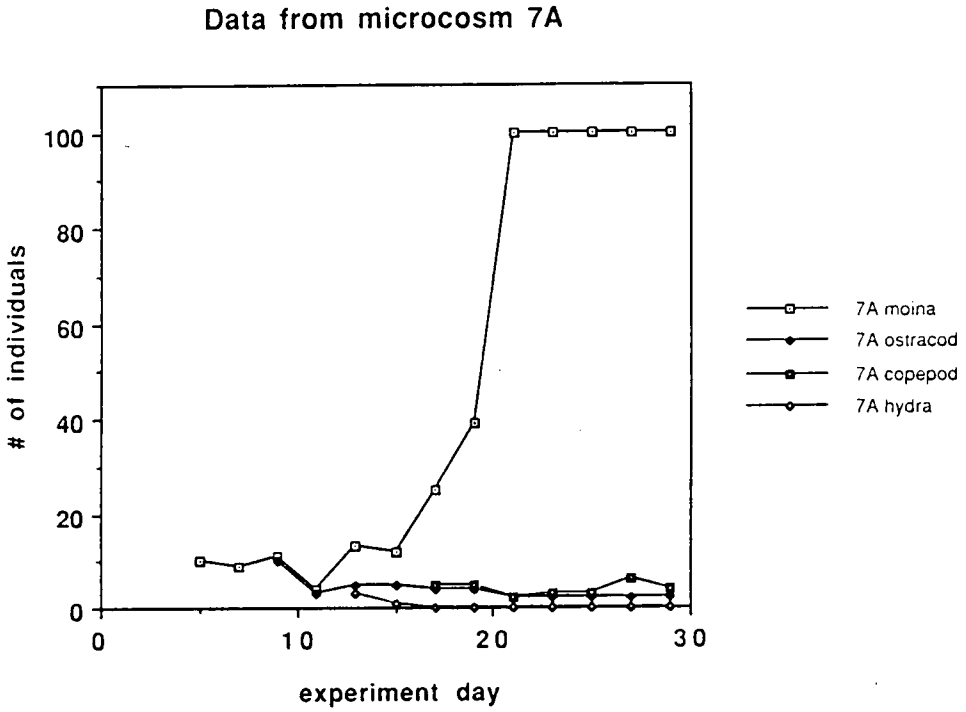

Data from microcosm 2A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
2A moina
2A ostracod
2A copepod
2A hydra

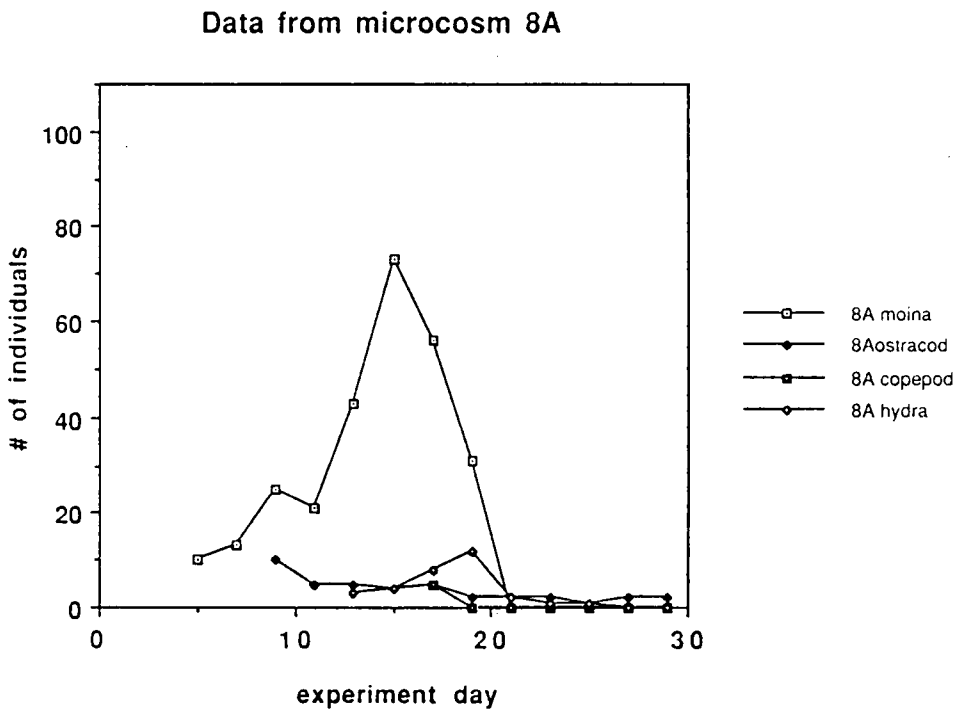

Data from microcosm 3A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
3A moina
3A ostracod
3A copepod
3A hydra

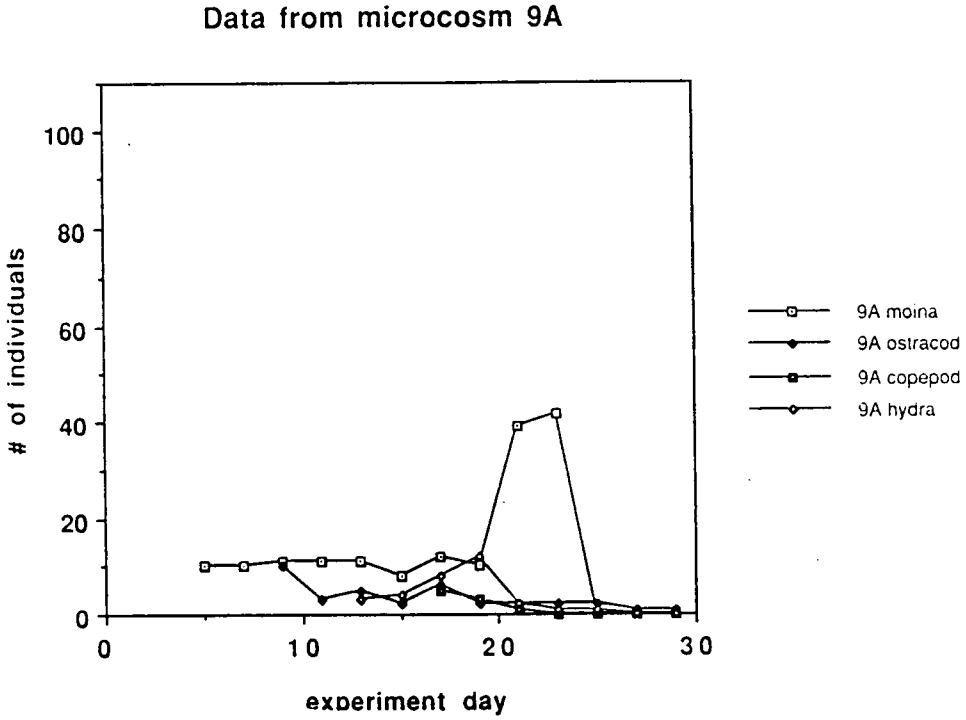

Data from microcosm 4A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
4A moina
4A ostracod
4A copepod
4A hydra

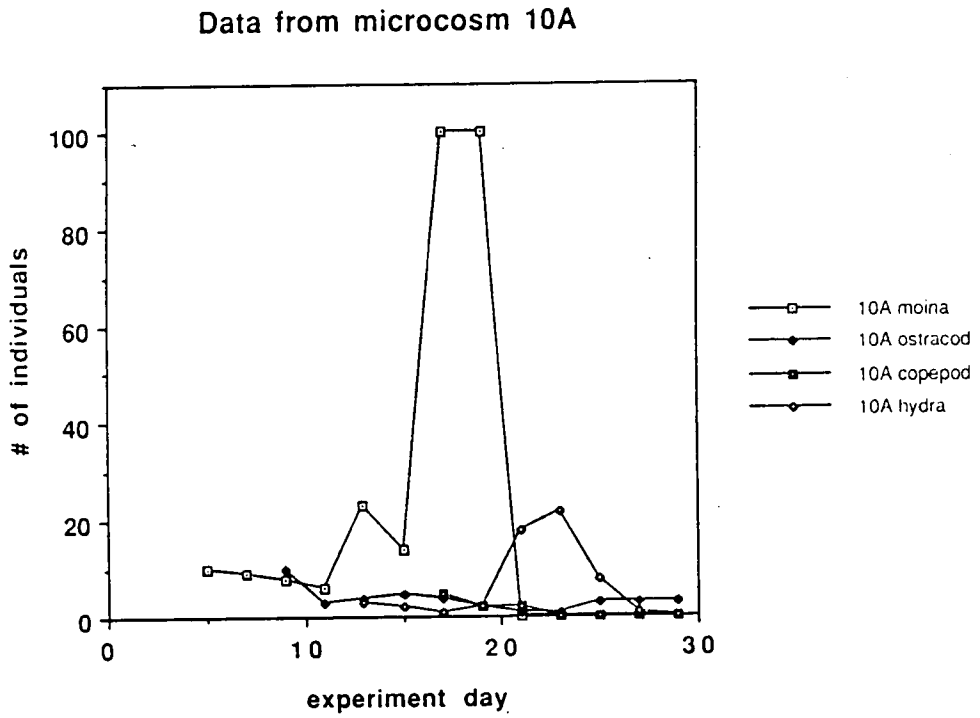

Data from microcosm 5A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
5A moina
5A ostracod
5A copepod
5A hydra

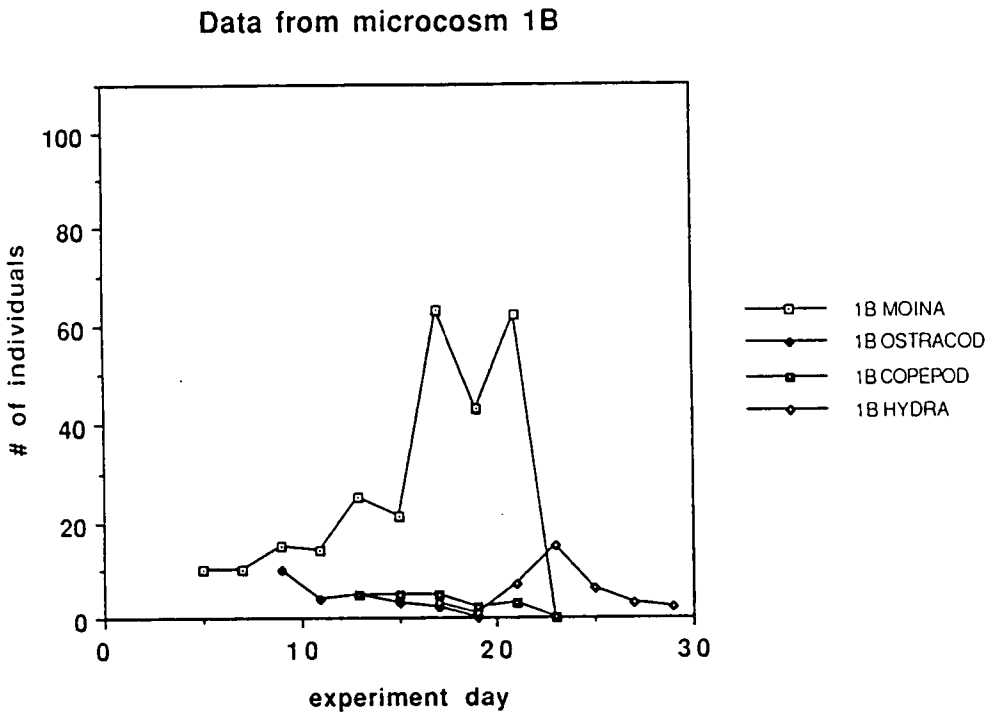

Data from microcosm 6A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
6A moina
6A ostracod
6A copepod
6A hydra


Data from microcosm 7A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
7A moina
7A ostracod
7A copepod
7A hydra

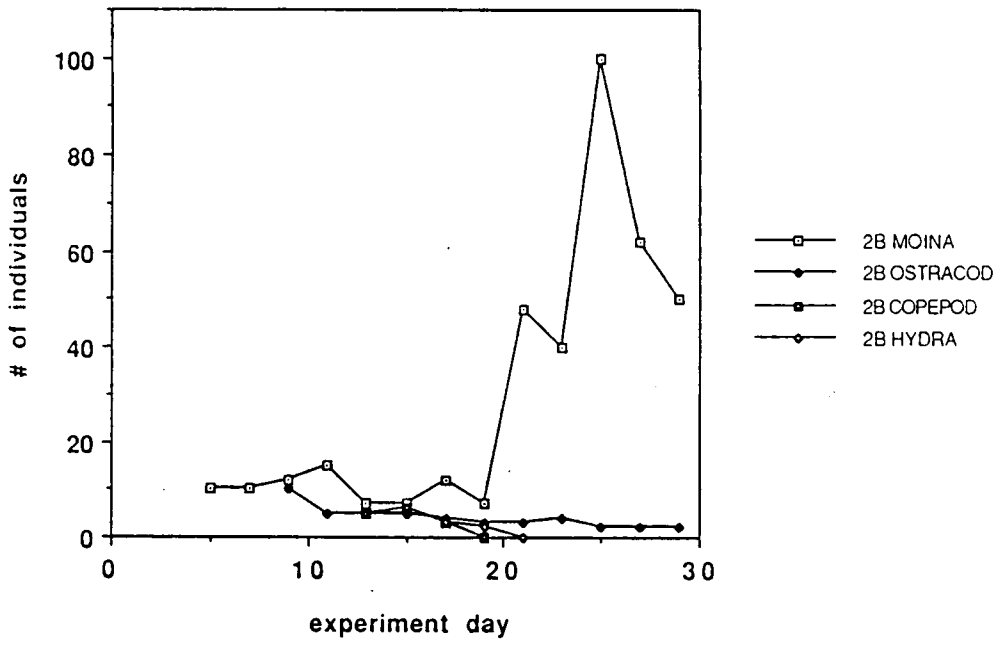

Data from microcosm 8A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
8A moina
8Aostracod
8A copepod
8A hydra

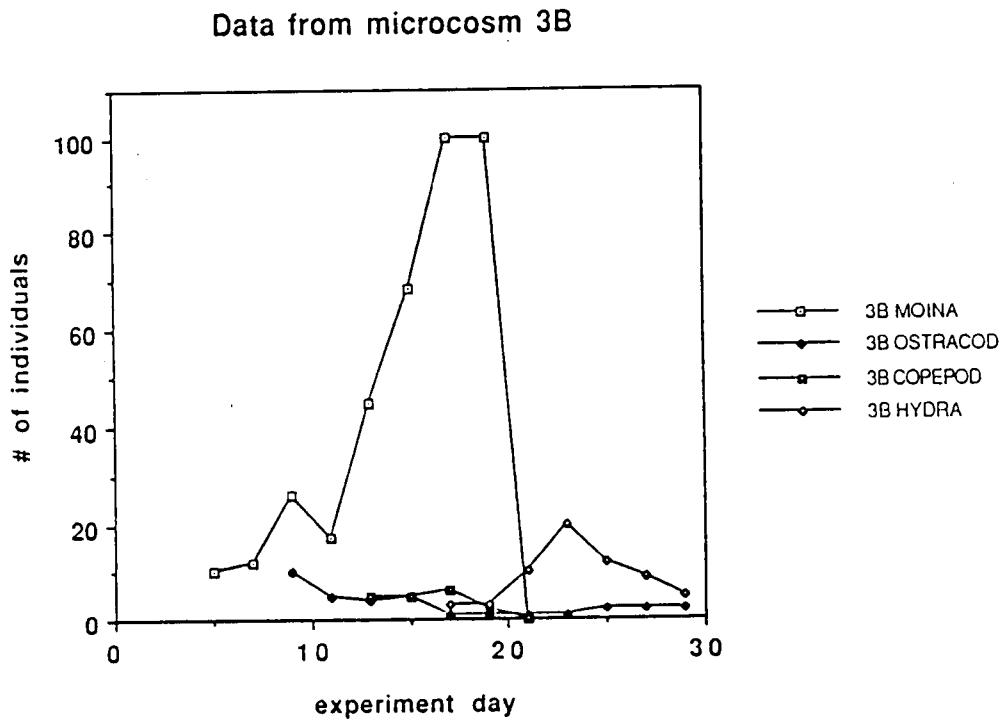

Data from microcosm 9A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
9A moina
9A ostracod
9A copepod
9A hydra

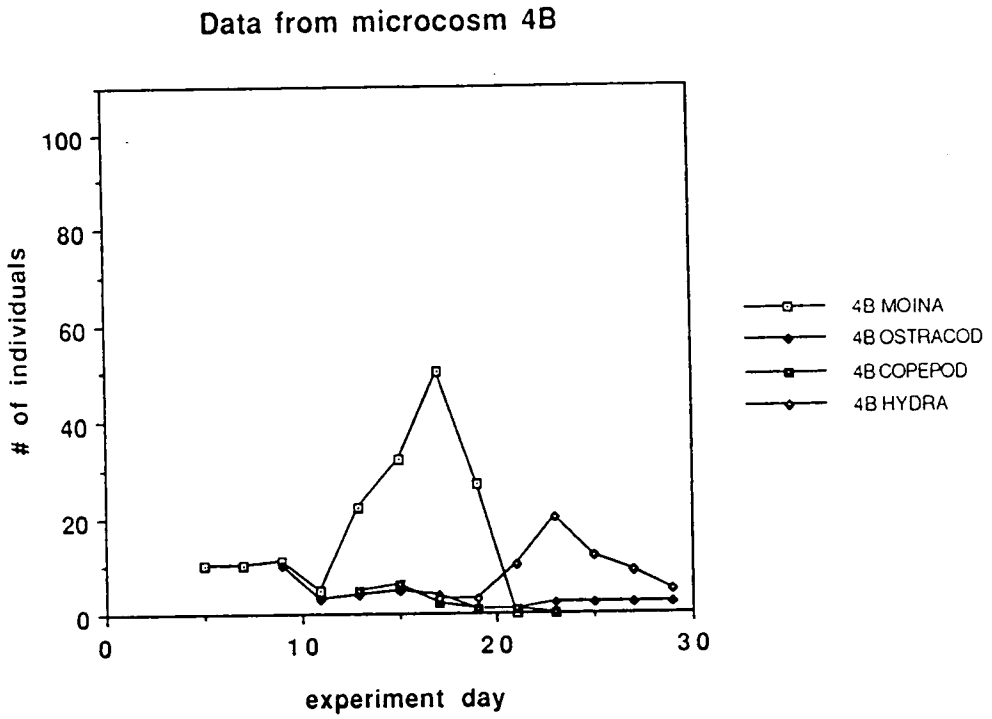

Data from microcosm 10A
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
10A moina
10A ostracod
10A copepod
10A hydra

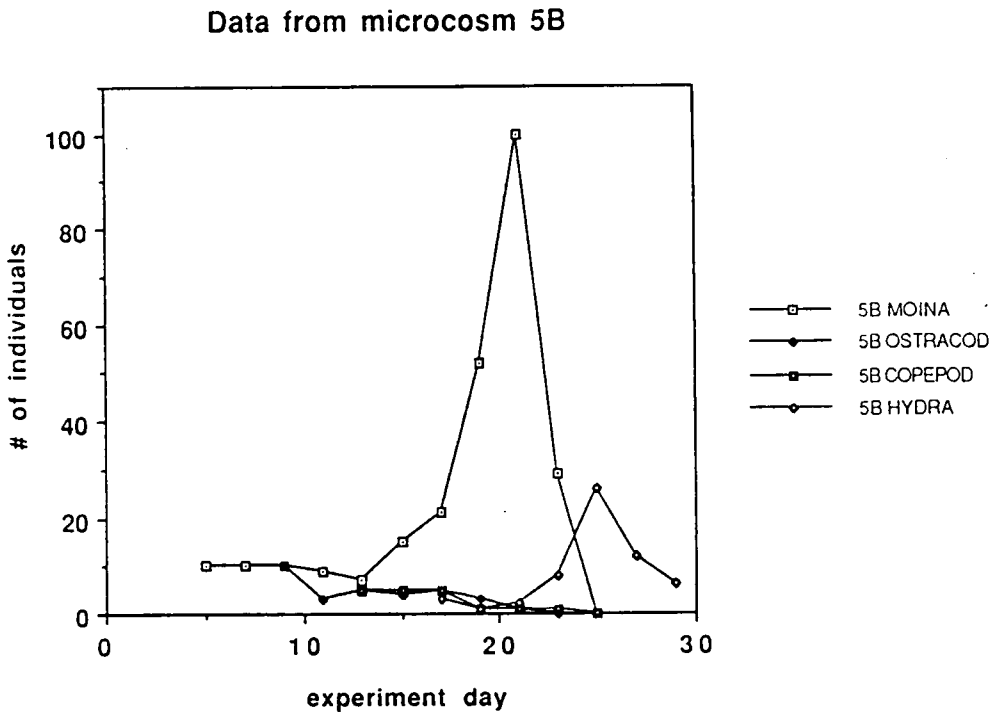

Data from microcosm 1B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
1B MOINA
1B OSTRACOD
1B COPEPOD
1B HYDRA

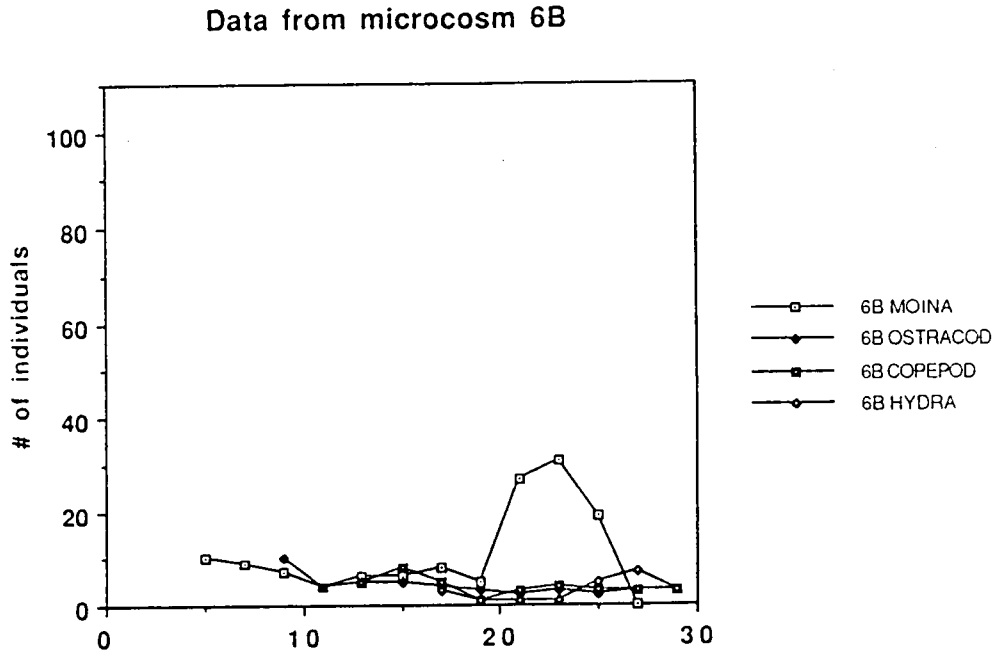
Data from microcosm 2B

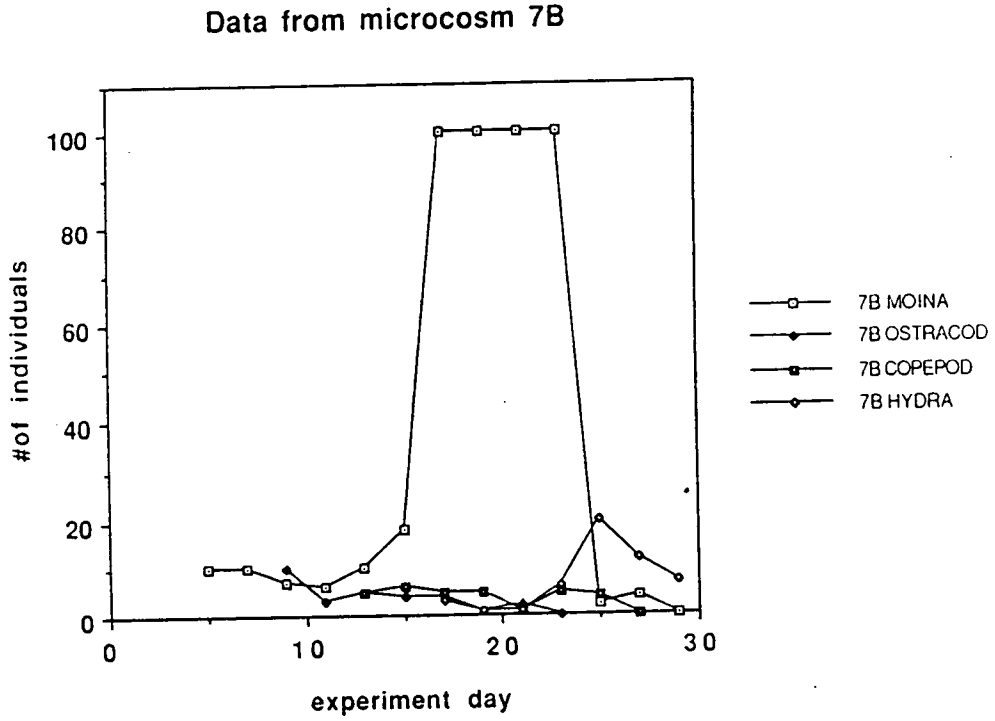


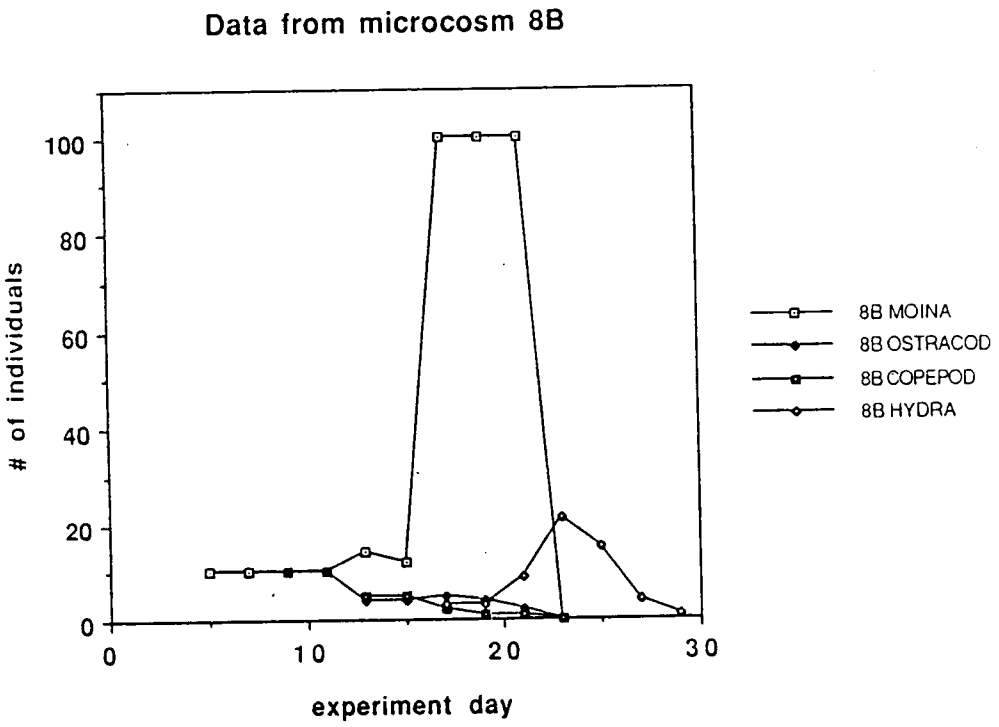

Data from microcosm 3B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
3B MOINA
3B OSTRACOD
3B COPEPOD
3B HYDRA

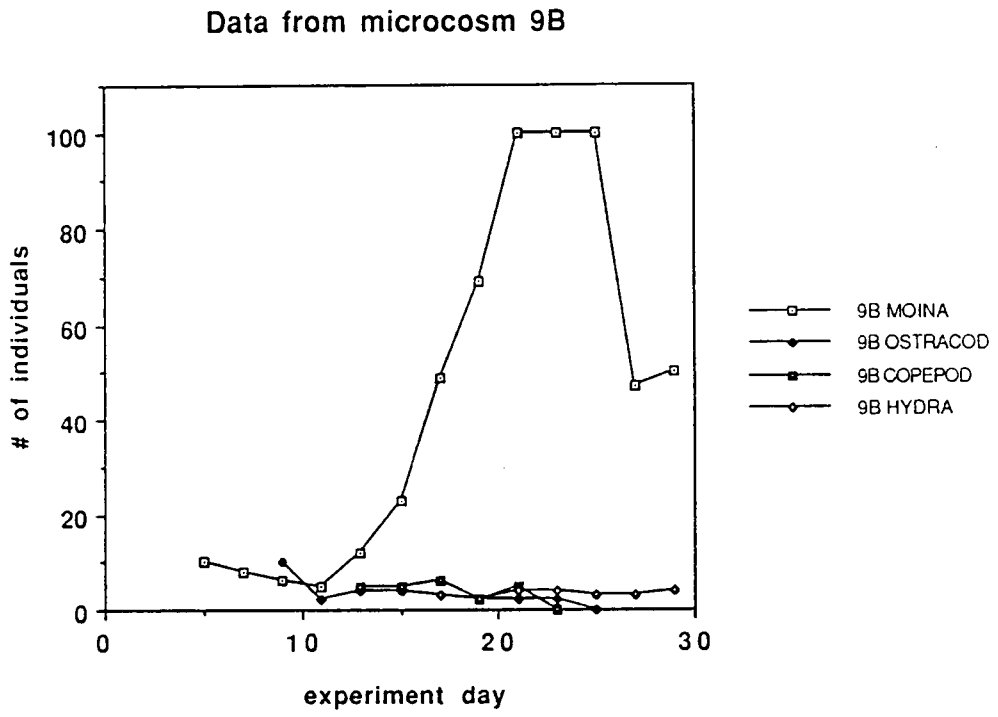

Data from microcosm 4B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
4B MOINA
4B OSTRACOD
4B COPEPOD
4B HYDRA

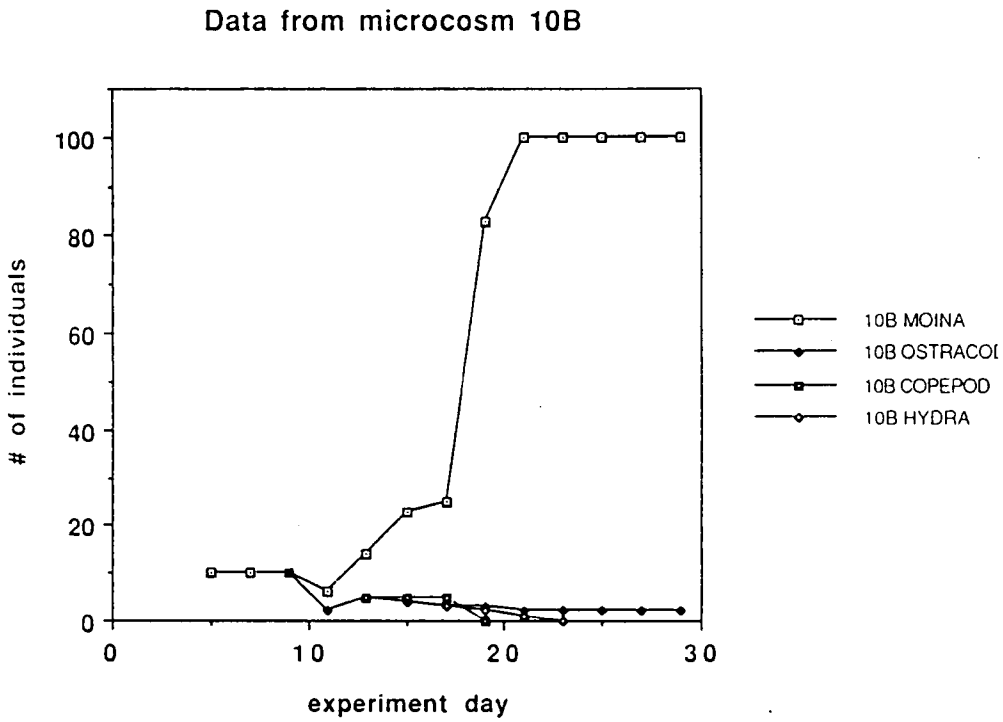

Data from microcosm 5B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
5B MOINA
5B OSTRACOD
5B COPEPOD
5B HYDRA


Data from microcosm 6B
# of individuals
100
80
60
40
20
0
0
10
20
30
6B MOINA
6B OSTRACOD
6B COPEPOD
6B HYDRA


Data from microcosm 7B
#of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
7B MOINA
7B OSTRACOD
7B COPEPOD
7B HYDRA


Data from microcosm 8B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
8B MOINA
8B OSTRACOD
8B COPEPOD
8B HYDRA


Data from microcosm 9B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
9B MOINA
9B OSTRACOD
9B COPEPOD
9B HYDRA


Data from microcosm 10B
# of individuals
100
80
60
40
20
0
0
10
20
30
experiment day
10B MOINA
10B OSTRACOI
10B COPEPOD
10B HYDRA

VITA

David Arthur Kenny was born in Virginia Beach, Virginia on April 24, 1965. He attended elementary school in Kingsport, Tennessee, however, where he graduated from Dobyns-Bennett High School in June 1983. After vascilating between majors in communications and pre-med at the University of Tennessee, Knoxville, he decided on zoology, and received his Bachelor of Arts in June 1987.

Though he never quite managed to transcend his bourgeoisie attitudes, the author did manage to broaden his conceptual horizons as a student in the graduate program in Ecology. He received his Master's of Science in May 1990.

The author is a member of Phi Eta Sigma, Phi Beta Kappa, and the Society for the Preservation of Stupid Cartoons. Mr. Kenny will be employed by the Tennessee Valley Authority after graduation.