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Title: The Role of Competition, Predation, Productivity, and
Temporal Heterogeneity in the Determination of System
Structure and Organization.

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William J. Liss

A model of the structure and organization of simple communities was developed and utilized to explain the structure of laboratory communities. Different rates of energy and material inputs and population exploitation defined environmental conditions. The laboratory systems were found to establish different steady-state structures under different sets of environmental conditions, in accordance with the general expectations of the model. In variable environments, community structure is continually changing and may be understood as being in pursuit of an ever-changing steady-state point. These studies support the view that predation/exploitation, competition, and productivity, and temporal heterogeneity can be understood to operate together in determining system structure including species diversity. As a result, classical interpretations of species interactions may not hold universally in multispecies interactive systems. Specifically, the expected results of the hypotheses of competition, predation, productivity, and/or temporal heterogeneity individually need not be reflected in the performances of the component populations and the system as a whole, even though each mechanism may be operating within the system and its environment.

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THE ROLE OF COMPETITION, PREDATION, PRODUCTIVITY,
AND TEMPORAL HETEROGENEITY IN THE DETERMINATION OF
SYSTEM STRUCTURE AND ORGANIZATION

by

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THE ROLE OF COMPETITION, PREDATION, PRODUCTIVITY,
AND TEMPORAL HETEROGENEITY IN THE DETERMINATION
OF SYSTEM STRUCTURE AND ORGANIZATION

INTRODUCTION

Historically the study of systems of populations or communities has been approached from at least two directions. Lindeman's (1942) trophic-dynamic or ecosystem theory has been generally viewed as a holistic approach in which rates of energy transfer from one trophic level to another become most important in understanding system structure and organization. Another approach, exemplified by Dayton (1971), is centered on defining the specific mechanisms that might underlie and so determine system structure and organization. A major aim of studies of community structure has been to understand patterns of species diversity. Hypotheses invoked to explain species diversity include competition (Dobzhansky 1950, C. B. Williams 1964), predation (Paine 1966), productivity (Ashby 1958, Connell and Orias 1964), spatial heterogeneity (Simpson 1964), climatic stability (Klopfer 1959), and time (Fischer 1960). Recently focus has centered on the relative importance of competition in structuring natural communities (Strong, Szyska, and Simberloff 1979, Connor and Simberloff 1979, Roughgarden 1982, Schoener 1982). Connell (1978) has viewed the problem of understanding species diversity in terms of steady-state vs. nonsteady-state explanations. He and others (e.g. Huston 1979) maintain that species diversity is greatest in nonsteady-state systems.

Presented individually as universal explanations for observed structure and organization, the diversity hypotheses tend to be simplistic. As the current controversy over the importance of competition testifies, no single hypothesis seems to be adequate in terms of generating understanding of structure and organization. This has been recognized previously, the result being the synthesis of two or more hypotheses into a framework for understanding observed community structure and organization (Menge and Sutherland 1976, Wiens 1977). Even so, emphasis is still placed upon the relative importance of one mechanism over another. For example, Menge and Sutherland suggested that the relative importance of competition as opposed to predation in structuring natural systems is dependent upon trophic level, while Wiens suggested that competition is perhaps intermittent in importance depending upon environmental conditions. These studies imply that specific mechanisms and their relative importance in determining structure can be isolated and identified empirically.

Isocline models as developed by Booty (1976) and expanded upon by Liss (1977) and Thompson (1981) provide a theoretical framework in which both steady-state and nonsteady-state system structure may be understood in terms of interactions between the populations composing a system and conditions in the environment of the system. This provides the potential for further theoretical unification of several of the diversity hypotheses. The goal of the research presented in this thesis has been to further advance understanding of structure and organization through the development of a unifying model and its use

in interpretation of observational experience. Attainment of this goal required two specific objectives:

1. Articulation of a multisteady-state isocline model that provides unification of the roles of productivity, predation and exploitation, competition, and temporal heterogeneity in determining structure and organization of simple communities.
2. To empirically determine and explain, in laboratory systems, the roles of productivity expressed as energy and material input, predator/exploitation, and competition in determining structure and organization.

Structure we defined as the apparent form of a system as a whole (Liss, et al. 1983). In simple systems, structure may be taken to be the kinds of species found in the system along with their distribution and abundance in space and time (Dayton 1971, Menge 1976).

Organization is taken to be more of a theoretical concept, in part entailing how species populations and their level-specific environments are interrelated and so incorporated into a system as a whole.

THEORETICAL FRAMEWORK

Isocline models symbolize, partially articulate, and provide a perspective on the structure and organization of natural systems. With these models, the structure and organization of a simple community (e.g. Fig. 1a) can be represented graphically with sets of isoclines on a series of interrelated phase planes (Fig. 2). There is no a priori limit to the complexity of systems that can be analyzed with isocline models, although complex systems can become intractable when trying to understand all possible isoclines on all possible phase planes. As a result, isocline models of simple systems will be discussed to simplify description of the basic features of isocline analysis. Even simple linear representations (Fig. 1) exhibit a richness of complexity when represented with systems of isoclines on phase planes.

In Figure 1a, the populations and the interactions between them may be taken to be the community while I (the rate of energy and material input or system productivity) and E (for the purposes of this paper, the number of units of effort harvesting the carnivore population) may be taken to define the environment of the system. Harvesting effort removes biomass from the carnivore population, while productivity in terms of energy and material input (L.G. Williams 1964), is representative of the rate at which plant resources are introduced into the system. Definition of the environment is not necessarily limited to only I and E. Their use demonstrates the effects that changes in both productivity (expressed in terms of changes in I) and harvesting (expressed in terms of changes in E and

- Figure 1. a. Digraph of a simple predation system. Populations of a carnivore (C), herbivore (H), plant (P) and plant resources (R) define the system. E, number of units of effort harvesting C and I, rate of energy and material input into the system comprise the environment of the system.
- b. Digraph of a predation-competition system in which carnivore population C2 competes with carnivore population C1 for the herbivore food resource. E and I comprise the environment of the system.

Figure 1.

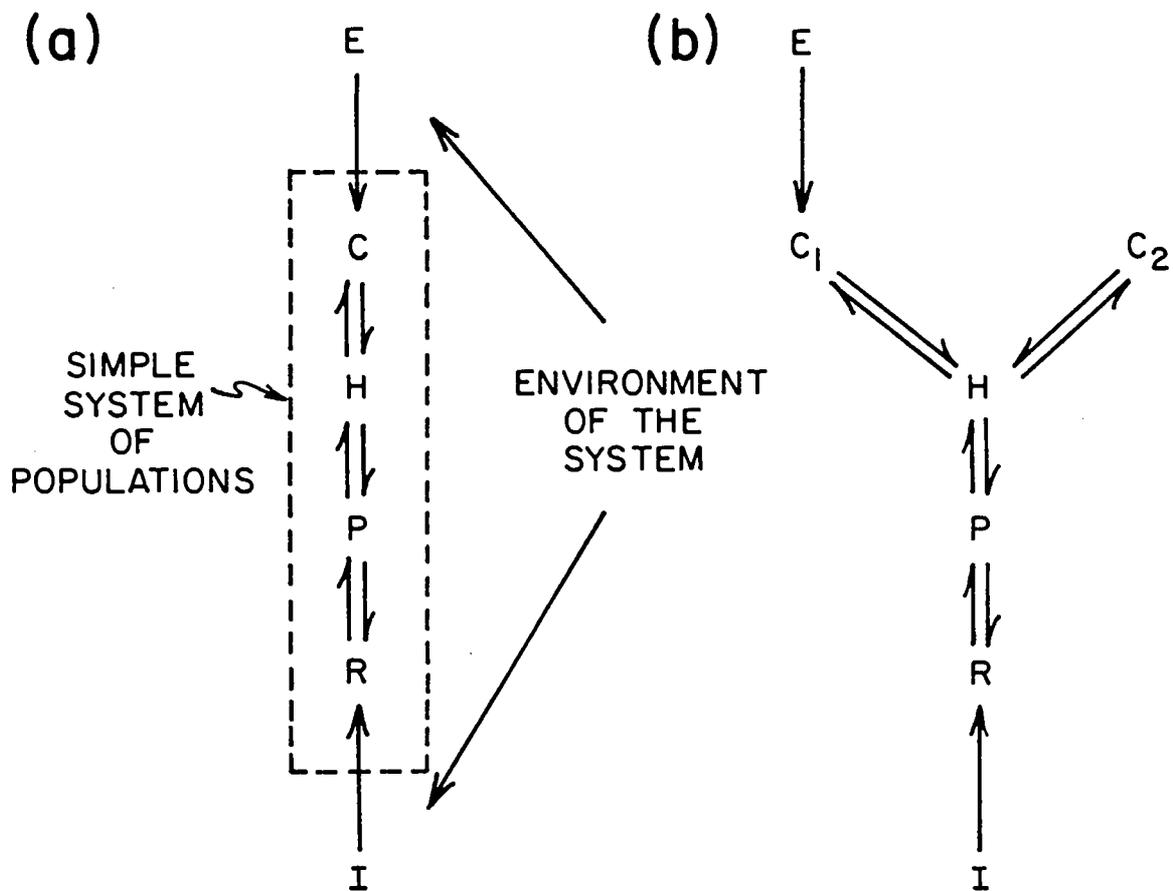
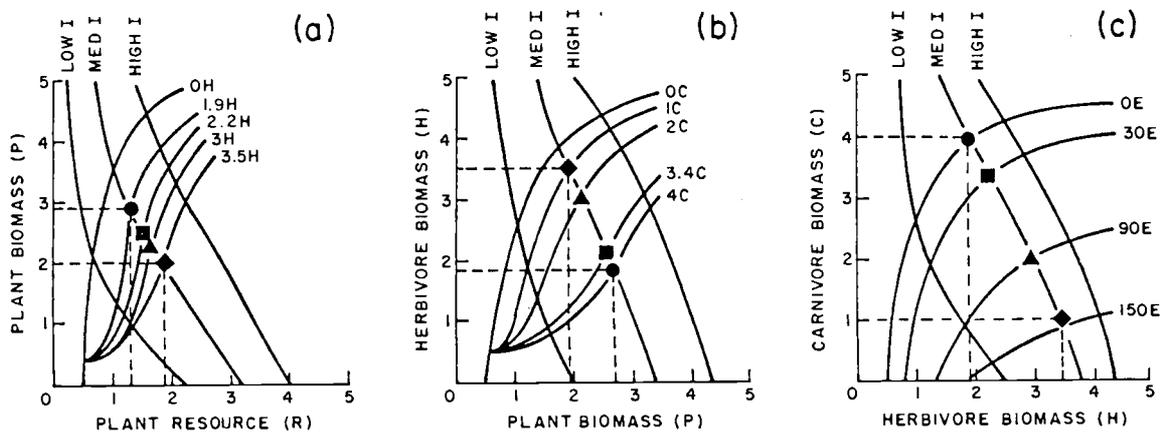


Figure 2. Phase planes and isocline systems derived for the system shown in figure 1a. Combinations of values of I and E define environmental states. Steady-state points that define the steady-state structure of the system at a medium rate of energy and material input, MED I , and levels of harvesting effort $0E$ (circles), $30E$ (squares), $90E$ (triangles), and $150E$ (diamonds) are shown. Each steady-state point on each phase plane is a two-dimensional projection of a single four-dimensional point in phase space. After Liss and Warren (1980).

Figure 2.



the consumer-resource links between component populations) may have on system structure and organization. Physical disturbances (e.g. wave shock; Menge 1976) may also be modeled as specific environmental parameters.

On each phase plane in Figure 2, resource density is plotted along the x-axis while consumer density is plotted along the y-axis. The descending isoclines, parameterized by different levels of I , are resource isoclines (Booty 1976). These represent the sets of biomasses of consumer and resource where the rate of change of resource biomass with time is zero. The common labeling of different isoclines on different phase planes results from the linked nature of the phase planes in n-dimensional phase space. The ascending isoclines on each phase plane are consumer isoclines. These represent the sets of biomasses of consumer and resource where the rate of change in consumer biomass with time is zero. These isoclines are parameterized by the density of the trophic level that utilizes the consumer in each consumer-resource interaction or, on the C-H phase plane, by different levels of E . Each intersection of a predator and prey isocline is a steady-state point where the rate of change of both predator and prey biomass with time is zero.

The isoclines can be generated in many ways. The system of populations may be defined by a set of non-linear differential equations, each representing the rate of change in biomass with time of a particular population. The components of the equations for each population model the rates of biomass gain due to recruitment and production and rates of biomass loss due to mortality from predation

or exploitation and non-predatory losses. The forms of these components determine the shapes of the isoclines (Booty 1976, Thompson 1981). For a zero rate of change, total loss rate must equal total gain rate. Steady-state points for each set of environmental conditions can be found by iterative solution of the set of equations (Thompson 1981). The isoclines can also be derived graphically (Booty 1976, Liss 1977).

Isocline models illustrate the following generalizations (Liss et al. 1983):

1. Under different environmental states a community will develop different steady-state structures and organizations and thus can be understood to be a multisteady-state system.
2. Changes in structure of an n-dimensional community can be understood as an n-dimensional trajectory in phase space in continuous pursuit of an n-dimensional steady-state point whose location in phase space is continually changing due to result of changes in the environment.

If I and E are fixed at medium input (MED I) and zero exploitation (OE), the system will converge upon the steady-state points defined by the solid circles (Fig. 2). The steady-state biomasses of the populations are $R = 1.3$, $P = 2.8$, $H = 1.9$, and $C = 4.0$. If I remains constant at MED I but E is increased to 150E, the system will converge upon the steady-state point defined by the solid diamond on all three phase planes. By increasing effort to this

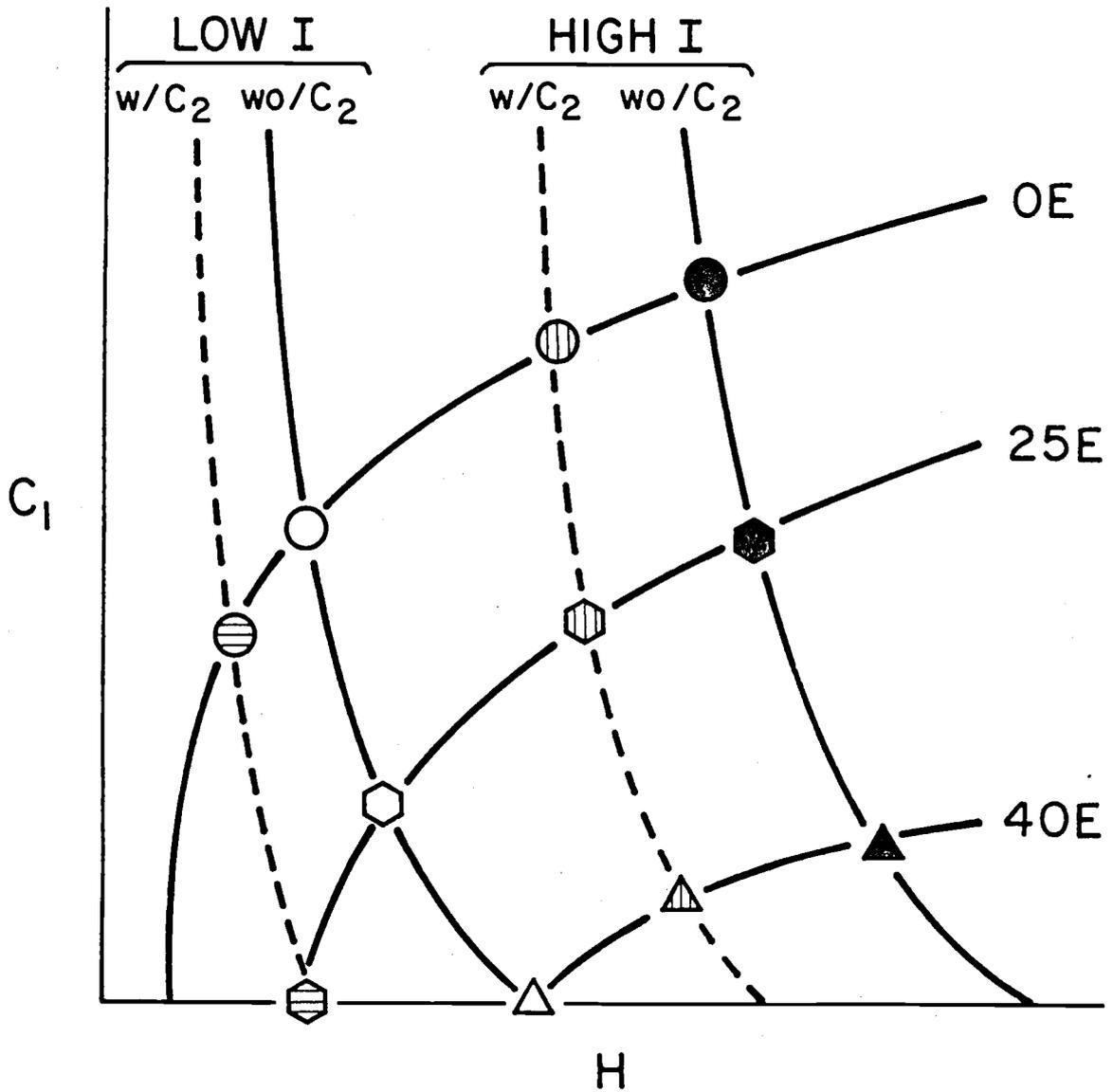
level, the system re-equilibrates with the carnivore experiencing a decline in steady-state biomass to 1.0 and the herbivore, under less predation pressure from the carnivore, increases in biomass to 3.5. The plant population, under increasing predation pressure, declines to approximately 2.0, while resources increase to 1.9.

For each set of environmental conditions a steady-state point exists on each phase plane. The set of these points defines the steady-state structure of the system (e.g. the solid circle and the solid diamond define steady-state structure at MED I, OE and MED I, 150E, respectively). Changes in environmental conditions bring about changes in steady-state structure and thus the system can be understood to be a multisteady-state system (Liss et al. 1983). For a single population or a community to reach steady-state, the environment (I and E in this case) must remain constant. Since environmental constancy rarely holds, change in structure and organization can be understood as a trajectory continuously pursuing an ever-changing steady-state point (Booty 1976, Liss 1977, Thompson 1981).

So far a community influenced by different rates of energy and material input and varying levels of exploitation of a single carnivore has been considered. What would happen if the organization of the system in Figure 1a were altered by the addition of a competing but non-exploited carnivore C2 (Figure 1b)? In this case, food resource competition will shift the solid prey isoclines to the left at each I (Figure 3, dashed isoclines; see Booty 1976; Liss 1977; Thompson 1981). Predation on H by C2 as well as C1 adds an additional

Figure 3. Phase plane and isocline systems representing the interaction between carnivore C_1 and its prey, herbivore H when the competing carnivore C_2 is present (w/C_2) and when it is absent (w_0/C_2).

Figure 3.



loss term due to consumption by C2 to the equation representing rate of change of H biomass, bringing about the leftward shift of the prey isoclines. Stated differently, competition between C1 and C2 acts through the resource, resulting in lower steady-state levels of H, C1, and C2 for a given set of values of I and E. At LOW I, 25E, if the predator C2 is absent, the system steady-state is defined by the open hexagon. If C2 is included and the values of I and E remain the same, C1 will be driven to extinction (the 40E predator isocline does not intersect in positive phase space the LOW I, w/C2 prey isocline; horizontally-lined hexagon). C1 and C2 can coexist if I (system productivity) is increased (vertically-lined hexagon), harvesting effort, E, on C1 is decreased (horizontally-lined circle), or both occur simultaneously (vertically lined circle). Hence, productivity, exploitation, predation between trophic levels, and competitive interactions may act together to determine system structure and organization.

METHODS

A digraph of the experimental systems used to investigate the roles of productivity, exploitation, predation, and competition in determining system structure and organization is shown in Figure 4. Previous work (Woltering 1981, Liss et al. 1983) indicated that food resource competition may take place between guppies and snails for the alfalfa ration with algae serving as an alternative prey for the snail populations. This design permits evaluation of community structure over a range of I and E when the competitors occur both allopatrically and sympatrically.

Thirty-two systems composed of populations of guppies (Poecilia reticulata), snails (family Planorbidae), and various taxa of algae were set up at Oak Creek Laboratory of Biology. Each resided in a 40 liter glass aquarium adapted for flow-through usage. Each tank received 200 ml min^{-1} of well water at $21^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and was subjected to a 14/10 hour light/dark cycle. Twenty-eight tanks were unshaded, receiving light intensities of 20.3 ± 2.3 quanta of light energy while the remaining four were shaded, receiving only 1.8 ± 0.5 quanta of light energy. Each tank had approximately 3,450 cubic cm of cover available to newborn guppies and snails in the form of floating plastic plants.

Fourteen of the unshaded aquaria received a low rate of energy and material input (80 percent alfalfa and 20 percent Oregon Test Diet, Sinnhuber et al. 1977) and the other fourteen unshaded tanks received a high rate of energy and material input (Table 1). These

Figure 4. Digraph of the inferred trophic relations between components in the experimental systems. G represents the guppy population, and S, the snail population. A and Al represent the alfalfa and algal assemblage respectively. G, S, A, and Al together define the community. E is the level of exploitation that the guppy population is exposed to, expressed as percent population biomass removed every 28 days. I_{alfalfa} and I_{light} are the energy and material input rates of alfalfa and light into the system. E, I_{alfalfa}, and I_{light} may be taken to define the environment of the laboratory systems.

Figure 4.

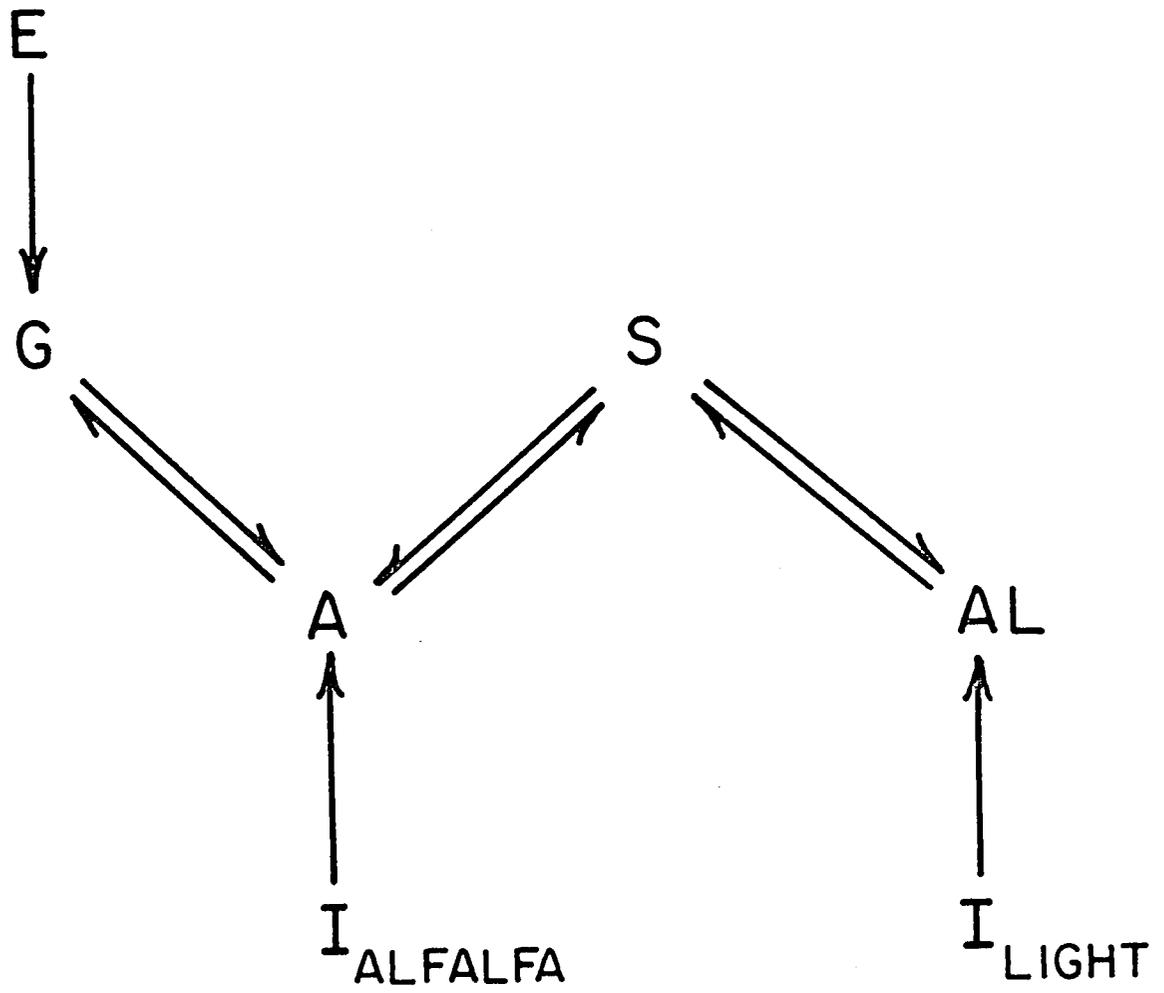


Table 1. Experimental design including species composition and environmental parameters for each system.

System	Number of Tanks	Input Rate ¹	Exploitation Rate ²
Snail-Alfalfa-Algae	2	0.6	-
	2	4.0	-
Guppy-Alfalfa-Algae	2	0.6	0
	2	0.6	25
	2	0.6	40
	2	4.0	0
	2	4.0	25
	2	4.0	40
Guppy-Snail-Alfalfa-Algae	2	0.6	0
	2	0.6	25
	2	0.6	40
	2	4.0	0
	2	4.0	25
	2	4.0	40
Guppy-Snail-Alfalfa (shaded system)	1	0.6	0
	1	0.6	40
	1	4.0	0
	1	4.0	40

¹Grams alfalfa ration day⁻¹

²Percent biomass removed every 28 days

will be referred to as LOW I and HIGH I, respectively. Twelve unshaded aquaria, six each at LOW I and HIGH I, had only guppy and algae populations, with two systems in each subgroup of six being exploited at 0, 25, or 40 percent of the biomass of the population present at the end of every 28 day period (0E, 25E, and 40E, respectively). On the phase plane in Figure 3, this set of twelve systems would be analogous to those represented by the solid and open steady-state points at the intersections of the solid predator and prey isoclines. The other twelve unshaded tanks were composed of guppy, snail, and algae populations with six each at LOW I and HIGH I. Again, two systems in each subgroup were exploited at 0, 25, or 40 percent. On the phase plane in Figure 3, this set would be analogous to those represented by the vertically- and horizontally-barred steady-state points found at the intersection of the solid predator and dashed prey isoclines. The remaining four unshaded aquaria, two at each I, had only snails and algae. The four shaded aquaria had only guppies and snails. In these systems, competitive outcomes when the populations were limited to a single resource, the alfalfa ration were examined.

At the beginning of the experiment, tanks were stocked so that the age structure and biomass of all guppy and snail populations were initially similar in all LOW I systems and HIGH I systems. Previous work (Woltering 1981, Liss et al. 1983) had shown that guppy and snail populations would maintain higher (near)steady-state (NSS) biomasses at HIGH I than at LOW I (NSS refers to the localized region of phase space which the system trajectories eventually occupied).

Consequently, HIGH I populations were stocked at higher biomasses than LOW I populations to speed the attainment of NSS.

Each system was sampled every 28 days. During sampling, all guppies and snails were removed from the tanks and their length, weight, and numbers were recorded. Each guppy population was exploited according to a schedule that provided for the removal of a proportion of the population corresponding to the exploitation rate (Liss 1974; Woltering 1981). Unharvested fish were returned to the tanks. Snail numbers and biomass were determined. The algal component was sampled by 32 plexiglass squares to each tank. The algae assemblage was brushed into an open container. At each sample period four squares were used to determine chlorophyll concentration. Chlorophyll was extracted from the sample (Strickland and Parsons, 1968). From this, the relative density of the algal assemblage in each sample was determined on a Beckman model 35 spectrophotometer utilizing the method and equations of Wetzel and Westlake (1969).

In addition, in order to keep micro-invertebrates at a minimal level, the accumulated sediments in each tank were siphoned out every four days. Twice a month the sediment samples from each tank were saved and dry weights were determined in order to keep track of changes in relative organic sediment densities through time. These sediments are composed of uneaten alfalfa ration and feces that collect on the bottom of the tanks. The biomass of uneaten alfalfa ration is determined by the rate that the ration is introduced into the tanks and the rate that it is consumed by guppies and snails.

Thus the density of uneaten alfalfa should bear some relationship to I, guppy biomass, and snail biomass. Organic sediment biomass is used as a nonlinear index of the density of the uneaten alfalfa ration. Three place running averages of the bi-monthly sediment samples were plotted against time. Organic sediment density for the dates upon which the systems were sampled were extrapolated from the time plots.

RESULTS

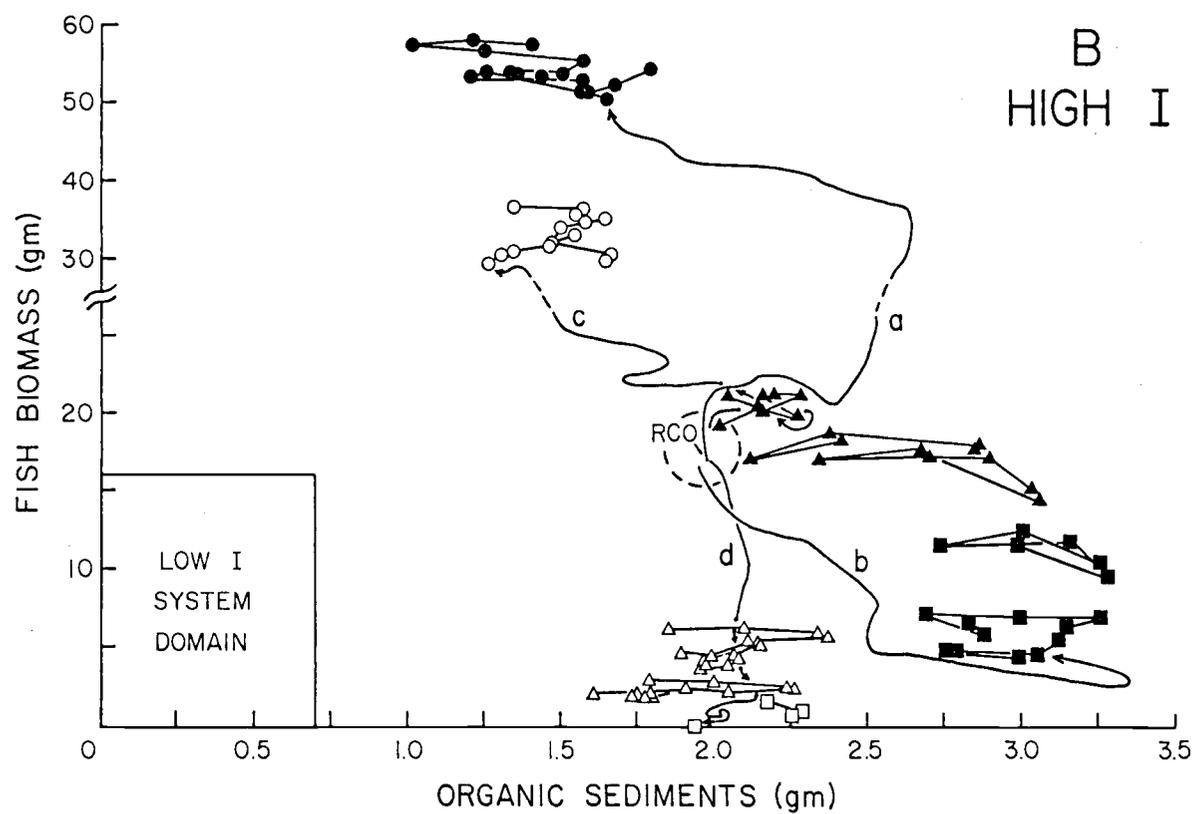
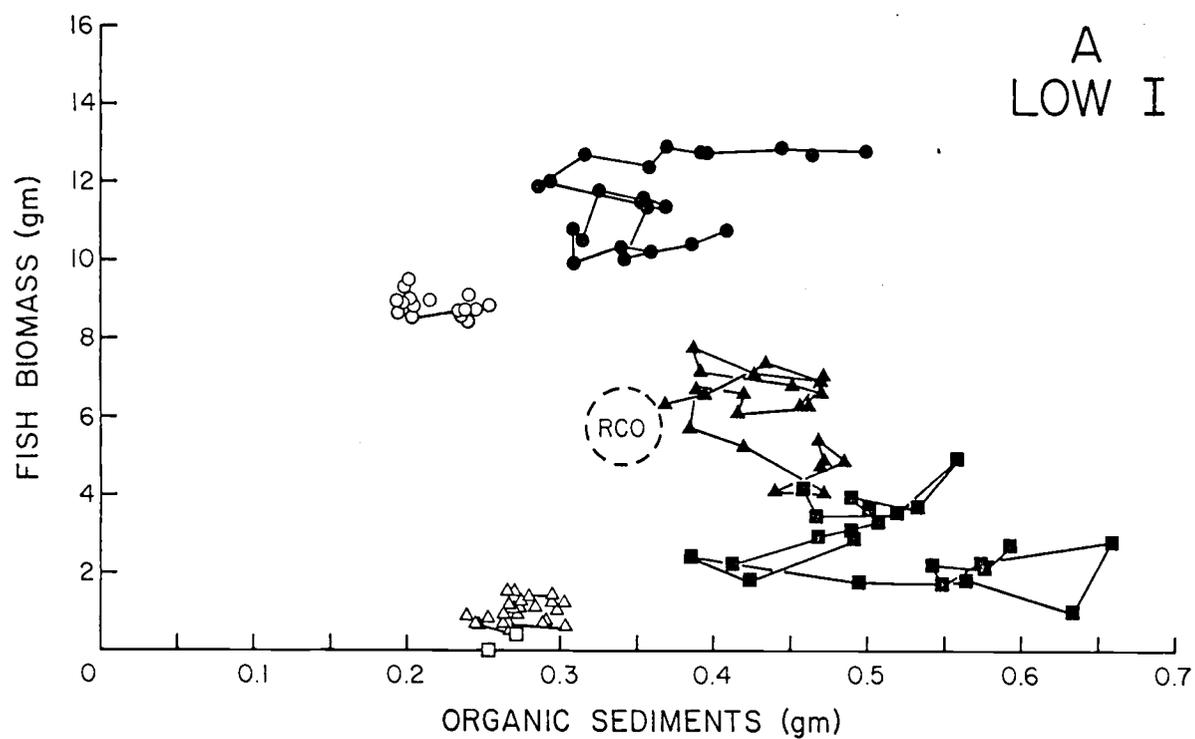
Phase plane relationships between fish biomass and organic sediment biomass at LOW I and HIGH I in the absence and presence of the snail competitor are shown in Figure 5. Regions of common origin (RCO) identify biomasses at the beginning of the experiment, i.e., the stocking densities. From the RCO, each system tracked towards different regions in phase space depending upon the levels of I and E and the organization of the systems (for example, trajectories a-d in Fig. 5b). When a trajectory remained in a localized region the community was considered to be at NSS (Woltering 1981, Liss et al. 1983). The NSS means, SE, and the number of observations at NSS (n) are given in Appendix 1.

At both LOW I and HIGH I, when the snail competitor is not present (solid symbols), an inverse relationship exists between NSS guppy and sediment biomasses, with increased E bringing about a reduction in NSS guppy biomass and an increase in the NSS biomass of sediments. The relationship between guppies and sediments was shifted to the right on the phase plane when I was increased from LOW I to HIGH I (Fig. 5b).

When the snail is present (open symbols), the relationship between guppies and sediments at each I is shifted to the left (Fig. 5). With snails present, guppies and sediments maintained considerably lower NSS biomasses at each E than when snails were absent. Presumably the snail reduced food availability for guppies. Consequently guppies did not maintain NSS biomasses as high as those maintained in systems lacking the snails.

Figure 5. Phase plane representing near steady-state (NSS) guppy and organic sediment biomasses at Low I (A) and High I (B) in the guppy-alfalfa-algae (G-A-Al) unshaded systems (solid symbols) and guppy-snail-alfalfa-algae (G-S-A-Al) unshaded systems (clear symbols). NSS system behavior of the systems at OE (circles), 25E (triangles), and 40E (squares) is shown. System trajectories for the G-A-Al systems at High I, OE and High I, 40E (a and b) and those for the G-S-A-Al systems at High I, OE and High I, 40E (c and d) are shown. The region of common origin (RCO) for systems at each I is also shown.

Figure 5.



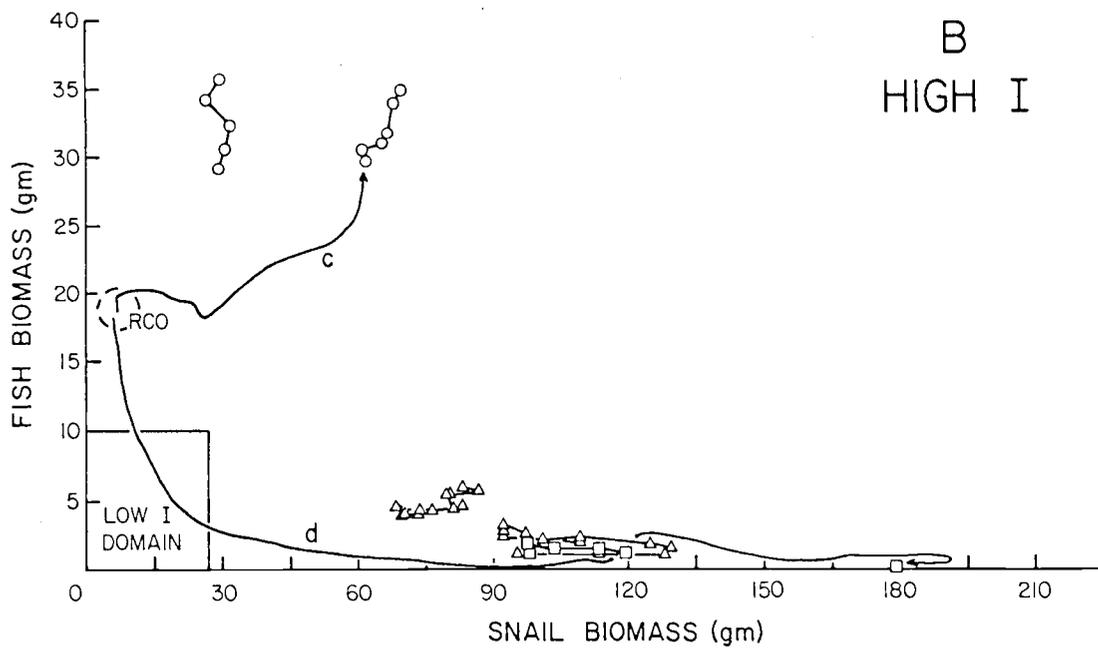
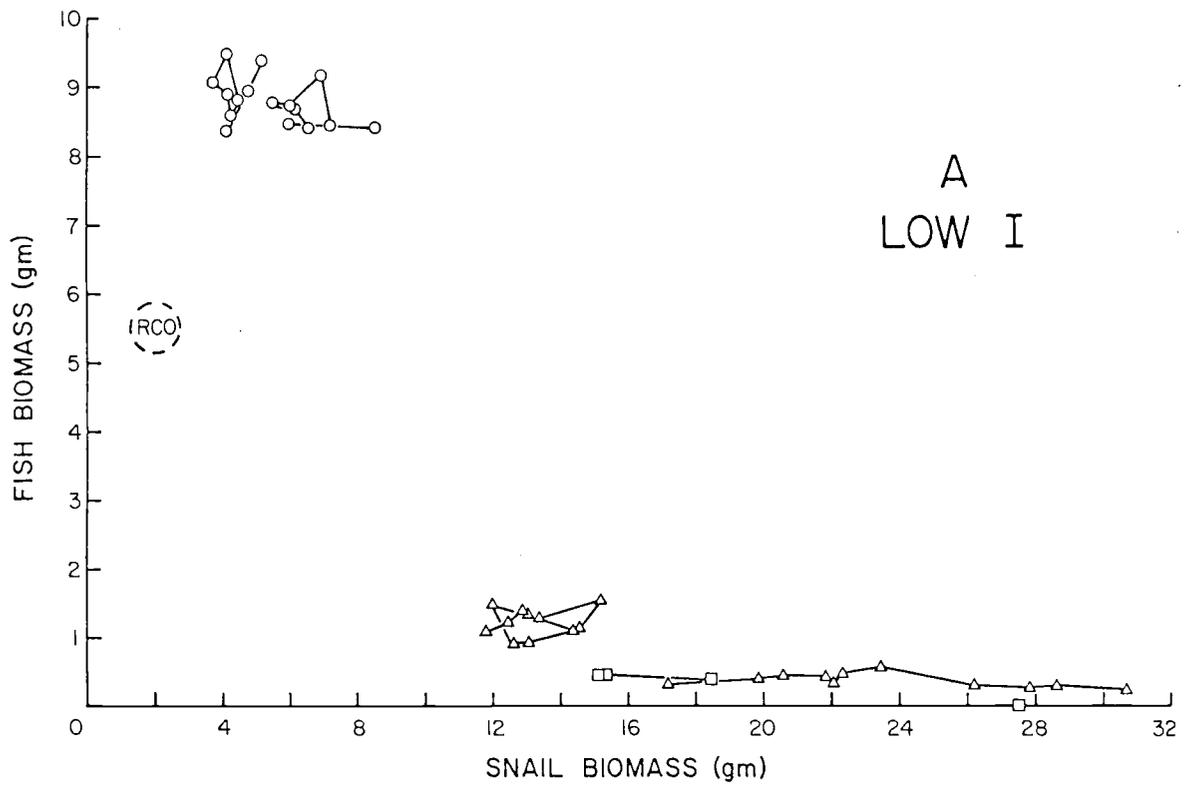
The interaction between fish and snails is shown on the competition phase plane in Figure 6. NSS fish biomass and snail biomass are inversely related, with the relationship being shifted up and to the right with increased I. At each I, increased E resulted in a decrease in NSS fish biomass and an increase in the NSS biomass of the snail competitor.

Competitive coexistence between fish and snails is dependent upon I, or system productivity, and level of exploitation of the fish population. If snails are absent, fish are able to persist when harvested at 40E at both LOW I and HIGH I (solid squares, Fig. 5). When the snail competitor is present, fish and snails in one replicate at LOW I, 40E, were not able to coexist, the fish being driven to extinction (open squares, Fig. 5). In the other replicate, the fish were persisting at a very low density when this research was discontinued. At this time there was no recruitment, no males, and only one small mature female in the population. Given more time the fish in this replicate would have suffered extinction. At HIGH I, the fish in one replicate could not persist in competition with snails. Fish in the other replicate were in no danger of extinction.

If the rate of exploitation of the fish is reduced, fish and snails are able to coexist. At both LOW I and HIGH I the fish at 0E and 25E were able to persist in competition with snails (open and closed circles and triangles, Fig. 5). At HIGH I, 40E, the fish population in one of the replicates was able to coexist with the snail competitor while the other was driven to extinction. The particular

Figure 6. Phase plane representing NSS guppy and snail biomasses at Low I (A) and High I (B) for the guppy-snail-alfalfa-algae unshaded systems at OE (circles), 25E (triangles), and 40E (squares). Trajectories c and d correspond to those shown in Figure 5b. The region of common origin (RCO) for Low I and High I systems is also shown.

Figure 6

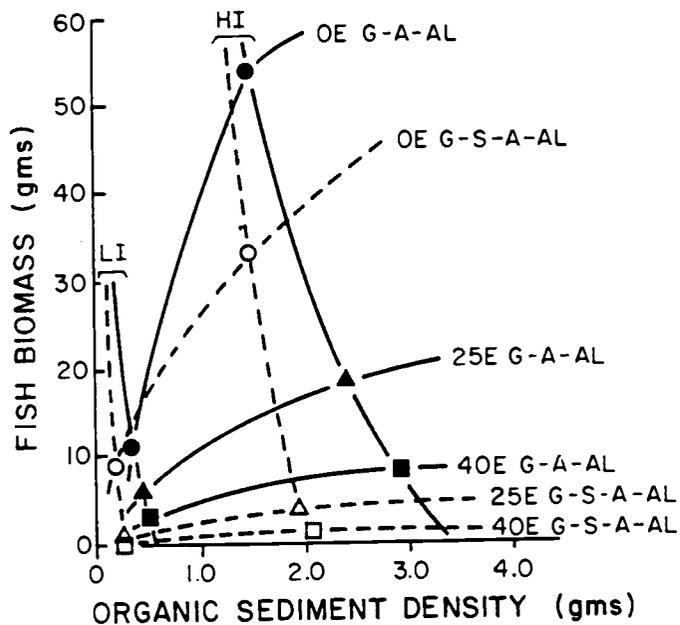


system in which the fish were unable to persist had a very high snail biomass, much higher than the biomass of snails in the other replicate at HIGH I, 40E (Fig. 6b). This unusually high snail biomass may have been responsible for fish extinction in this system. The isocline model indicates that in simple systems increased I may facilitate coexistence of competing populations (Fig. 3). As will become apparent in the discussion, fish and snails may have been able to coexist at LOW I, 40E if the snail populations had been harvested at sufficiently high levels.

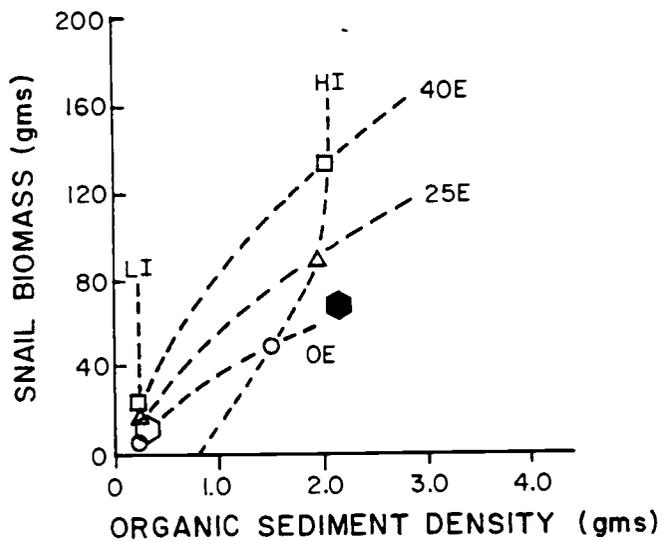
To better illustrate and discuss the multisteady-state perspective, the grand weighted means of the individual NSS regions for the systems are plotted as points on isoclines in Figures 7 and 8. Figures 7a and 7c are another form of Figures 5 and 6. In Figure 7b, mean NSS relationships between snails and organic sediment is shown. It might be expected that the greatest snail biomass would be found in the snail-alfalfa-algae (S-A-Al) communities, since the fish competitor was never present in these systems. Yet at both levels of I, mean NSS snail biomass was lower than that in systems at 25E and 40E in which fish were present. Further, in the communities at 40E in which the fish populations were driven extinct, snails maintained mean NSS biomasses at LOW I and HIGH I of 21.5 grams and 132.9 grams, respectively. Snails in the S-A-Al communities maintained mean NSS biomasses of 12.5 and 68.4 grams at LOW I and HIGH I, respectively. However, at each I, the average number of snails in the S-A-Al communities was greater than that in the systems at 40E at the time of

Figure 7. Linked series of phase planes representing the structure of the guppy-alfalfa-algae (G-A-Al) unshaded systems (solid symbols connected by solid predator and prey isoclines) and the guppy-snail-alfalfa-algae (G-S-A-Al) unshaded systems (clear symbols connected by dashed predator and prey isoclines) at Low I and High I at 0E (circles), 25E (triangles), and 40E (squares). Snail and organic sediment performances in the snail-alfalfa-algae (S-A-Al) systems at Low I (open hexagon) and High I (closed hexagon) are shown in Figure 7b. Each point is the grand weighted mean of each system and its replicate. The grand weighted mean for a given system type at each level of I and E is calculated by summing the NSS sample values for all individual component population biomasses of both replicates and dividing by the total number of NSS samples taken from both replicates.

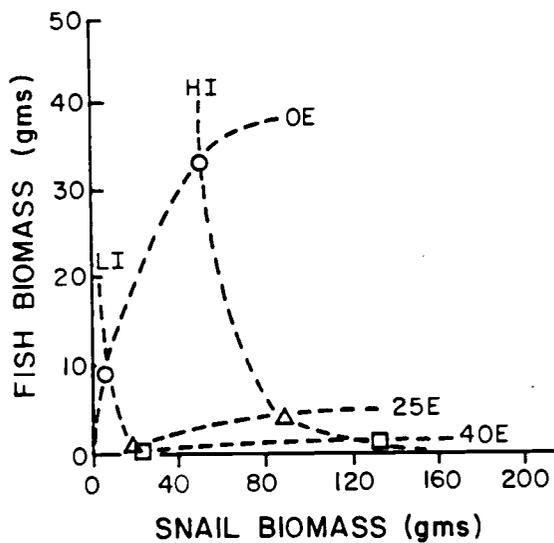
Figure 7.
(a)



(b)



(c)



fish extinction even though biomass was lower. In the S-A-Al communities system, average snail numbers were 229 at LOW I and 644 at HIGH I. In the systems at 40E in which the fish were driven extinct, snails numbered 181 at LOW I and 457 at HIGH I. Thus, while biomass did not follow the expected result, numbers did.

The reasons for this disparity are not well understood. Guppies were observed harassing and possibly preying on young snails. Fish were observed to pick at and dislodge snails up to 3 mm in diameter. As a result, in systems in which fish were present, most newborn snails were found in relatively protected areas, for example behind algae sampling squares, to a higher degree than in the S-A-Al communities (pers. obs.). Moreover, over the first three months of the study, initial egg deposition by the snails was in the open corners and edges of the tanks; almost none occurred in the plastic plants. After three months, there was less egg deposition in the open corners and edges by snails in tanks containing fish and more on the plastic plants. This behavior was not exhibited to such a degree in the S-A-Al systems. It is conceivable that harassment and possible predation on newborn snails by fish reduced snail numbers enough to cause a reduction in intraspecific competition and, through a process of intra-population competitive release, allow the remaining individuals to grow faster and to attain a larger size.

It is interesting to note that snail population number, biomass, and size structure in the systems in which fish were driven extinct started to change; beginning to resemble that of the snail populations

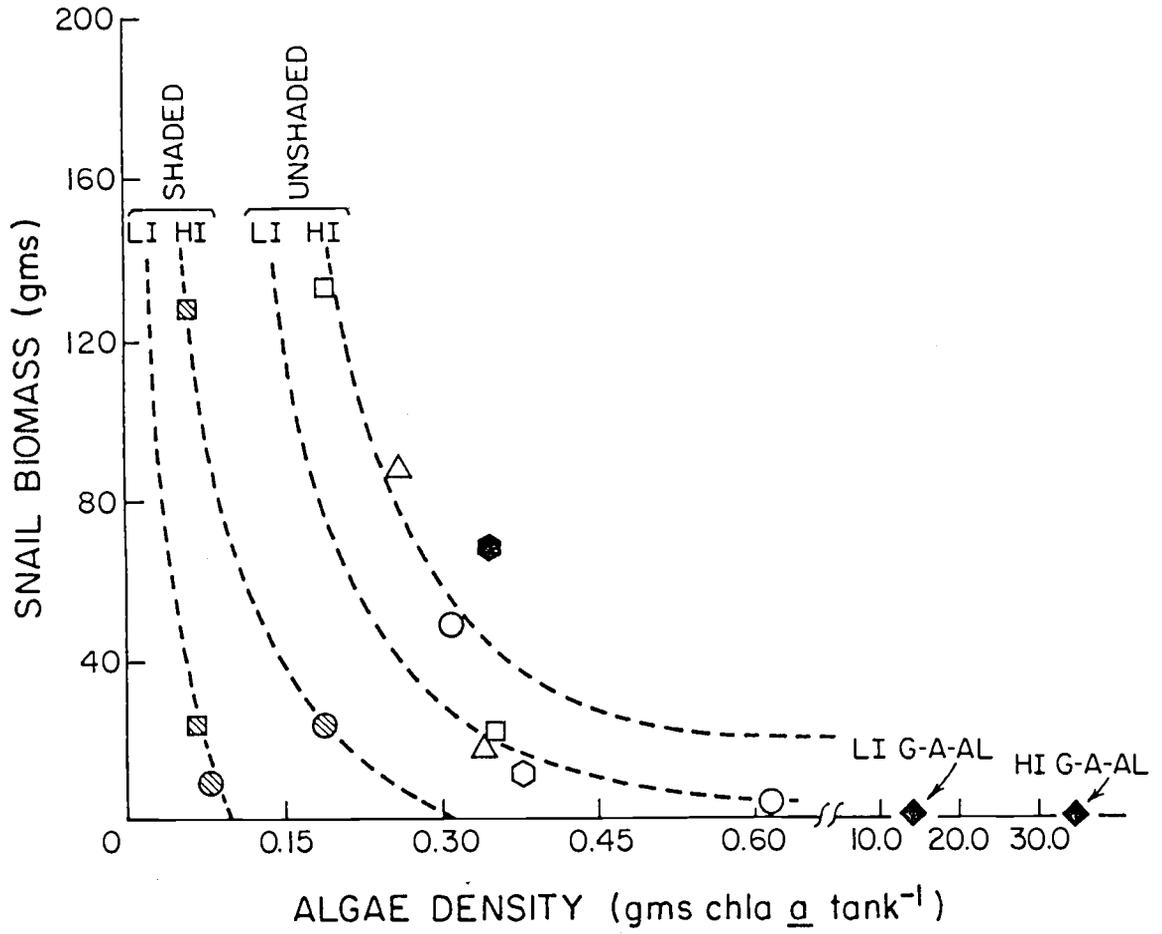
in the S-A-Al systems. Thus, depending upon E, fish may have not only a negative effect on snail biomass through competition, but they may also have a facilitating effect upon their biomass. The biomasses that snails maintain may be an outcome of both these processes.

Figure 8 is a representation of the interaction between snails and algae utilizing the grand weighted means of the NSS regions. The standard errors of the mean NSS algal densities are larger than that of the other components of the community (Appendix 1). This is partially due to large sampling variability and partially due to the fact that the assemblages are composed of many algae species that occur in different relative densities from one system to another. This adds confusion to a simple index of density such as that derived from chlorophyll a concentration. When the algae sample squares were held up to the light, a collage of algal colonies of different species could be seen. When comparing sample squares between replicates by this method, the algal assemblages were visually very similar, but a single change in system organization, I, and/or E resulted in a visible change in assemblage structure. Nevertheless, some general relationships between mean NSS snail biomass and algal density are apparent.

When snails were not present, the algal assemblage maintained a relatively high density (solid diamonds). In these systems algal density was greater at HIGH I than at LOW I, perhaps because of the greater availability of plant nutrients derived from the more abundant alfalfa ration. When snails were present the algal assemblages

Figure 8. Phase plane representing grand weighted mean biomass of snails and algae for the guppy-snail-alfalfa-algae (G-S-A-Al) unshaded systems at 0E, 25E, and 40E (clear circles, triangles, and squares, respectively), the G-S-A-Al shaded systems at 0E and 40E (cross-hatched circles and squares, respectively), and snail-alfalfa-algae (S-A-Al) unshaded systems (clear and solid hexagons at LI and HI respectively). The solid diamonds are average algae densities for all Low I and High I guppy-alfalfa-algae (G-A-Al) unshaded systems. Each point is the grand weighted mean of each system and its replicate at a given level of I and E with exception of the solid diamonds which are the grand weighted mean of all Low I and High I G-A-Al systems. The grand weighted mean for a given system type of each level of I and E is calculated by summing the NSS sample values for all individual component population biomasses and dividing by the total number of NSS samples taken from both replicates.

Figure 8.



maintained much lower densities due to snail grazing. Upon visual inspection of the tanks, the difference in algal densities between systems with and without snails was readily apparent. In both shaded and unshaded tanks reduction in I shifts the inverse relationship between snails and algae to the left on the phase plane. This means that a given biomass of snails will maintain the algal assemblage at a lower density at LOW I than at HIGH I. The potential of the systems with snails to maintain a greater density of algae at HIGH I again may be related to the greater availability of plant nutrients.

Even though the relationship between snails and algae was shifted to the left on the phase plane, at each E the algal assemblage maintained a greater density at LOW I than at HIGH I. At LOW I, snails maintained much lower biomasses than at corresponding E at HIGH I due to a lower availability of the alfalfa ration. Consequently, at LOW I, there was probably not as much grazing pressure by snails on the algae and the algae were able to maintain higher densities in spite of the lower availability of plant nutrients.

The inverse relationships between snails and algae in the shaded systems (hatched symbols) lies farther to the left on the phase plane than the relationships between these components in the unshaded systems (open symbols). Interestingly, with the exception of HIGH I, OE, snails maintained about the same mean NSS biomass at each level of I and E as those in the shaded systems. It is possible that the presence of the algae may not play a large role in the maintenance of snail biomass. Apparently feeding on the alfalfa ration maintains

snail biomasses at levels high enough to keep the algal assemblage grazed down. Thus, although changes in snail biomass can alter algal density, the densities (and probably production) of algal assemblages are always maintained at levels that are too low to contribute much to the energy and material intake of the snails.

In these systems the density of algae is jointly determined by I, the rate of input of energy and materials in the form of light energy and plant nutrients derived from the alfalfa ration, and by snail biomass. Snail biomass, in turn, is determined by the rate of input of the alfalfa ration, which is the major food of the snail, and by the biomass of the guppy competitor. Guppy biomass is determined by E as well as alfalfa input. Thus exploitation of guppies indirectly affects algae populations through its indirect impact on snails.

It is clear that the structures of the communities--the kinds and densities of the species populations composing them--is related to their organization--the interrelations between the populations such as predation and competition--and to the state of their environment. That is, predation, competition, productivity (expressed as energy and material input) and exploitation played interactive roles in the determination of system structure. Competitive coexistence and thus species diversity was jointly determined by the levels of system productivity and competitor exploitation. At different levels of I and E the communities established different NSS structures (Fig. 5, 6, 7, 8) and thus, could be understood as multisteady-state systems, in the sense that that concept has been used here.

DISCUSSION

Though all of the diversity hypotheses are by definition couched in terms of species diversity, in many respects they address the basic question: what are the major determinants of community structure at any given point in space and time? Typically the question has revolved around the relative importance of a specific mechanism such as competition, predation, productivity, temporal and/or spatial heterogeneity in determining system structure. The focus on diversity or system structure has often been concerned with which mechanism is the most important in all cases at all times. Such a focus tends to lead one to think in terms of single causative factors rather than networks of causative factors. This is not always the case; many have opted for a synthesis of two or more hypotheses into a framework for understanding observed structure. Notable among these include the synthesis of predation, competition, and temporal heterogeneity by Menge and Sutherland (1976) and the synthesis of competition and climatic stability by Wiens (1977). Even so, many today still focus on single mechanisms and attempt to prove or disprove their importance by various means (Strong et al. 1979, Connor and Simberloff 1979).

If interactions between component populations themselves and between populations and their physical environment play important roles in the determination of system structure, it may be valuable to develop frameworks that better address such concerns. Towards this goal, isocline models as advanced by Booty (1976) and extended by Liss

(1977) and Thompson (1981) provide a framework within which competition, exploitation/predation, productivity in terms of energy and material inputs, and temporal heterogeneity as can be shown to operate unified and as inseparable determinants of system structure. The spatial heterogeneity hypothesis has not been included in this unification. Habitat structure and organization cannot be handled adequately with the kind of isocline models used here.

To better address the question of hypothesis unification, an isocline model of a simple community (Fig. 9) was developed. Two carnivores, C1 and C2, compete for the common prey, herbivore H, and are individually exposed to exploitation. The herbivore feeds the plant, P, which in turn uses energy and material resources, R. The phase planes and production curves in Figures 10, 11, and 12 are the specific solution of one model of this system which is described in more detail in Appendix 2.

In Figure 10a, relationships between C1 and H when C2 is not present in the system (OC2) are essentially similar to those between fish and organic sediments empirically defined in the laboratory systems in which the snail competitor was absent (Figs. 5, 7a). For example, a change in I from 1I, OC2 to 5I, OC2 results in a rightward shift of the prey isocline (from the solid prey isocline defined by clear symbols to that defined by the solid symbols). At both levels of I, as E1 increases the steady-state biomass of C1 decreases and the steady-state biomass of H increases. As before, these same steady-state points can be traced back through the system to give the

Figure 9. Digraph of a system in which carnivores C1 and C2 compete for the common prey herbivore (H). H preys upon the plant population P which in turn preys upon plant resources R. I represents the rate of input of energy and materials or plant resources into the system, while E1 and E2 represent given levels of exploitation of C1 and C2, respectively. C1, C2, H, P, and R comprise the system of populations while I, E1, and E2 comprise the environment of the system.

Figure 9.

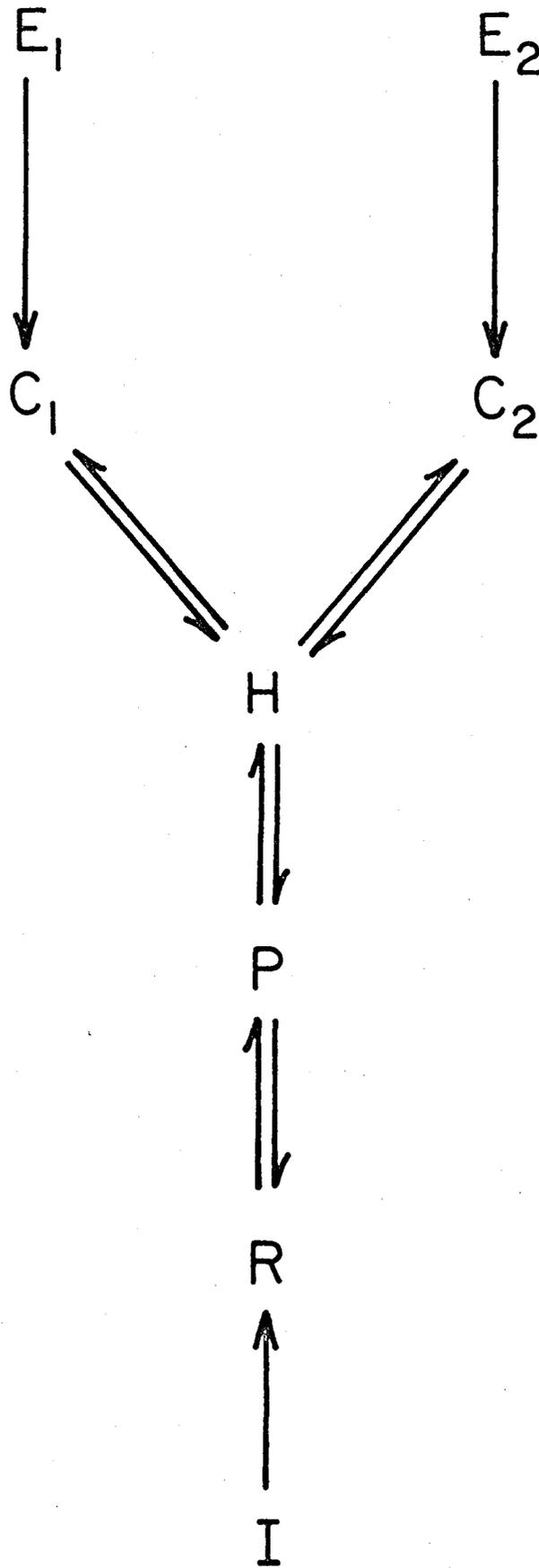
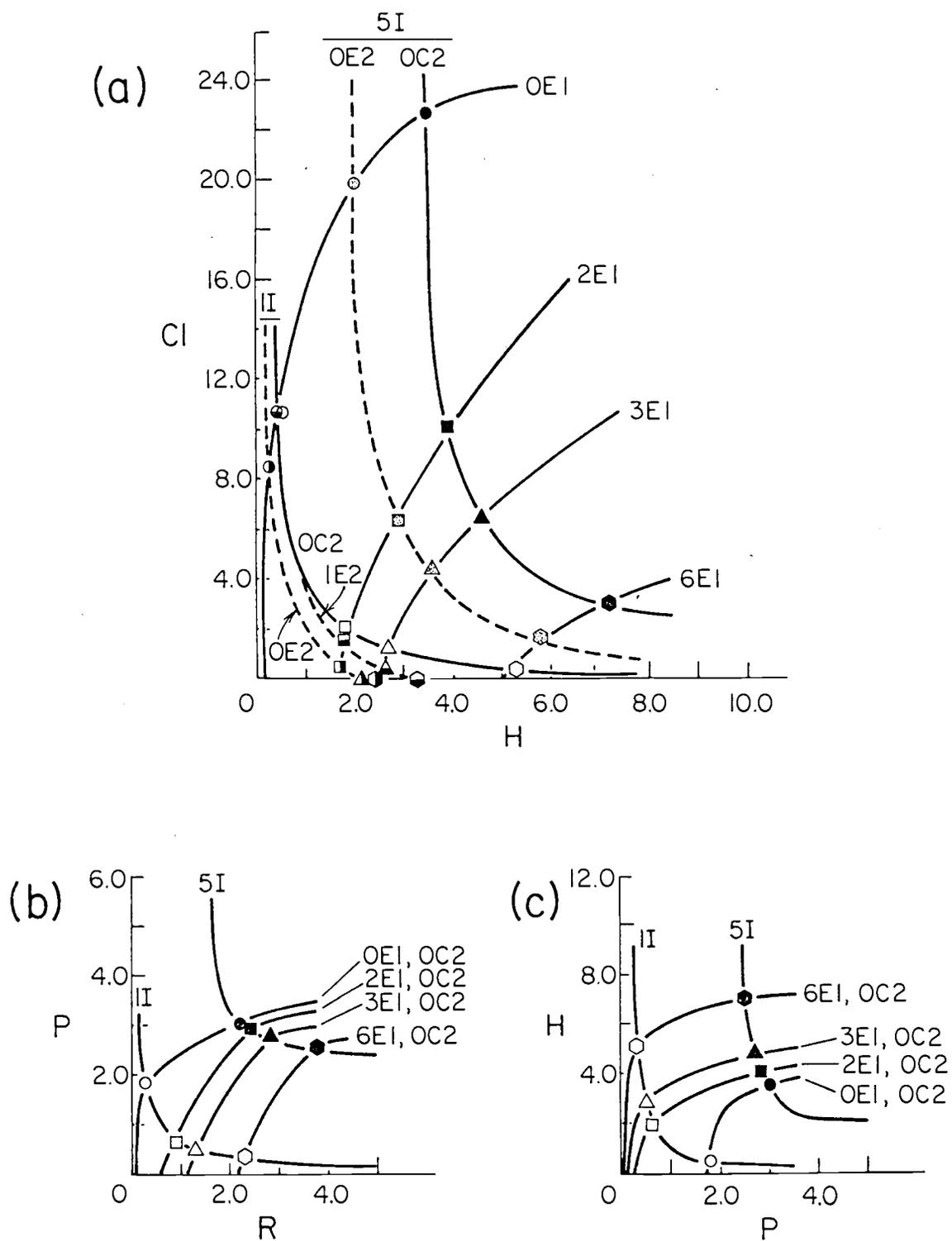


Figure 10. Phase planes and isocline systems representing different steady-state structures of the system shown in Figure 9 given different levels of I , E_1 , and E_2 . Solid and clear points connected by solid predator and prey isoclines on all three phase planes represent steady-state system structures at $5I$ (High I) and $1I$ (Low I) with C_2 absent from the system (OC_2), while the stippled, horizontally half-solid, and vertically half-solid points connected by dashed prey and solid predator isoclines on Figure 10a represent steady-state system structures at $5I$, OE_2 , $1I$, $1E_2$, respectively. Levels of harvesting of C_1 are OE_1 (circles), $2E_1$ (squares), $3E_1$ (triangles), and $6E_1$ (hexagons). E_2 is an additional parameter on the prey isoclines in Figure 10a because the competitive interaction between C_1 and C_2 is mediated through the common prey H . If a predator isocline parameterized by a given level of E_1 does not intersect a prey isocline parameterized by a given level of I and E_2 , C_1 will be drive to extinction under that set of conditions (eg. $1I$, OE_2 , $3E_1$; vertically half-solid triangle). The isocline systems on these phase planes were generated by computer iteration using the simulation command control language SIMCON (Worden 1976, Thompson 1981). The model is given in Appendix 2.

Figure 10.



system steady-state structure for each set of environmental conditions.

The effects of introduction of the competitor C2 are analogous to those empirically observed in the laboratory systems in which the snail competitor was present. E2, the level of harvesting of C2, becomes an additional parameter on the prey isoclines. At each I, the addition of C2 causes a leftward shift in the prey isoclines. For example, at 1I, if C2 is introduced into the system and harvested at 1E2, there is a leftward shift from the solid prey isocline defined by clear symbols to the dashed prey isocline defined by the horizontally half-solid symbols. If C2 is completely released from harvesting pressure (OE2), there is a further leftward shift to the dashed prey isocline defined by vertically half-solid symbols. The same kind of shift of the prey isocline also occurs at 5I. In the laboratory systems, the presence of the unharvested snail competitor shifted the prey isoclines defining the NSS relationships between guppies and organic sediments to the left at each I (Figs. 5, 7a).

The densities of the competing species and their coexistence are determined by the state of the environment of the system, that is, by the levels of E1, E2, and I. If a predator isocline identified by a particular level of E1 does not intersect a prey isocline identified by particular levels of I and E2 in positive phase space, then C1 will not be able to persist under that set of conditions; it will have been excluded from the system by C2. With OC2, C1 is able to persist at both 1I, 3E1 (clear triangle) and 1I, 6E1 (clear hexagon). In the presence of an unexploited competitor (OE2), C1 is driven to

extinction at both 1I, 3E1 (vertically half-solid triangle) and 1I, 6E1 (vertically half-solid hexagon). C1 and C2 are able to coexist if C2 is exploited. For example, at 1I, 3E1 if C2 is harvested at 1E2 (horizontally half-solid triangle). This is an illustration of the predation hypothesis; increased mortality of a "dominant" competitor reduces its density and consequently the intensity of competition, enabling an inferior competitor to successfully colonize the system and persist (Paine 1966). However, if C1 is more heavily exploited, say at 6E1, C1 will still be excluded at 1I if C2 is exploited at 1E2 (horizontally half-solid hexagon). At 1I, 6E1, for coexistence to occur, C2 must be harvested at a level greater than 1E2.

Exploiting C2 is not the only way in which exclusion of C1 can be prevented. If the level of harvesting of C1 is reduced, C1 and C2 are able to coexist. For example, at 1I, OE2 coexistence of C1 and C2 can be brought about if E1 (and thus mortality of C1) is reduced from 3E1 (vertically half-solid triangle) to 2E1 (vertically half-solid square) or OE1 (vertically half-solid circle). Thus, at a given I, coexistence depends upon the level of mortality of each competing species. High levels of E2 in relation to E1 may, in effect, lead to exclusion of the "dominant" competitor C2 by the "inferior" competitor C1. For example C2 is unable to persist in competition with C1 at 1I, OE1 if it is harvested at a level greater than or equal to 1E2 (horizontally half-solid circle).

Competition and predation alone do not determine the structure of communities. Productivity, expressed in terms of energy and material

inputs also plays an important and inseparable role in the determination of structure. A change in I with E1 and E2 held constant results in a change in steady-state structure of the system. Further, changes in I affect competitive coexistence. For example, C1 and C2 are able to coexist at OE2, 3E1 if I is increased from 1I (vertically half-solid triangle) to 5I (stippled triangle).

Results of the laboratory experiments are analogous to the theoretically derived results shown here even though organization of the systems is different. When the snail competitor was absent, fish were able to persist when heavily exploited at 40E at both LOW I and HIGH I, (Figs. 5 and 6). When the snail was present, fish in both replicates at LOW I, 40E and in one replicate at HIGH I, 40E were either driven to extinction or were about to be driven to extinction. Co-existence occurred at LOW I in systems in which the fish population was exploited at a lower rate, either 25E or OE. Further, at HIGH I, the likelihood of competitive coexistence of these species was increased. Perhaps, if I had been increased to some level greater than 4.0 grams of alfalfa ration per day, coexistence would have been assured.

Connell (1978) suggests that there are steady-state and nonsteady-state explanations for species diversity. The question involves the relative importance of temporal heterogeneity (particularly the intermediate disturbance and gradual change hypotheses) versus steady-state explanations such as niche diversification (competition and climatic stability in their classical forms), circular networks of species interactions, and compensatory

mortality (the predation hypothesis in its classical form). The isocline models developed here provide a framework in which both steady-state and nonsteady-state system structure can be examined in relation to conditions in the environment of the system. Changes in environmental conditions, or temporal heterogeneity, alter the location of steady-state points in phase space. If environmental conditions are constantly changing, a system trajectory is in continuous pursuit of an evershifting steady-state point.

Shown on the competition phase plane in Figure 11 is a trajectory generated by changing levels of I , E_1 and E_2 , that is, resulting from temporal heterogeneity in environmental conditions. In this model, competitive exclusion of C_1 takes place if the system establishes a steady-state as occurs, for example, at $1I$ OE_2 , $3E_1$ (Figs. 10a, 11, vertically half-solid triangle). Environmental conditions that would ultimately lead to exclusion (e.g. $1I$ OE_2 , $3E_1$) may not persist for long enough periods of time for the system to establish a steady-state and thus for exclusion to occur. Environmental conditions may become more favorable for coexistence and thus the trajectory would be deflected toward a new steady-state point that is located in positive phase space (e.g. $5I$ OE_2 , $3E_1$; stippled triangle). In this way, the nonsteady-state nature of systems may facilitate competitive coexistence. Of course, if environmental conditions changed but were still unfavorable for coexistence (e.g. to $1I$ OE_2 , $6E_1$; vertically half-solid hexagon), exclusion would occur.

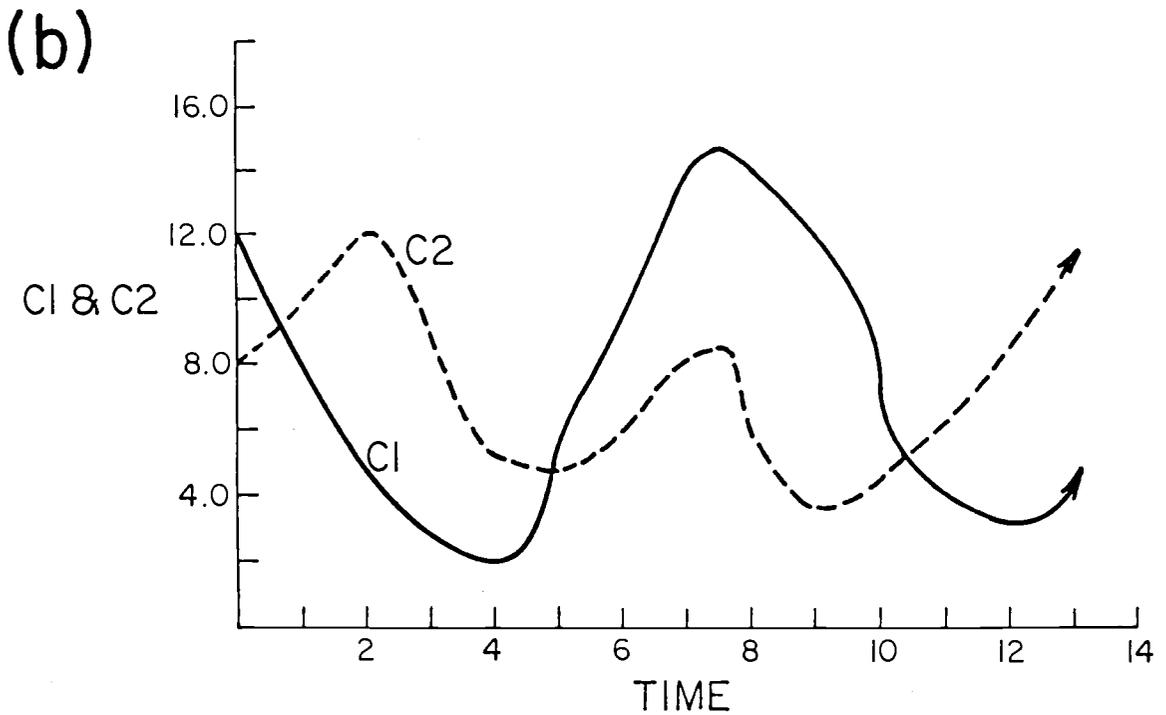
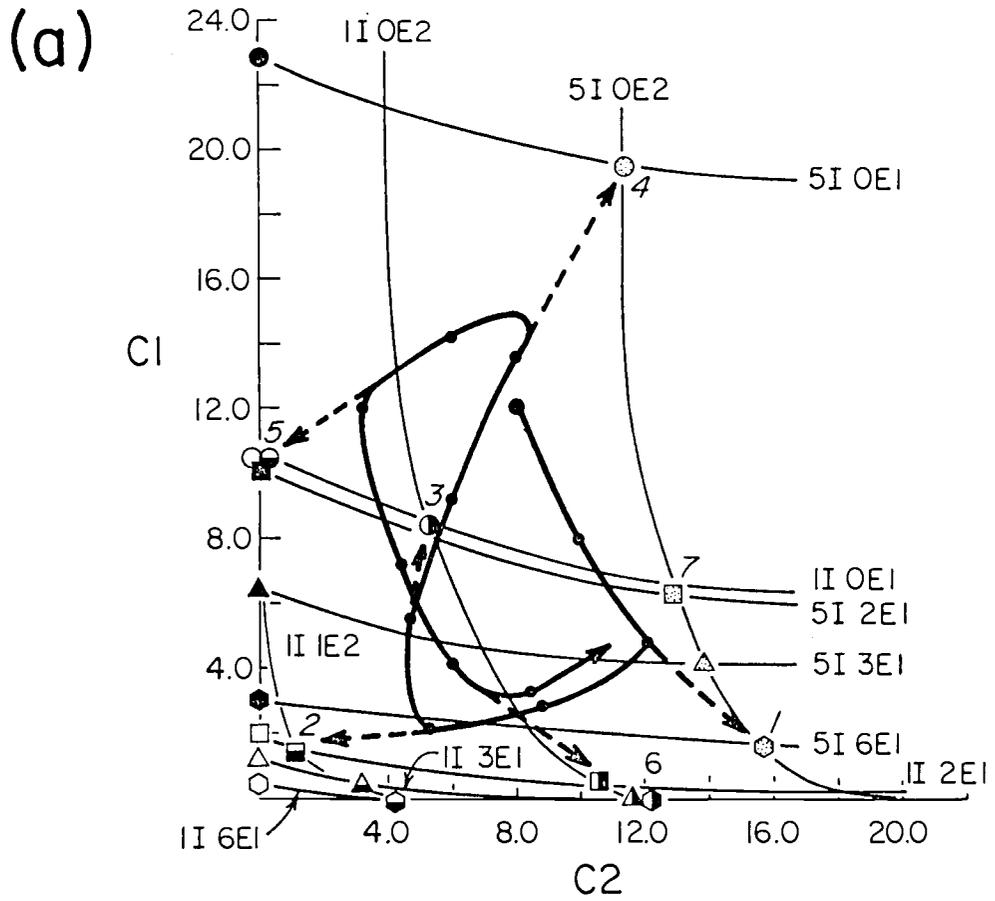
From inspection of Figure 11 it is clear that trajectories have no unique or universal form. For example, there do not necessarily

Figure 11. C1-C2 competition phase plane with a system trajectory superimposed upon it (a) and a graph of C1 and C2 biomasses against time derived from the system trajectory (b). Those isoclines that intersect the C1 axis and slightly decline from left to right are parameterized by I and E1 while those isoclines that steeply descend from left to right and intersect the C2 axis are parameterized by I and E2. Only the intersections of those isoclines parameterized by the same level of I represent operative steady-state points. The symbols at these steady-state points correspond to those in Figure 10a. The structure of the system tracks towards the steady-state point delineated by the number 1 but before it can get there, conditions change again to that defined by the number 2. Before it can get there, conditions change again to that defined by the steady-state point delineated by the number 3 and so on. At any given point on the trajectory, the system is not at steady-state even though it is tracking a given steady-state point.

Pattern of environmental change:

1. 5I OE2, 6E1
2. 1I 1E2, 2E1
3. 1I OE2, OE1
4. 5I OE2, OE1
5. 1I 1E2, OE1
6. 1I OE2, 3E1
7. SI OE2, 2E1

Figure 11.



have to be, although there could be, inverse dynamic relationships between populations of competitors. That is, one population need not decrease in density when the other increases in density. The form of a trajectory is determined by the characteristics and interactions between the species composing the system and by the way in which the steady-state point the system is going toward is shifted in phase space as the environment changes. Thus, organization generally cannot be inferred simply from the form of the nonsteady-state relationships between populations. In nonsteady-state systems, measurements of population densities and system structure are merely points on trajectories that are moving throughout phase space.

Isocline models provide a convenient way of illustrating that productivity, exploitation and predation, competition, and temporal heterogeneity can act in a unified way to determine system structure including species diversity. Further, the laboratory community studies provide an empirical demonstration of the mutual operation of these determinants of system structure.

How universal are statements such as the diversity hypotheses that attempt to say very particularly how changes in system productivity, predation, competition, etc. affect system structure? For example, the predation hypothesis implies that predation on a superior competitor will permit coexistence. However, in the system shown in Figure 10, increased E_2 may not be sufficient to bring about coexistence of C_1 and C_2 if E_1 is also increased (e.g. from vertically half-solid triangle at $1I, 0E_2, 3E_1$ to horizontally half-solid hexagon $1I, 1E_2, 6E_1$) or I is decreased (e.g. from the stippled hexagon at $5I,$

OE2, 6E1 to the horizontally half-solid hexagon at 1I, 1E2, 6E1).

Further, an increase in productivity may not be sufficient to bring about coexistence if there is a concomitant increase in E1 or a decrease in E2.

The effect on structure of changes in I (productivity hypothesis) or changes in E2 (predation hypothesis) depends upon how other factors in the environment are changing. The structure of communities is affected by the state of their environment as a whole. The insistence upon trying to statistically prove or disprove the importance of specific mechanisms in the determination of structure is confounded by the fact that all mechanisms are inseparably linked together thus negating the classical expectations by which they are interpreted. Thus, a single hypothesis cannot be isolated and "tested" independent of the system of hypotheses. Further, the outcomes of competition, and the effects of predation, changes in exploitation or changes in productivity also depend upon the organization of the system--the kinds of species composing the it and the network of interrelations linking them all (Riebesell 1974, Levine 1976, Vandermeer 1980, Thompson 1981). Thus systems with different organizations may respond quite differently to the same set of environmental factors.

A further problem with the application of the diversity hypotheses has to do with how they are empirically addressed. Perhaps the best example of the confusion generated by using different measures may be found in conjunction with the productivity hypothesis. "Productivity" has been taken to mean rate of plant production (Connell and Orias 1964), plant biomass (Hohn 1961, Hulburt 1963),

and energy and material inputs (L.G. Williams 1964). Increased "productivity" has been found to both increase (Patten et al. 1963) and decrease (Whiteside and Harmsworth 1967) species diversity. The productivity hypothesis and its relationship to system structure can be examined with the model developed here.

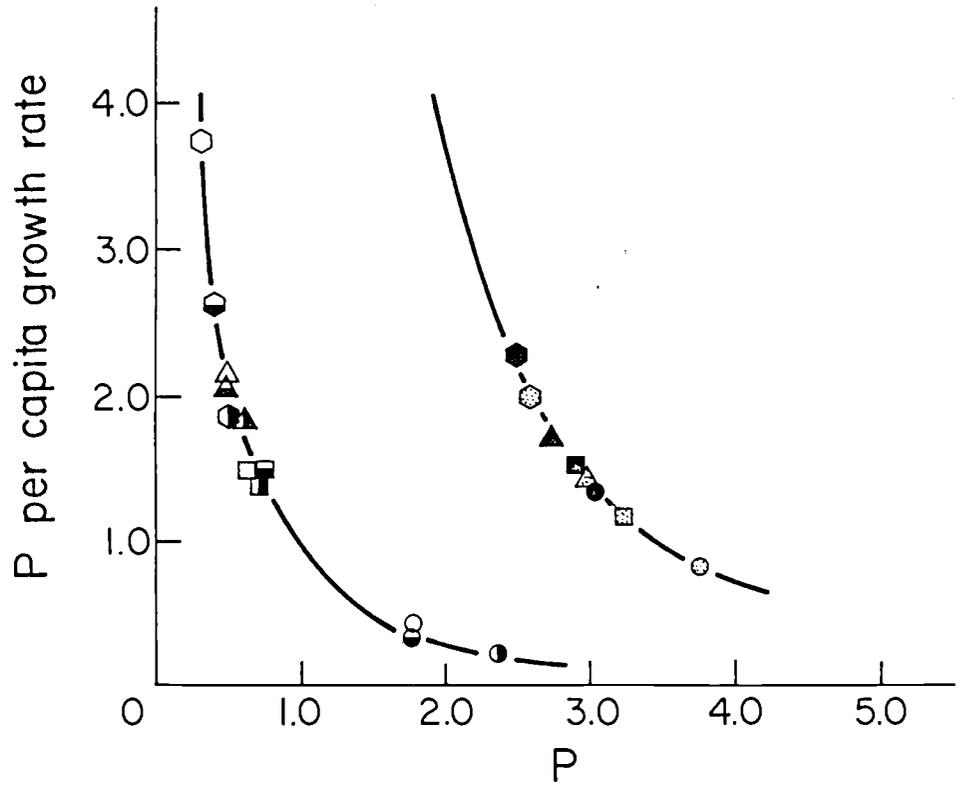
In the model used here, per capita plant growth rate is assumed to be density-dependent (Figure 12a). Gains in plant biomass are attributed to plant reproduction and plant production, both of which are a function of P and R. Biomass losses are attributed to consumption of plants by herbivores which is a function of P and H and non-predatory losses (Appendix 2). Plant production rate is defined as the total amount of tissue elaborated per unit of time through body growth of all individuals in the plant population. It can be calculated as the product of per capita plant growth rate (the average growth rate of an individual plant) and plant biomass (Warren 1971). Plant production curves are shown in Figure 12. The symbols that lie along each of the curves in Figure 12 correspond to the particular plant growth rate and production rate occurring at each steady-state point in Figure 10a. Changes in energy and material input (I) as well as changes in other physico-chemical factors and certain kinds of changes in the organization of the system are among the factors that may alter magnitudes of the growth rate and production curves (Booty 1976, Liss 1977). For example, the shift from 1I to 5I causes a rightward shift in the growth rate curve in Figure 12a and a corresponding increase in the magnitude of the production curve in

Figure 12. a. Density-dependent steady-state per capita plant growth rate curves at 1I and 5I for the system shown in Figure 9.

b. Steady-state plant production curves at 1I and 5I. Per capita growth rate is the average of the change in weight per unit of time of each individual in the population. Plant production or total tissue elaboration by the population is the product of per capita growth rate and population biomass.

Figure 12.

(a)



(b)

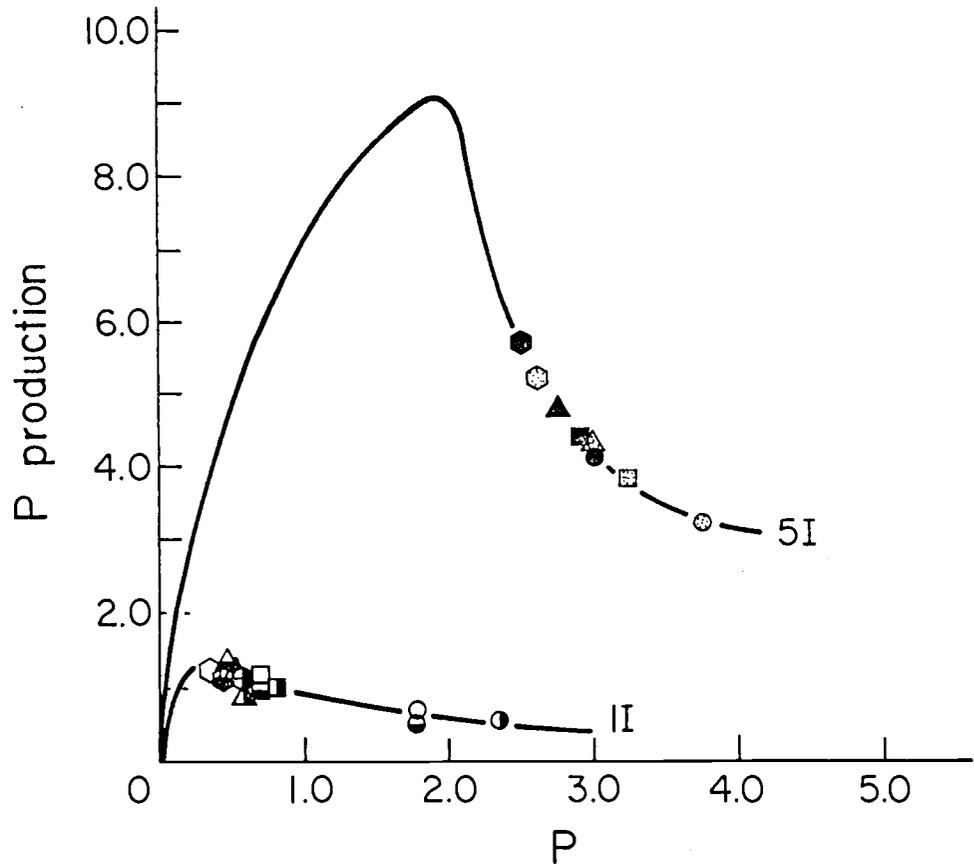


Figure 12b. There are conceivably an infinite number of possible plant growth rate and production curves (Booty 1976, Liss 1977).

Plant biomass and thus plant growth and production is determined by the biomass of H as well as I (Fig. 10b). Further, at a given I, the biomass of H is determined by the densities of C1 and C2, which in turn depend on E1 and E2 (Fig. 10a). For example, at 5I 0C2, 0E1 (solid circle) the steady-state structure of the system and the plant growth and production rates occurring under this set of conditions is indicated by the solid circle (Figs. 10, 12). At 5I 0C2, 6E1 (solid hexagon), C1 has decreased, H has increased, P has decreased, and R has increased. There has been a corresponding increase in plant growth rate and production rate due to a decrease in P and an increase in R, the steady-point being shifted upward along the descending limb of the production curve. As I, E1, and E2 change, the steady-state structure of the system changes. Changes in structure resulting from the interaction of competition, predation/exploitation, and I are associated with changes in steady-state plant growth rate and production rate.

Table 2 shows the relationship of various measures of "productivity"--plant per capita growth rate, plant biomass, plant production, and I--to constant, increasing, decreasing, and increasing then decreasing species richness under different sets of environmental conditions. At least in the simple theoretical system developed here, per capita plant growth rate, plant biomass, plant production rate, or I, as measures of productivity, do not have any necessary correlation with species diversity, expressed as species richness. The results in

Table 2. Relation of plant per capita growth rate, plant biomass, and energy and material inputs to species richness under different sets of environmental conditions.

PATTERN OF SPECIES RICHNESS	SYMBOLIC SHIFT IN F. 10a-12	RESULTANT DIRECTIONAL SHIFT IN :			
		P P.C. GROWTH RATE	P BIOMASS	P PRODUCTION	I
CONSTANT	 → 	↓	↓	↓	↓
	 → 	↓	↑	↑	↑
	 → 	N.C.	N.C.	N.C.	N.C.
	 → 	↑	SLIGHT ↓	SLIGHT ↓	N.C.
4 → 5	 → 	↓	↑	N.C.	N.C.
	 → 	↓	↑	↓	N.C.
	 → 	↑	↑	↑	↑
	 → 	↓	↓	↓	↓
5 → 4	 → 	↑	↓	↑	N.C.
	 → 	↓	↓	↓	↓
	 → 	↑	↑	↑	↑
4 → 5 → 4	 →  → 	↓	↑	SLIGHT ↓	N.C.
	 →  → 	↑-↓	↓	↓	↓
	 →  → 	↓-↑	↓	↓-↑	↓
	 →  → 	N.C.	↓	N.C. - ↓	↓

Table 2 are certainly not universal predictions of how these are related to species richness, they are merely examples derived from the particular model used here and illustrate that each of these "productivity" measures need not bear any simple relationship to species richness.

In this view, per capita growth, production, and biomass of the plant population or any population in the system are structural properties or performances of the system as a whole and as such will vary with changes in system organization or environment. Energy and material input is modeled as a factor in the environment of the system. But system structure and species diversity are determined by the state of the environment as a whole (E1 and E2 as well as I in this example) and not by any single factor. In light of all of this, it is not at all surprising that "productivity" has been found to increase, decrease, and not affect species diversity; it is expected.

Although algal production was not determined in the laboratory systems, the relationship of algal density to I, E, and system structure is similar to the theoretically derived relationships shown in Figure 12. In the laboratory communities, algal density was jointly determined by the rate of energy and material input in the form of light energy and plant nutrients and the biomass of the herbivorous snail (Fig. 8). At each I, snail biomass was related to the biomass of its competitor, the guppy, whose biomass was related to E.

Universal statements about system structure probably cannot be of the very particular form of the diversity hypotheses; they cannot say,

for example, that predation, competition, and increased productivity will generally and invariantly increase species diversity, for the response of species diversity and more generally community structure depends upon the environment and the organization of the community. This is not intended as a criticism of the hypotheses in their present form, for several of these have been very useful in explaining the structure of particular kinds of systems. It is only an attempt to assess the universality of such specific generalizations.

Further, the particular theoretical results derived with the isocline model developed here and the empirical results of the laboratory community studies are intended to demonstrate unification of the hypotheses and illustrate their inseparability. The models provide a perspective on total experience within a domain; they provide a way of thinking about or talking about things (Warren et al. 1983). The particular effects of changes in I and exploitation, and the outcomes of competition and predation derived and demonstrated here are not taken to be universal, for theoretical or empirical systems with different organizations may respond differently to these factors.

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APPENDICES

APPENDIX 1

NSS mean biomass, standard errors, and number of NSS data points (n) for each population in each experimental system.

System	Replicate	Populations			
		Fish (g)	Snails (g)	Organic sediments (g)	Algae (mg)
Guppy-alfalfa-algae systems (unshaded)					
LOW I, OE	1	10.76 ± 0.60 (13)	- -	0.353 ± 0.034 (13)	11.5 ± 1.3 (12)
	2	12.48 ± 0.47 (11)	- -	0.380 ± 0.070 (11)	9.0 ± 3.4 (10)
LOW I, 25E	1	6.89 ± 0.45 (10)	- -	0.425 ± 0.037 (10)	9.0 ± 0.7 (9)
	2	5.67 ± 0.95 (16)	- -	0.449 ± 0.032 (16)	7.8 ± 0.8 (12)
LOW I, 40E	1	2.19 ± 0.59 (13)	- -	0.537 ± 0.079 (13)	32.0 ± 3.0 (12)
	2	3.38 ± 0.73 (13)	- -	0.492 ± 0.045 (13)	12.1 ± 3.8 (13)
HIGH I, OE	1	52.37 ± 1.46 (10)	- -	1.58 ± 0.24 (10)	46.4 ± 11.2 (10)
	2	56.01 ± 1.82 (9)	- -	1.40 ± 0.25 (9)	18.3 ± 4.2 (9)
HIGH I, 25E	1	20.69 ± 1.04 (10)	- -	2.17 ± 0.08 (10)	34.2 ± 7.0 (10)
	2	16.88 ± 1.16 (13)	- -	2.64 ± 0.28 (13)	44.3 ± 17.9 (13)
HIGH I, 40E	1	5.42 ± 1.28 (13)	- -	2.90 ± 0.23 (13)	36.9 ± 8.7 (12)
	2	11.76 ± 1.40 (8)	- -	3.02 ± 0.21 (8)	23.9 ± 4.0 (8)
Guppy-Snail-Alfalfa-Algae Systems (unshaded)					
LOW I, OE	1	8.80 ± 0.42 (13)	4.10 ± 0.64 (13)	0.210 ± 0.017 (13)	0.664 ± 0.126 (12)
	2	8.56 ± 0.27 (12)	6.35 ± 1.57 (12)	0.234 ± 0.021 (12)	0.537 ± 0.119 (12)
LOW I, 25E	1	0.72 ± 0.21 (14)	24.31 ± 3.85 (14)	0.265 ± 0.018 (14)	0.311 ± 0.042 (12)
	2	1.25 ± 0.19 (14)	12.48 ± 1.93 (14)	0.284 ± 0.016 (14)	0.359 ± 0.049 (13)

Appendix 1. Continued

System	Replicate	Populations			
		Fish (g)	Snails (g)	Organic sediments (g)	Algae (mg)
LOW I, 40E	1	0.00 ± 0.00 (2)	27.38 ± 0.92 (6)	0.247 ± 0.012 (6)	0.404 ± 0.110 (5)
	2	0.48 ± 0.07 (7)	16.44 ± 2.14 (7)	0.280 ± 0.021 (7)	0.297 ± 0.065 (6)
HIGH I, OE	1	32.15 ± 2.02 (9)	68.10 ± 4.62 (9)	1.49 ± 0.15 (9)	0.361 ± 0.080 (8)
	2	34.07 ± 3.14 (8)	27.31 ± 3.67 (8)	1.54 ± 0.11 (8)	0.253 ± 0.097 (7)
HIGH I, 25E	1	2.22 ± 0.34 (12)	104.70 ± 10.17 (12)	1.87 ± 0.18 (12)	0.348 ± 0.042 (11)
	2	4.92 ± 0.76 (16)	75.64 ± 10.48 (16)	2.07 ± 0.14 (16)	0.181 ± 0.031 (12)
HIGH I, 40E	1	0.00 ± 0.00 (4)	185.70 ± 5.91 (4)	1.86 ± 0.61 (4)	0.281 ± 0.027 (3)
	2	1.18 ± 0.38 (8)	106.52 ± 9.06 (8)	2.14 ± 0.12 (8)	0.148 ± 0.026 (7)
Guppy-Snail-Alfalfa-Algae Systems (shaded)					
LOW I, OE	1	6.36 ± 0.66 (11)	9.55 ± 1.13 (11)	0.265 ± 0.048 (11)	0.081 ± 0.023 (10)
LOW I, 40E	1	0.00 ± 0.00 (4)	23.80 ± 3.29 (9)	0.297 ± 0.013 (9)	0.069 ± 0.044 (8)
HIGH I, OE	1	44.98 ± 1.28 (8)	23.58 ± 1.41 (8)	1.51 ± 0.07 (8)	0.193 ± 0.058 (7)
HIGH I, 40E	1	0.00 ± 0.00 (4)	126.88 ± 30.57 (5)	2.12 ± 0.03 (5)	0.056 ± 0.011 (4)
Snail-Alfalfa-Algae-systems (unshaded)					
LOW I, -E	1	- -	12.72 ± 1.77 (13)	0.308 ± 0.048 (13)	0.398 ± 0.103 (13)
	2	- -	12.21 ± 1.43 (13)	0.295 ± 0.046 (13)	0.363 ± 0.063 (12)
HIGH I, -E	1	- -	70.95 ± 23.36 (13)	2.09 ± 0.22 (13)	0.347 ± 0.070 (12)
	2	- -	65.87 ± 17.46 (13)	2.21 ± 0.32 (13)	0.347 ± 0.030 (13)

APPENDIX 2

ECOSYS3 was designed by Thompson (1981) using the simulation command control language SIMCON (Worden 1976). The complete program listing and variable default and/or test values have been listed below. Briefly the program finds the steady-state solution of a series of linked differential equations of the general form outlined by Liss (1977) given a certain set of environmental conditions (I, E1, and E2 in this case). Manipulation of environmental parameters allows for the determination of isocline networks between any two component populations in the system.

```

SUBROUTINE UMODEL(IT)
REAL I,MAXCH
COMMON PR(5),OR(2),GV(5),RV(5),PV1(5),PV2(5),OV(2)
COMMON GH1(5),RH1(5),PH1(10),OH1(2)
COMMON GH2(5),RH2(5),PH2(10),OH2(2)
COMMON GC1(10),GC2(10),RC1(10),RC2(10)
COMMON PC1E1(5),PC2E1(5),PC1E2(5),PC2E2(5),OC1(2),OC2(2)
COMMON UE1(5),UE2(5),CE1(2),CE2(2),PRI1(2),PRI2(2)
COMMON R,V,H1,H2,C1,C2,E1,E2,P1,P2
COMMON AK1,AK2,D1,D2,DIV,DR,I,ITIME,TK1,TK2,YMODE
COMMON CS1,CS2,DSW,EE1,EE2,MAXCH,OTHLC1,OTHLC2,OTHLH1,OTHLH2
COMMON OTHLR,OTHLV,PREDH1,PREDH2,PREDR,PREDV,PRODC1,PRODC2
COMMON PRODH1,PRODH2,PRODV,RECTC1,RECTC2,RECTH1,RECTH2,RECTV
COMMON PROF1,PROF2,SW,TP1,TP2,TR1,TR2,UTILE1,UTILE2
COMMON Y1E1,Y2E1,Y1E2,Y2E2,Y11M,Y12M,Y21M,Y22M,Y1MKT,Y2MKT
COMMON CHNGR,CHNGV,CHNGH1,CHNGH2,CHNGC1,CHNGC2
COMMON CHNGE1,CHNGE2,CHNGP1,CHNGP2

```

C
C
C

DETERMINE CHANGE VALUES OF R AND V

```

    PREDR = PR(1)*(1.-EXP(-PR(2)*(R-PR(3))))*
$ (1.-EXP(-PR(4)*(V-PR(5))))
    OTHLR = OR(1)*(EXP(OR(2)*R)-1.)
    CHNGR = I-PREDR-OTHLR
    PRODV = GV(1)*(1.-EXP(-GV(2)*(V-GV(3))))*
$ (1.-EXP(-GV(4)*(R-GV(5))))
    RECTV = RV(1)*(V-RV(2))*EXP(-RV(3)*V)*
$ (1.-EXP(-RV(4)*(R-RV(5))))
    PREDV = PV1(1)*(1.-EXP(-PV1(2)*(V-PV1(3))))*
$ (1.-EXP(-PV1(4)*(H1-PV1(5))))
$ +PV2(1)*(1.-EXP(-PV2(2)*(V-PV2(3))))*
$ (1.-EXP(-PV2(4)*(H2-PV2(5))))
    OTHLV = OV(1)*(EXP(OV(2)*V)-1.)
    CHNGV = PRODV+RECTV-PREDV-OTHLV

```

C
C
C

DETERMINE CHANGE VALUES OF H1 AND H2

```

    PRODH1 = GH1(1)*(1.-EXP(-GH1(2)*(H1-GH1(3))))*
$ (1.-EXP(-GH1(4)*(V-GH1(5))))
    RECTH1 = RH1(1)*(H1-RH1(2))*EXP(-RH1(3)*H1)*
$ (1.-EXP(-RH1(4)*(V-RH1(5))))
    PREDH1 = PH1(1)*(1.-EXP(-PH1(2)*(H1-PH1(3))))*
$ (1.-EXP(-PH1(4)*(C1-PH1(5))))
$ +PH1(6)*(1.-EXP(-PH1(7)*(H1-PH1(8))))*
$ (1.-EXP(-PH1(9)*(C2-PH1(10))))
    OTHLH1 = OH1(1)*(EXP(OH1(2)*H1)-1.)
    CHNGH1 = PRODH1+RECTH1-PREDH1-OTHLH1
    PRODH2 = GH2(1)*(1.-EXP(-GH2(2)*(H2-GH2(3))))*
$ (1.-EXP(-GH2(4)*(V-GH2(5))))
    RECTH2 = RH2(1)*(H2-RH2(2))*EXP(-RH2(3)*H2)*
$ (1.-EXP(-RH2(4)*(V-RH2(5))))
    PREDH2 = PH2(1)*(1.-EXP(-PH2(2)*(H2-PH2(3))))*
$ (1.-EXP(-PH2(4)*(C1-PH2(5))))
$ +PH2(6)*(1.-EXP(-PH2(7)*(H2-PH2(8))))*
$ (1.-EXP(-PH2(9)*(C2-PH2(10))))
    OTHLH2 = OH2(1)*(EXP(OH2(2)*H2)-1.)
    CHNGH2 = PRODH2+RECTH2-PREDH2-OTHLH2

```

C
C
C

DETERMINE YIELDS

```

    IF (YMODE .EQ. 1.) GO TO 1
    Y1E1 = PC1E1(1)*((C1-PC1E1(3))*PC1E1(2))*
$ ((E1-PC1E1(5))*PC1E1(4))
    Y2E1 = PC2E1(1)*((C2-PC2E1(3))*PC2E1(2))*
$ ((E1-PC2E1(5))*PC2E1(4))
    Y1E2 = PC1E2(1)*((C1-PC1E2(3))*PC1E2(2))*
$ ((E2-PC1E2(5))*PC1E2(4))
    Y2E2 = PC2E2(1)*((C2-PC2E2(3))*PC2E2(2))*
$ ((E2-PC2E2(5))*PC2E2(4))

```

1

CONTINUE

```

Y1E1 = PC1E1(1)*(1.-EXP(-PC1E1(2)*(C1-PC1E1(3))))*
$ (1.-EXP(-PC1E1(4)*(E1-PC1E1(5))))
Y2E1 = PC2E1(1)*(1.-EXP(-PC2E1(2)*(C2-PC2E1(3))))*
$ (1.-EXP(-PC2E1(4)*(E1-PC2E1(5))))
Y1E2 = PC1E2(1)*(1.-EXP(-PC1E2(2)*(C1-PC1E2(3))))*
$ (1.-EXP(-PC1E2(4)*(E2-PC1E2(5))))
Y2E2 = PC2E2(1)*(1.-EXP(-PC2E2(2)*(C2-PC2E2(3))))*
$ (1.-EXP(-PC2E2(4)*(E2-PC2E2(5))))
2 CONTINUE
IF (D1 .EQ. 0.) GO TO 3
Y1MKT = (ALOG(D1)-ALOG(P1)-PRI1(1))/PRI1(2)
3 CONTINUE
Y11M = Y1E1
IF (Y1MKT .LT. (Y1E1+Y1E2)) Y11M = Y1E1*Y1MKT/(Y1E1+Y1E2)
Y12M = Y1E2
IF (Y1MKT .LT. (Y1E1+Y1E2)) Y12M = Y1E2*Y1MKT/(Y1E1+Y1E2)
IF (D2 .EQ. 0.) GO TO 4
Y2MKT = (ALOG(D2)-ALOG(P2)-PRI2(1))/PRI2(2)
4 CONTINUE
Y21M = Y2E1
IF (Y2MKT .LT. (Y2E1+Y2E2)) Y21M = Y2E1*Y2MKT/(Y2E1+Y2E2)
Y22M = Y2E2
IF (Y2MKT .LT. (Y2E1+Y2E2)) Y22M = Y2E2*Y2MKT/(Y2E1+Y2E2)
C
C DETERMINE CHANGE VALUES OF C1 AND C2
C
PRODC1 = GC1(1)*(1.-EXP(-GC1(2)*(C1-GC1(3))))*
$ (1.-EXP(-GC1(4)*(H1-GC1(5))))
$ +GC1(6)*(1.-EXP(-GC1(7)*(C1-GC1(8))))*
$ (1.-EXP(-GC1(9)*(H2-GC1(10))))
RECTC1 = RC1(1)*(C1-RC1(2))*EXP(-RC1(3)*C1)*
$ (1.-EXP(-RC1(4)*(H1-RC1(5))))
$ +RC1(6)*(C1-RC1(7))*EXP(-RC1(8)*C1)*
$ (1.-EXP(-RC1(9)*(H2-RC1(10))))
OTHLC1 = OC1(1)*(EXP(OC1(2)*C1)-1.)
CHNGC1 = PRODC1+RECTC1-Y1E1-Y1E2-OTHLC1
PRODC2 = GC2(1)*(1.-EXP(-GC2(2)*(C2-GC2(3))))*
$ (1.-EXP(-GC2(4)*(H1-GC2(5))))
$ +GC2(6)*(1.-EXP(-GC2(7)*(C2-GC2(8))))*
$ (1.-EXP(-GC2(9)*(H2-GC2(10))))
RECTC2 = RC2(1)*(C2-RC2(2))*EXP(-RC2(3)*C2)*
$ (1.-EXP(-RC2(4)*(H1-RC2(5))))
$ +RC2(6)*(C2-RC2(7))*EXP(-RC2(8)*C2)*
$ (1.-EXP(-RC2(9)*(H2-RC2(10))))
OTHLC2 = OC2(1)*(EXP(OC2(2)*C2)-1.)
CHNGC2 = PRODC2+RECTC2-Y2E1-Y2E2-OTHLC2
C
C DETERMINE CHANGE VALUES OF E1, E2, P1, AND P2
C
UTILE1 = UE1(1)*(1.-EXP(-UE1(2)*(E1-UE1(3))))*(1.-
$ EXP(-UE1(4)*((Y1E1+Y2E1)-UE1(5))))
UTILE2 = UE2(1)*(1.-EXP(-UE2(2)*(E2-UE2(3))))*(1.-
$ EXP(-UE2(4)*((Y1E2+Y2E2)-UE2(5))))
CHNGE1 = P1*Y11M+P2*Y21M+UTILE1

```

```

$ -CE1(1)*TK1*(EXP(CE1(2)*E1)-1.)
CHNGE2 = P1*Y12M+P2*Y22M+UTILE2
$ -CE2(1)*TK2*(EXP(CE2(2)*E2)-1.)
CHNGP1 = D1*EXP(-PRI1(1)-PRI1(2)*(Y1E1+Y1E2))-P1
CHNGP2 = D2*EXP(-PRI2(1)-PRI2(2)*(Y2E1+Y2E2))-P2

```

C
C
C

POLICY VARIABLES

```

CS1 = (D1/PRI1(2))*(1.-EXP(-PRI1(1)-PRI1(2)*Y1MKT))-P1*Y1MKT
$ +PRI1(1)*(D1*EXP(-PRI1(1))-P1)/PRI1(2)
$ -D1*(1.-EXP(-PRI1(1)))/PRI1(2)
CS2 = (D2/PRI2(2))*(1.-EXP(-PRI2(1)-PRI2(2)*Y2MKT))-P2*Y2MKT
$ +PRI2(1)*(D2*EXP(-PRI2(1))-P2)/PRI2(2)
$ -D2*(1.-EXP(-PRI2(1)))/PRI2(2)
PROF1 = P1*Y11M+P2*Y21M-CE1(1)*TK1*(EXP(CE1(2)*E1)-1.)
PROF2 = P1*Y12M+P2*Y22M-CE2(1)*TK2*(EXP(CE2(2)*E2)-1.)
TP1 = CE1(1)*TK1*(EXP(CE1(2)*EE1)-1.)
$ -CE1(1)*TK1*(EXP(CE1(2)*E1)-1.)
$ -(EE1-E1)*CE1(1)*CE1(2)*TK1*EXP(CE1(2)*E1)
TP2 = CE2(1)*TK2*(EXP(CE2(2)*EE2)-1.)
$ -CE2(1)*TK2*(EXP(CE2(2)*E2)-1.)
$ -(EE2-E2)*CE2(1)*CE2(2)*TK2*EXP(CE2(2)*E2)
TR1 = CE1(1)*(TK1-AK1)*(EXP(CE1(2)*E1)-1.)
TR2 = CE2(1)*(TK2-AK2)*(EXP(CE2(2)*E2)-1.)
SW = CHNGE1+CHNGE2+TR1+TR2+CS1+CS2-TP1-TP2
DSW = SW/(1.+DR)**IT+DSW
ITIME=IT

```

C
C
C

DETERMINE MAXIMUM CHANGE, AND UPDATE COMPONENTS

```

MAXCH = AMAX1(ABS(CHNGR),ABS(CHNGV),ABS(CHNGH1),ABS(CHNGH2),
$ ABS(CHNGC1),ABS(CHNGC2),ABS(CHNGE1),ABS(CHNGE2),
$ ABS(CHNGP1),ABS(CHNGP2))
R = R+CHNGR/DIV
V = V+CHNGV/DIV
H1 = H1+CHNGH1/DIV
H2 = H2+CHNGH2/DIV
C1 = C1+CHNGC1/DIV
C2 = C2+CHNGC2/DIV
EE1 = E1+CE1(1)*(TK1-AK1)*(EXP(CE1(2)*E1)-1.)/DIV+CHNGE1/DIV
EE2 = E2+CE2(1)*(TK2-AK2)*(EXP(CE2(2)*E2)-1.)/DIV+CHNGE2/DIV
E1 = E1+CHNGE1/DIV
E2 = E2+CHNGE2/DIV
P1 = P1+CHNGP1/DIV
P2 = P2+CHNGP2/DIV

```

C
C
C

CHECK TO MAKE SURE ALL VALUES ARE NON-NEGATIVE

```

IF (R .LT. 0.) R = 0.
IF (V .LT. 0.) V = 0.
IF (H1 .LT. 0.) H1 = 0.
IF (H2 .LT. 0.) H2 = 0.
IF (C1 .LT. 0.) C1 = 0.
IF (C2 .LT. 0.) C2 = 0.

```

```

IF (E1 .LT. 0.) E1 = 0.
IF (E2 .LT. 0.) E2 = 0.
IF (P1 .LT. 0.) P1 = 0.
IF (P2 .LT. 0.) P2 = 0.

```

C

```

RETURN
END

```

C

C SUBROUTINE UINIT - READS IN VALUES FROM DATA3 FILE

C

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SUBROUTINE UINIT
COMMON PR(5),OR(2),GV(5),RV(5),PV1(5),PV2(5),OV(2)
COMMON GH1(5),RH1(5),PH1(10),OH1(2)
COMMON GH2(5),RH2(5),PH2(10),OH2(2)
COMMON GC1(10),GC2(10),RC1(10),RC2(10)
COMMON PC1E1(5),PC2E1(5),PC1E2(5),PC2E2(5),OC1(2),OC2(2)
COMMON UE1(5),UE2(5),CE1(2),CE2(2),PRI1(2),PRI2(2)
COMMON R,V,H1,H2,C1,C2,E1,E2,P1,P2
COMMON AK1,AK2,D1,D2,DIV,DR,I,ITIME,TK1,TK2,YMODE
COMMON CS1,CS2,DSW,EE1,EE2,MAXCH,OTHLC1,OTHLC2,OTHLH1,OTHLH2
COMMON OTHLR,OTHLV,PREDH1,PREDH2,PREDR,PREDV,PRODC1,PRODC2
COMMON PRODH1,PRODH2,PRODV,RECTC1,RECTC2,RECTH1,RECTH2,RECTV
COMMON PROF1,PROF2,SW,TP1,TP2,TR1,TR2,UTILE1,UTILE2
COMMON Y1E1,Y2E1,Y1E2,Y2E2,Y11M,Y12M,Y21M,Y22M,Y1MKT,Y2MKT
COMMON CHNGR,CHNGV,CHNGH1,CHNGH2,CHNGC1,CHNGC2
COMMON CHNGE1,CHNGE2,CHNGP1,CHNGP2
REWIND 44
READ (44,5) PR(1),PR(2),PR(3),PR(4),PR(5)
READ (44,6) OR(1),OR(2)
READ (44,5) GV(1),GV(2),GV(3),GV(4),GV(5)
READ (44,5) RV(1),RV(2),RV(3),RV(4),RV(5)
READ (44,5) PV1(1),PV1(2),PV1(3),PV1(4),PV1(5)
READ (44,5) PV2(1),PV2(2),PV2(3),PV2(4),PV2(5)
READ (44,6) OV(1),OV(2)
READ (44,5) GH1(1),GH1(2),GH1(3),GH1(4),GH1(5)
READ (44,5) GH2(1),GH2(2),GH2(3),GH2(4),GH2(5)
READ (44,5) RH1(1),RH1(2),RH1(3),RH1(4),RH1(5)
READ (44,5) RH2(1),RH2(2),RH2(3),RH2(4),RH2(5)
READ (44,5) PH1(1),PH1(2),PH1(3),PH1(4),PH1(5)
READ (44,5) PH1(6),PH1(7),PH1(8),PH1(9),PH1(10)
READ (44,5) PH2(1),PH2(2),PH2(3),PH2(4),PH2(5)
READ (44,5) PH2(6),PH2(7),PH2(8),PH2(9),PH2(10)
READ (44,6) OH1(1),OH1(2)
READ (44,6) OH2(1),OH2(2)
READ (44,5) GC1(1),GC1(2),GC1(3),GC1(4),GC1(5)
READ (44,5) GC1(6),GC1(7),GC1(8),GC1(9),GC1(10)
READ (44,5) GC2(1),GC2(2),GC2(3),GC2(4),GC2(5)
READ (44,5) GC2(6),GC2(7),GC2(8),GC2(9),GC2(10)
READ (44,5) RC1(1),RC1(2),RC1(3),RC1(4),RC1(5)
READ (44,5) RC1(6),RC1(7),RC1(8),RC1(9),RC1(10)
READ (44,5) RC2(1),RC2(2),RC2(3),RC2(4),RC2(5)
READ (44,5) RC2(6),RC2(7),RC2(8),RC2(9),RC2(10)
READ (44,5) PC1E1(1),PC1E1(2),PC1E1(3),PC1E1(4),PC1E1(5)
READ (44,5) PC2E1(1),PC2E1(2),PC2E1(3),PC2E1(4),PC2E1(5)

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READ (44,5) PC1E2(1),PC1E2(2),PC1E2(3),PC1E2(4),PC1E2(5)
READ (44,5) PC2E2(1),PC2E2(2),PC2E2(3),PC2E2(4),PC2E2(5)
READ (44,6) OC1(1),OC1(2)
READ (44,6) OC2(1),OC2(2)
READ (44,5) UE1(1),UE1(2),UE1(3),UE1(4),UE1(5)
READ (44,5) UE2(1),UE2(2),UE2(3),UE2(4),UE2(5)
READ (44,6) CE1(1),CE1(2)
READ (44,6) CE2(1),CE2(2)
READ (44,6) PRI1(1),PRI1(2)
READ (44,6) PRI2(1),PRI2(2)
READ (44,7) R,V,H1,H2,C1,C2,E1,E2,P1,P2
READ (44,8) AK1,AK2,D1,D2,DIV,DR,DSW,I,TK1,TK2,YMODE
READ (44,6) EE1,EE2
READ (44,6) Y1MKT,Y2MKT
5  FORMAT (5(F5.1))
6  FORMAT (2(F5.1))
7  FORMAT (10(F5.1))
8  FORMAT (11(F5.1))
C
      RETURN
      END
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C  SUBROUTINE CCOM
C
      SUBROUTINE CCOM
      REAL I
      COMMON PR(5),OR(2),GV(5),RV(5),PV1(5),PV2(5),OV(2)
      COMMON GH1(5),RH1(5),PH1(10),OH1(2)
      COMMON GH2(5),RH2(5),PH2(10),OH2(2)
      COMMON GC1(10),GC2(10),RC1(10),RC2(10)
      COMMON PC1E1(5),PC2E1(5),PC1E2(5),PC2E2(5),OC1(2),OC2(2)
      COMMON UE1(5),UE2(5),CE1(2),CE2(2),PRI1(2),PRI2(2)
      COMMON R,V,H1,H2,C1,C2,E1,E2,P1,P2
      COMMON AK1,AK2,D1,D2,DIV,DR,I,ITIME,TK1,TK2,YMODE
      COMMON CS1,CS2,DSW,EE1,EE2,MAXCH,OTHLC1,OTHLC2,OTHLH1,OTHLH2
      COMMON OTHLR,OTHLV,PREDH1,PREDH2,PREDR,PREDV,PRODC1,PRODC2
      COMMON PRODH1,PRODH2,PRODV,RECTC1,RECTC2,RECTH1,RECTH2,RECTV
      COMMON PROF1,PROF2,SW,TP1,TP2,TR1,TR2,UTILE1,UTILE2
      COMMON Y1E1,Y2E1,Y1E2,Y2E2,Y11M,Y12M,Y21M,Y22M,Y1MKT,Y2MKT
      COMMON CHNGR,CHNGV,CHNGH1,CHNGH2,CHNGC1,CHNGC2
      COMMON CHNGE1,CHNGE2,CHNGP1,CHNGP2
C
      RETURN
      END
EOI ENCOUNTERED.
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D PR(1) PR(2) PR(3) PR(4) PR(5)
PR          ( 1) = 10.00000
PR          ( 2) =  1.00000
PR          ( 3) =  0.
PR          ( 4) =  .2500000
PR          ( 5) =  0.
? D OR(1) OR(2)
OR          ( 1) =  1.00000
OR          ( 2) =  .1000000
? D GV(1) GV(2) GV(3) GV(4) GV(5)
GV          ( 1) = 10.00000
GV          ( 2) =  1.00000
GV          ( 3) =  0.
GV          ( 4) =  .2500000
GV          ( 5) =  0.
? D RV(1) RV(2) RV(3) RV(4) RV(5)
RV          ( 1) = 10.00000
RV          ( 2) =  0.
RV          ( 3) =  .5000000
RV          ( 4) =  .5000000
RV          ( 5) =  0.
? D PV *DEL*
D PV(1) PV(2) PV(3) PV(4) PV(5)
UNKNOWN COMMAND
DD PV(1) PV(2) PV(3) PV(4) PV(5)
? D PV(1) PV(2) PV(3) PV(4) PV(5)
PV          WAS NOT FOUND IN COMMON
? D PV1(1) PV1(2) PV1(3) PV1(4) PV1(5)
PV1         ( 1) = 15.00000
PV1         ( 2) =  1.00000
PV1         ( 3) =  0.
PV1         ( 4) =  .2500000
PV1         ( 5) =  0.
? D PV2(1) PV2(2) PV2(3) PV2(4) PV2(5)
PV2         ( 1) =  5.00000
PV2         ( 2) =  .5000000
PV2         ( 3) =  0.
PV2         ( 4) =  .5000000
PV2         ( 5) =  0.
? D OV(1) OV(2)
OV          ( 1) =  1.00000
OV          ( 2) =  .1000000
? D GH1(1) GH1(2) GH1(3) GH1(4) GH1(5)
GH1         ( 1) = 15.00000
GH1         ( 2) =  1.00000
GH1         ( 3) =  0.
GH1         ( 4) =  .2500000
GH1         ( 5) =  0.
? D GH2(1) GH2(2) GH2(3) GH2(4) GH2(5)

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GH2          ( 1) = 1.000000
GH2          ( 2) = .5000000
GH2          ( 3) = 0.
GH2          ( 4) = .5000000
GH2          ( 5) = 0.
? D RH1(1) RH1(2) RH1(3) RH1(4) RH1(5)
RH1          ( 1) = 15.00000
RH1          ( 2) = 0.
RH1          ( 3) = .5000000
RH1          ( 4) = .5000000
RH1          ( 5) = 0.
? D RH2(1) RH2(2) RH2(3) RH2(4) RH2(5)
RH2          ( 1) = 5.000000
RH2          ( 2) = 0.
RH2          ( 3) = .5000000
RH2          ( 4) = .5000000
RH2          ( 5) = 0.
? D PH1(1) PH1(2) PH1(3) PH1(4) PH1(5)
PH1          ( 1) = 15.00000
PH1          ( 2) = 1.000000
PH1          ( 3) = 0.
PH1          ( 4) = .2500000
PH1          ( 5) = 0.
? D PH1(6) PH1(7) PH1(8) PH1(9) PH1(10)
PH1          ( 6) = 5.000000
PH1          ( 7) = 1.000000
PH1          ( 8) = 0.
PH1          ( 9) = .2500000
PH1          (10) = 0.
? PH2(1) PH2(2) PH2(3) PH2(4) PH2(5)
UNKNOWN COMMAND
PH2(1) PH2(2) PH2(3) PH2(4) PH2(5)
? D PH2(1) PH2(2) PH2(3) PH2(4) PH2(5)
PH2          ( 1) = 5.000000
PH2          ( 2) = .5000000
PH2          ( 3) = 0.
PH2          ( 4) = .5000000
PH2          ( 5) = 0.
? D PH2(6) PH2(7) PH2(8) PH2(9) PH2(10)
PH2          ( 6) = 5.000000
PH2          ( 7) = .5000000
PH2          ( 8) = 0.
PH2          ( 9) = .5000000
PH2          (10) = 0.
? D OH1(1) OH1(2)
OH1          ( 1) = 1.000000
OH1(2)      WAS NOT FOUND IN COMMON
? D OH1(1) OH2(2)
OH1          ( 1) = 1.000000
OH1          ( 2) = .1000000
? D OH2(1) OH2(2)

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OH2          ( 1) = 1.000000
OH2          ( 2) = .1000000
? D GC1(1) GC1(2) GC1(3) GC1(4) GC1(5)
GC1          ( 1) = 15.00000
GC1          ( 2) = 1.000000
GC1          ( 3) = 0.
GC1          ( 4) = .2500000
GC1          ( 5) = 0.
? D GC1(6) GC1(7) GC1(8) GC1(9) GC1(10)
GC1          ( 6) = 1.000000
GC1          ( 7) = .5000000
GC1          ( 8) = 0.
GC1          ( 9) = .5000000
GC1          (10) = 0.
? D GGC1(7) GGC1(8) GGC1(9) GC2(4) GC2(5)
GC2
WAS NOT FOUND IN COMMON
? D GC2(1) GC2(2) GC2(3) GC2(4) GC2(5)
GC2          ( 1) = 5.000000
GC2          ( 2) = 1.000000
GC2          ( 3) = 0.
GC2          ( 4) = .2500000
GC2          ( 5) = 0.
? D GC2(6) GC2(7) GC2(8) GC2(9) GC2(10)
GC2
ERROR MAXIMUM SUBSCRIPT EXCEEDED FOR GC2
? D GC2(6) GC2(7) GC2(8) GC2(9) GC2(10)
GC2          ( 6) = 1.000000
GC2          ( 7) = .5000000
GC2          ( 8) = 0.
GC2          ( 9) = .5000000
GC2          (10) = 0.
? D RC1(1) RC1(2) RC1(3) RC1(4) RC1(5)
RC1          ( 1) = 5.000000
RC1          ( 2) = 0.
RC1          ( 3) = .5000000
RC1          ( 4) = .5000000
RC1          ( 5) = 0.
? D RC1(6) RC1(7) RC1(8) RC1(9) RC1(10)
RC1          ( 6) = 5.000000
RC1          ( 7) = 0.
RC1          ( 8) = .5000000
RC1          ( 9) = .5000000
RC1          (10) = 0.
? D RC2(1) RC2(2) RC2(3) RC2(4) RC2(5)
RC2          ( 1) = 5.000000
RC2          ( 2) = 0.
RC2          ( 3) = .5000000
RC2          ( 4) = .5000000
RC2          ( 5) = 0.
? D RC2(6) RC2(7) RC2(8) RC2(9) RC2(10)
RC2          ( 6) = 5.000000

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RC2          ( 7) = 0.
RC2          ( 8) = .5000000
RC2          ( 9) = .5000000
RC2          (10) = 0.
? D PC1E1(1) PC1E1(2) PC1E1(3) PC1E1(4) PC1E1(5)
PC1E1        ( 1) = 20.00000
PC1E1        ( 2) = 1.000000
PC1E1        ( 3) = 0.
PC1E1        ( 4) = .2500000
PC1E1        ( 5) = 0.
? D PC2E1(1) PC2E1(2) PC2E1(3) PC2E1(4) PC2E1(5)
PC2E1        ( 1) = 0.
PC2E1        ( 2) = 1.000000
PC2E1        ( 3) = 0.
PC2E1        ( 4) = .1000000
PC2E1        ( 5) = 0.
? D PC1E2(1) PC1E2(2) PC1E2(3) PC1E2(4) PC1E2(5)
PC1E2        ( 1) = 0.
PC1E2        ( 2) = 1.000000
PC1E2        ( 3) = 0.
PC1E2        ( 4) = .1000000
PC1E2        ( 5) = 0.
? D PC2E2(1) PC2E2(2) PC2E2(3) PC2E2(4) PC2E2(5)
PC2E2        ( 1) = 20.00000
PC2E2        ( 2) = 1.000000
PC2E2        ( 3) = 0.
PC2E2        ( 4) = .2500000
PC2E2        ( 5) = 0.
? D OC1(1) OC1(2)
OC1          ( 1) = 1.000000
OC1          ( 2) = .1000000
? D OC2(1) OC2(2)
OC2          ( 1) = 1.000000
OC2          ( 2) = .1000000
? D UE1(1) UE1(2) UE1(3) UE1(4) UE1(5)
UE1          ( 1) = 0.
UE1          ( 2) = .5000000
UE1          ( 3) = 0.
UE1          ( 4) = .5000000
UE1          ( 5) = 0.
? D UE2(1) UE2(2) UE2(3) UE2(4) UE2(5)
UE2          ( 1) = 0.
UE2          ( 2) = .5000000
UE2          ( 3) = 0.
UE2          ( 4) = .5000000
UE2          ( 5) = 0.
? D CE1(1) CE1(2)
CE1          ( 1) = 0.
CE1          ( 2) = .1000000
? D CE2(1) CE2(2)
CE2          ( 1) = 0.

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CE2                ( 2) = .1000000
? D PRII(1) PRI1(2)
PRI1               ( 1) = .5000000
PRI1               ( 2) = .1000000
? D PRI2(1) PRI2(2)
PRI2               ( 1) = .5000000
PRI2               ( 2) = .1000000
? D AKI AKQ2D1 D2 TK1 TK2 YMODE
AKI                WAS NOT FOUND IN COMMON
? D AK1 AK2 D1 D2 TK1 TK2 YMODE
AK1                = 1.000000
AK2                = 1.000000
D1                 = 0.
D2                 = 0.
TK1                = 1.000000
TK2                = 1.000000
YMODE              = 1.000000
? QUIT
      8.542 CP SECONDS EXECUTION TIME.
/BYE
UN=BRAQ5C  LOG OFF  10.27.36.
JSN=ADZE   SRU-S    26.584

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