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Title: EFFECTS OF PERTURBATION ON COMMUNITY STRUCTURE AND

ORGANIZATION OF AQUATIC MICROCOSMS

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Aquatic communities consisting of guppies, amphipods, copepods, snails, nematodes, rotifers, protozoans, euglenoid flagellates, and other microorganisms were established in sixteen laboratory microcosms. Guppies were exploited at four different levels (0 percent, 10 percent, 20 percent, and 40 percent of the population biomass) with four communities at each level of exploitation. An alfalfa ration (0.4 g/day) was introduced as a nutrient source for the communities.

The general objective of this study was to advance the understanding of community structure and organization by conceptualizing communities as hierarchical arrangements of subsystems influenced by the external environment and by explaining how both the interactive performances of these subsystems and the external environmental conditions may influence the dynamics of community structure. Environmental perturbations imposed on the sixteen communities included introduction of a toxicant, dieldrin, an increase

in nutrient input and habitat availability, and exploitation of the guppy populations at four levels.

The level of guppy exploitation had a direct effect on community structure. The biomasses of the guppy populations that were maintained in the systems decreased as the level of exploitation increased. The guppies apparently preyed on the amphipod and nematode populations as well as competed with the amphipods for the alfalfa nutrient source. As the biomass of the guppy populations decreased with increased exploitation, the populations of amphipods and nematodes increased.

Dieldrin was introduced into four systems (one at each level of exploitation) after these systems had exhibited near steady-state behavior on a guppy-amphipod phase plane for approximately one year. The most direct impact of the toxicant was on the guppy population. Guppy biomass was decreased substantially at 0 percent exploitation, 10 percent exploitation, and 20 percent exploitation. A subsequent increase in amphipods occurred as a result of the decreased intensity of predation and competition. New near steady-state biomasses were established for these populations. The system at 40 percent guppy exploitation showed no apparent immediate response to the dieldrin. Microinvertebrate populations also showed no apparent response to the toxicant.

In eight of the remaining systems, nutrient input was increased and additional rock habitat was introduced to provide increased cover for the invertebrates. This environmental perturbation greatly altered community structure. Immediate and dramatic increases in the

guppy and amphipod populations occurred. The increased rock cover caused an oxygen depletion in the sediments and thus decreased the habitat available for the microinvertebrates. Substantial decreases occurred in the populations of nematodes, protozoans, and other previously abundant organisms.

A system of intersecting isoclines is used to explain the general locations of the domains of behavior of these systems in phase space before and after the introduction of dieldrin and before and after the increase in nutrient and habitat availability. The increase in nutrient and habitat availability altered the domain of behavior for the communities more dramatically than did dieldrin.

Effects of Perturbation on Community Structure and Organization

in Aquatic Microcosms

by

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EFFECTS OF PERTURBATION ON COMMUNITY STRUCTURE AND ORGANIZATION IN AQUATIC MICROCOSMS

INTRODUCTION

The concept of community organization has been interpreted in many different ways throughout the ecological literature. The terms organization and structure are often used interchangeably. Here, organization and structure will be defined as separate concepts. Organization will be employed as a theoretical concept entailing the general ways of incorporation and concordance of subsystems within a community. Structure, on the other hand, will be defined as an observational concept. It is an empirical representation and may include such measurable characteristics as species composition, distribution, and relative abundance. An explanation of the organization of a community based solely on its structure is inadequate. However, structure is certainly an integral part of community organization. Structure entails the arrangement of the parts of a community through space and time. Organization includes not only the arrangement of these parts, but also their interrelationships, concordance, and incorporation within the community. It is through understanding organization that one can explain community structure.

Because of the recent emphasis on trophic relations, habitat and life history organization of subsystems forming communities have not been sufficiently considered. Elton (1966) suggested that in

addition to the food consumed and its characteristics, feeding strategies and the habitat from which the food was taken were important in community organization. Elton conceived of the community as a group of interlocking community units bound together by a system of girders representing organismic transfers between habitat systems. A stable community would consist of a group of tightly interlocking units.

Clements (1916, 1928) compared a community passing through the stages of succession to an organism as it goes through a life cycle. A community, like an organism, is born, grows, matures, reproduces, and dies. The importance of this recognition of the community as a complete entity extending through time and space has not always been appreciated. Gleason's (1926) individualistic population concept of communities was more generally accepted and tended to reduce community thinking to population thinking. In plant ecology, this appears in gradient analysis (Whittaker 1967) and in ordination (Bray and Curtis 1957). In animal ecology, it appears in resource partitioning within guilds (Root 1967). Even studies of "community structure" have been mainly of species diversity and relative abundance within selected taxonomic groups (e.g., Fisher, Corbet, and Williams 1943; Hairston and Beyers 1954; Pielou 1975; May 1975). These tendencies are, in part, related to the difficulty of adequately conceiving and studying such relatively unbounded and high dimensional systems as communities.

The study of some aspects of community organization and structure may be facilitated by development and use of laboratory systems. Such microcosms provide an opportunity to establish a community with defined boundaries, lower dimensionality, and a controlled environment, to perturb that community, and then to observe the responses of the community to the disturbance. The importance of microcosm studies is found not in their direct representation of a natural system, but in that their simplicity and manipulability may facilitate insight into community organization. The ultimate goal of this investigation is to advance the understanding of the structure and organization of communities as organismic systems, conceptualized as being simple, unified, and ordered, which seems to be necessary for human understanding. More specific explanatory objectives are:

1) To conceptualize communities as hierarchical organizations of interacting subsystems influenced indirectly and sometimes directly by the external environment.

2) To explain the dynamics of community structure on the basis of the interactive performances of these subsystems.

3) To explain how external environmental conditions such as nutrient input, habitat availability, toxicant introduction, and exploitation may influence the dynamics of community structure.

MATERIALS AND METHODS

Sixteen aquatic microcosms were established at the Oak Creek Laboratory of Biology. Each multispecies system was maintained in a fiberglass tank measuring 1.2 m x 1.06 m x 0.42 m and supplied with a continous flow (600 ml/min) of well water. Light intensity (20 foot candles), photoperiod (14 hr light/10 hr dark), and temperature (21°C) remained constant. These communities included (1) a vertebrate predator, the guppy (Poecilia reticulata), (2) macroinvertebrates, an amphipod (Gammarus fasciatus), a copepod (Cyclops sp.), and snails, and (3) numerous species of microorganisms (bacteria, euglenoid flagellates, rotifers, nematodes, gastrotrichs, and four protozoan species). A representation of the probable interrelationships between these organisms is shown in Figure 1. Fifty grams of the aquatic plant Ceratophyllum demersum provided cover necessary to protect the newborn guppies from the cannibalistic adults. Initially, all sixteen systems were of identical design. Three circular rock nests of 1.5 cm quartzite gravel covered 25 percent of each tank bottom and supplied habitat and escape cover for the invertebrate populations. A daily introduction of 0.6 g of alfalfa ration into each system was the primary source of energy and materials for the guppy and invertebrate populations. The alfalfa ration was a gelatinous mixture of 60 percent alfalfa and 40 percent Oregon Test Diet (See Appendix II). This was frozen during storage and introduced

Figure 1. Diagramatic representation of the interrelationships

between the most abundant organisms within the community.

All organisms compete either directly or indirectly for

the alfalfa ration.

EXPLOITATION

GUPPY

NEMATODE

AMPHIPODS   PROTOZOANS   ROTIFER

SNAILS

BACTERIA

DETRITUS AND SEDIMENTS

ALFALFA RATION

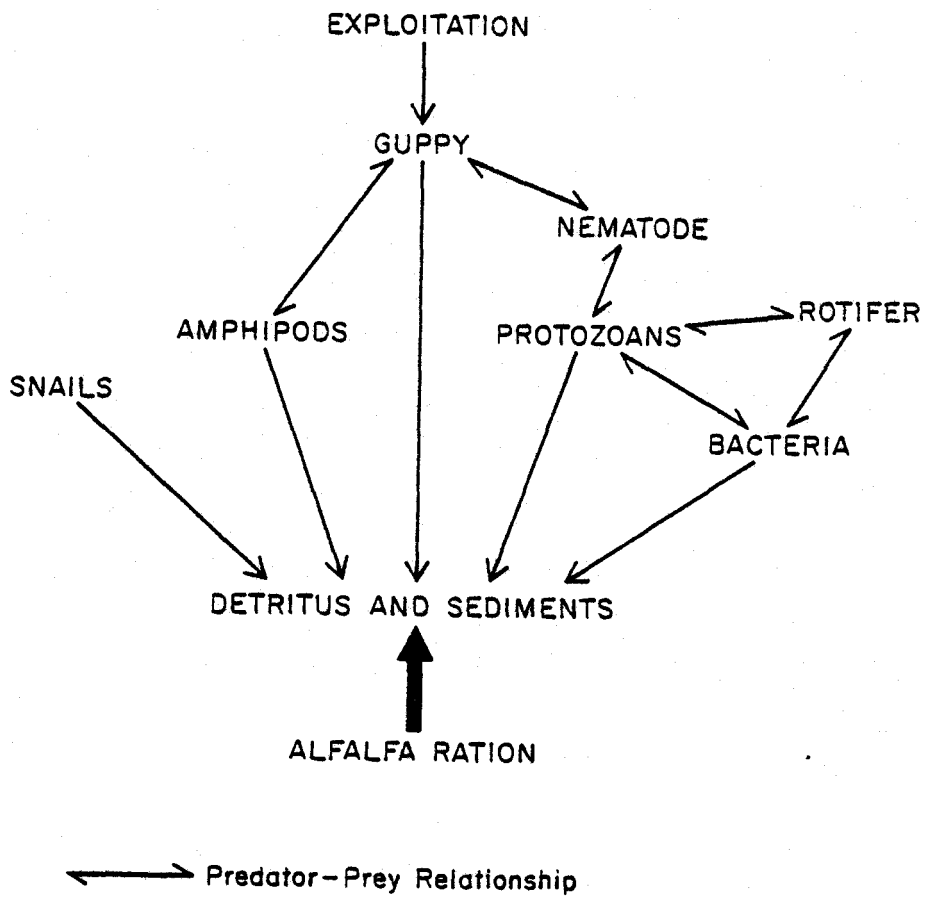Predator–Prey Relationship

Figure 1.

as a pellet over each rock nest. Experimental modifications to be explained later were made in this original design.

In April 1975, each tank was stocked with a population of 200 amphipods, the populations in the 16 tanks having similar size distributions. The amphipods were taken from native populations of the Neuse River in North Carolina. Copepods from the same area were introduced inadvertently into the systems at that time. The systems remained relatively undisturbed during the next year, except for periodic sampling to monitor the development of the invertebrate populations. In April 1976, a monthly sampling program was initiated and guppies were introduced into three systems for a preliminary determination of (1) the behavior of the systems with the addition of a vertebrate predator, (2) the approximate biomass and density of guppies the system could support, and (3) levels of exploitation that could be imposed upon the guppy and still allow the systems to persist. In November 1976, each of the remaining systems was stocked with 37 guppies having a total biomass of 4.5 g. Monthly exploitation rates for the guppies were set at 0, 10, 20, and 40 percent of the biomass with four systems being exploited at each level.

Sampling involved placing metal sampling cylinders simultaneously around the three rock nest areas. The cylinders provided artificial boundaries around each rock nest so that the organisms in each nest area could be sampled separately. All guppies were then removed from the tank by means of a small mesh net.

Gravel rock nests were next removed and the remaining sediment and invertebrates were taken from each cylinder with a fine mesh net and a siphon. Sediment and invertebrates outside the nests in the remaining area of the tank were removed in the same manner. Direct counts of amphipods and copepods were recorded. Amphipods were grouped into six size classes, and a mean individual biomass was determined for each class (Table 1). The estimate of total biomass of amphipods in a system was the sum of the biomasses from all size classes. All copepods were considered to be in the same size class. The mean biomass of a single copepod was estimated to be 6.0×10^{-5} g.

Table 1. Size range and mean individual biomass for each class of amphipods.

Size range (mm)	Biomass (g)
< 0.5	4.00×10^{-5}
$0.5 - 1.9$	1.50×10^{-4}
$2.0 - 3.9$	3.20×10^{-4}
$4.0 - 5.9$	5.60×10^{-4}
$6.0 - 7.9$	1.86×10^{-3}
≥ 8.0	3.94×10^{-3}

Following the removal of the macroinvertebrates, the sediment was subdivided into ten equal subsamples by means of a sample splitter. Nine of the subsamples were returned to the tank. The remaining subsample was then subdivided into ten equal subsamples. Each of these subsamples represented 1 percent of the total amount of sediment in the tank. One subsample was dried and weighed in order to estimate the total weight of sediment in the tank. It was then ashed for 3 hours at 500°C to determine the percent organic matter in the sediment. Another subsample of sediment was used to estimate densities of the microinvertebrate populations. These densities were estimated by means of a Sedgewick Rafter Cell (APHA 1971) and converted to biomass estimates with values from Fenchel (1978). A third subsample was analyzed by means of the standard micro-Kjeldahl technique. To return the community components to a tank, the metal sampling cylinders were replaced in the tank. Rock nests were replaced and sediment and invertebrates were returned to the nest from which they were removed. After the sediment had settled, the sampling cylinders were removed and guppies were returned to the tank. Extreme care was taken to perturb the systems as little as possible.

Experimental Modifications

In March 1978, eight of the systems were altered to establish a higher level of productivity. Four large rock nests covering approximately 95 percent of the bottom of each tank were introduced,

and the ration of alfalfa was increased to 4.0 g daily. The sampling procedure was identical to that previously described, except the metal sampling cylinders were no longer used.

At the same time, four of the remaining eight systems (one at each exploitation rate were chosen for perturbation with a pesticide. Dieldrin was introduced continuously in the exchange flow at a concentration of 1 part per billion (ppb). Figure 2 summarizes the experimental design and the time frame of the study including these experimental modifications. The study presented in this thesis is a part of a continuing investigation.

Figure 2. Time schedule and experimental design of the study. The
level of guppy exploitation (0, 10, 20, and 40 percent)
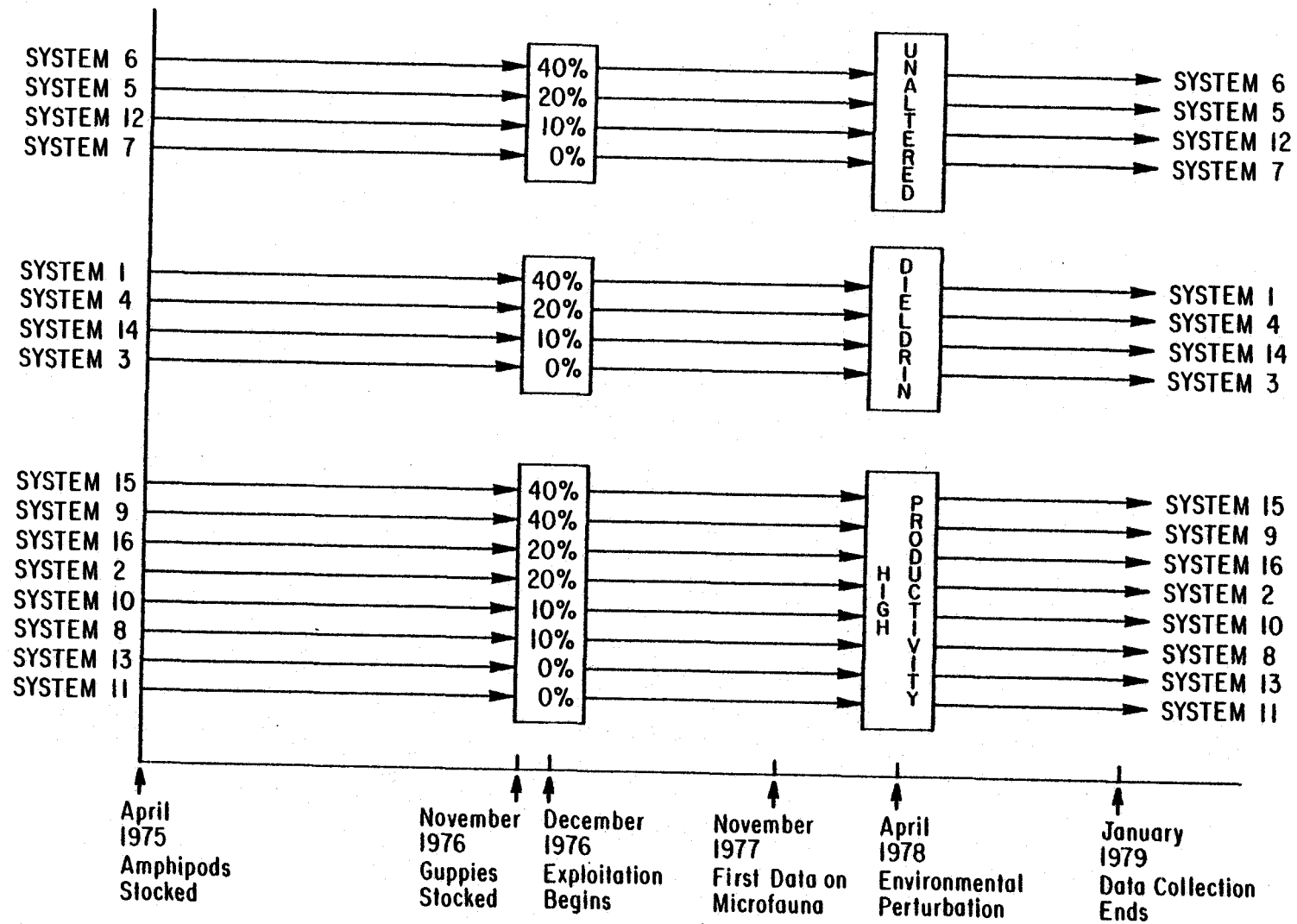for each system is indicated in the boxes centered above
December 1976.

Figure 2.

CONCEPTUAL FOUNDATION

Satisfying explanations of biological systems at the community level are rare, due largely to the difficulties involved in adequately conceiving of a community. Regier (1974) noted that ecologists have often failed to realize that community level science can be developed without reference to the previously existing models of population dynamics. The community may be best understood as being more than an assemblage of interacting populations, as being a system of systems of populations. A community can be conceived as a distinct organismic system, composed of a number of related subsystems, yet having its own level-specific capacity, environment, and performances through space and time (Warren and Liss 1977; Warren, Allen, and Haefner 1979). This concept of an organismic system encompasses the development of a community from its initial colonization through various successional stages to its climax.

The community can be conceived as consisting of a hierarchical arrangement of a few high level subsystems, each of which includes lower level subsystems. As an organismic system, the community at any stage of development incorporates its subsystems as well as their level-specific environments. Each of these subsystems must function in concordance, or harmony, with other subsystems to maintain a stable and persistent community. Incorporation and concordance of subsystems within the community is taken to be a universal property of communities. Insight into the nature of this property by microcosm

studies, other empirical studies, and theoretical investigations should, accordingly, advance understanding of communities.

At any point in time and space, a given community will have a specific performance or state attributable to the capacity of that community and the environment. The capacity of a system theoretically entails all possible performances of that system in all possible environments. At any stage in its development, a community has a realized capacity to do certain things such as exhibit structure, develop further, and persist. The prevailing environmental conditions will determine the actual pattern of development for the system. Since the performance of the community is determined by the environmental variables influencing it, communities having identical capacities will exhibit a variety of performances in different environments. Environmental factors that might cause these performances to be variable include differences in nutrient or habitat availability, exploitation, or toxicant presence. Capacity of a system is a theoretical concept and can never be fully and directly determined for any natural system. Realized capacity can change through time in accordance with system development and evolution. Though a particular performance may not be possible at one stage of development, the potential for that performance to occur at some future time can exist. As an organismic system, a community at its origin can be conceived to have some potential capacity. This potential capacity encompasses all realized capacities that could develop in all

possible environments, only some of which will occur during the development of the community in any particular environment through time. The relation of the environment to the development of the community from potential capacity to realized capacity to performance is illustrated in Figure 3. This abstract notion of potential and realized capacities is perhaps the most fundamental notion required in the explanation of biological systems.

Implicit in the understanding of the concept of community capacity is the recognition of the community as a complete entity extending through time and space. Performances of the community as a whole include structure, development, and persistence. Since structure is an empirical community level performance, a histogram that incorporates the biomasses of all community components for a given period of time is useful in allowing one to visually assess the community as a whole without losing awareness of the next lower level parts. Through the development of such histograms, the community is given a unique symbolic identity. It assumes a well defined form, which in itself reflects structural aspects of that particular community. Each component is represented by its biomass for that particular point in space and time. From this community representation species composition, relative abundance, diversity, and total biomass are readily extractable. But, most importantly, with a series of histograms through time, one can see what form a community takes and how that form may change relative to fluctuations in the environment.

Figure 3. A diagramatic view of a community as an organismic system.

Any particular series of realized capacities that may

develop are determined by the potential capacity of that

system and the prevailing environment. Exploitation of

the top predator in a community would have a major impact

on the development of that community. Community structures

that might be observed at a low level of exploitation

(Realized Capacity 1) or a high level of exploitation

(Realized Capacity 2) would be different. An increase in

nutrient input or other change in the developmental

environment would further alter the realized capacity and

result in different community performances.

COMMUNITY LEVEL PERFORMANCES:
            DEVELOPMENT···D
            STRUCTURE
                    PRESENT··Ⓢ
                    FUTURE···(Ⓢ)
            PERSISTENCE····P
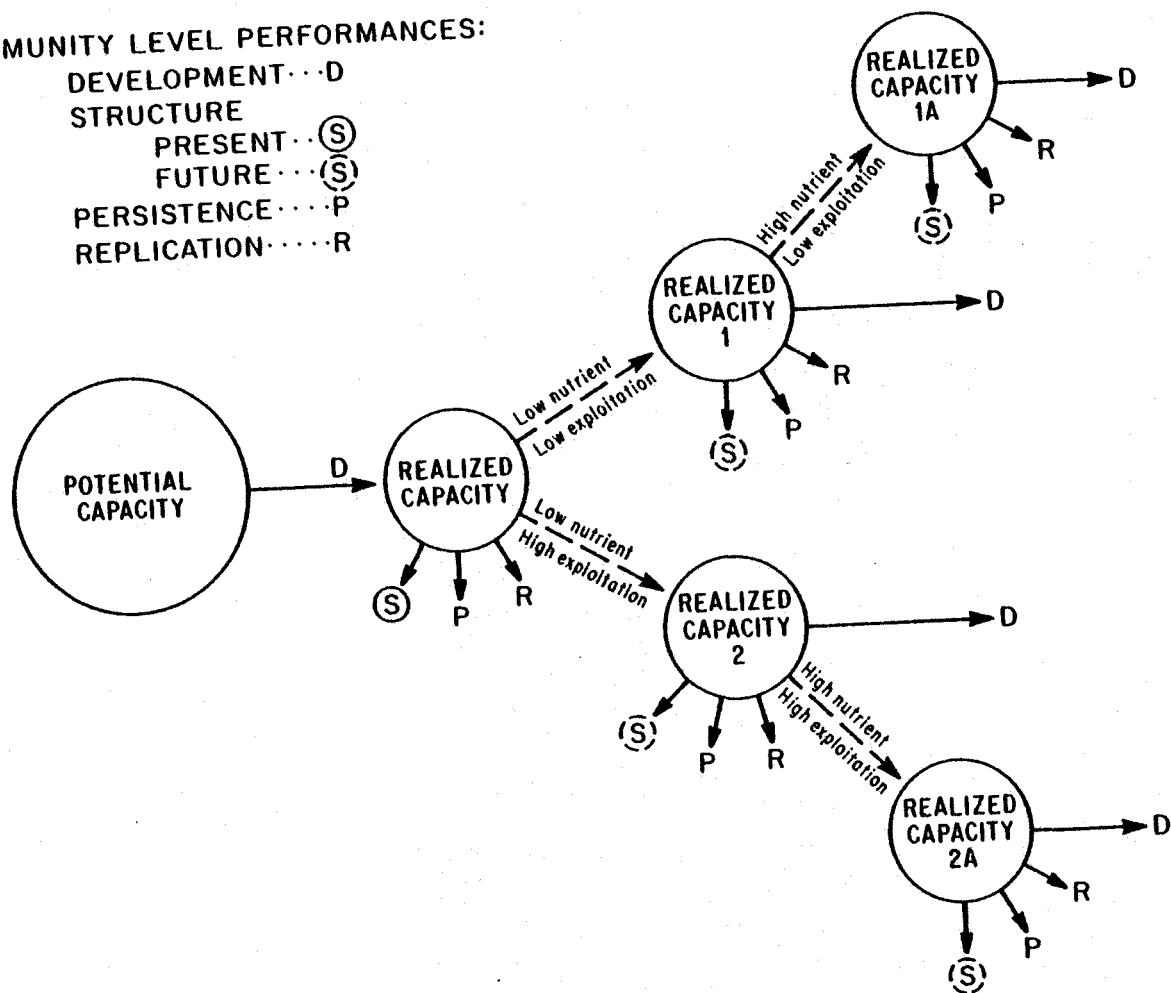   REPLICATION····R

Figure 3.

Performances of subsystems are, of course, useful in advancing understanding of communities. Operational, or "mechanistic", accounts of community level performances are based on conceptions of how the performances of lower level systems interact to produce them. But, in a very fundamental sense, a performance of a subsystem is a performance of the community as a whole, since the environment leading to a performance of that subsystem includes other subsystems and is largely incorporated by the community as a whole. The performance of a population is in this sense also a community level performance. To think otherwise is to uncouple the population from the community and to fail to account adequately for performance of the population.

To understand in greater detail the interactions between the populations of organisms within the subsystems and their relationships to community structure, one can define a simple hypothetical community as a sequence of predator-prey interactions:

$$E \longrightarrow C \rightleftharpoons H \rightleftharpoons P \rightleftharpoons R \longleftarrow I$$

Such a community is composed of a carnivore population, C, a herbivore population, H, a plant population, P, and the plant resource, R. E, the level of fishing effort (i.e., exploitation rate), and I, rate of plant resource input, form the environment of the community. Population interactions and the steady-state structure of this community can be represented by interrelated systems of isoclines and phase planes (Booty 1975; Liss 1977). Representative phase planes

are shown in Figure 4. Because phase plane analysis of population
interrelations will be employed in this thesis, I will briefly outline
their interpretation.

On each phase plane, the resource or prey is plotted on the
x-axis and the utilizer or predator is plotted on the y-axis. The
descending curves on each phase plane are resource isoclines. Each
resource isocline is a set of utilizer and resource levels or densities
at which the rate of change of resource level or density with time is
zero (dR/dt = 0 on the P-R phase plane, dP/dt = 0 on the H-P phase
plane, and dH/dt = 0 on the C-H phase plane). The ascending curves
on each phase plane are utilizer isoclines. Each of the utilizer
isoclines is a set of levels or densities of utilizer and resource at
which the rate of change of the utilizer level or density with time is
zero (dP/dt = 0 on the P-R phase plane, dH/dt = 0 on the H-P phase
plane, and dC/dt = 0 on the C-H phase plane). Any intersection of a
utilizer and resource isocline is a possible steady-state point, or
equilibrium point, where both utilizer and resource do not change with
time. The resource isoclines are all identified by plant resource
input rate. The utilizer isoclines on the P-R phase plane are
identified by herbivore density, on the H-P phase plane by carnivore
density, and on the C-H phase plane by level of fishing effort.

The positions and forms of the isoclines on the phase planes
have been graphically deduced from response functions that represent
population recruitment, production, loss to predation or exploitation,

Figure 4.   Phase planes and isocline systems representing the

interrelationships between populations in a predation

system. Predator biomass is plotted on the y-axis of

each phase plane and prey biomass is plotted on the

x-axis. On each phase plane, the descending lines

identified by different rates of plant resource input, I,

are prey isoclines. The ascending lines on the phase

planes are predator isoclines. 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. At a particular level of I and E, a single

steady-state point exists on each phase plane, the set of

these points defining the steady-state biomasses of C, H,

P, and R. The points that define the steady-state

biomasses of C, H, P, and R at Med I and 0 E (open circles),

30 E (squares), 90 E (triangles), and 150 E (closed circles)

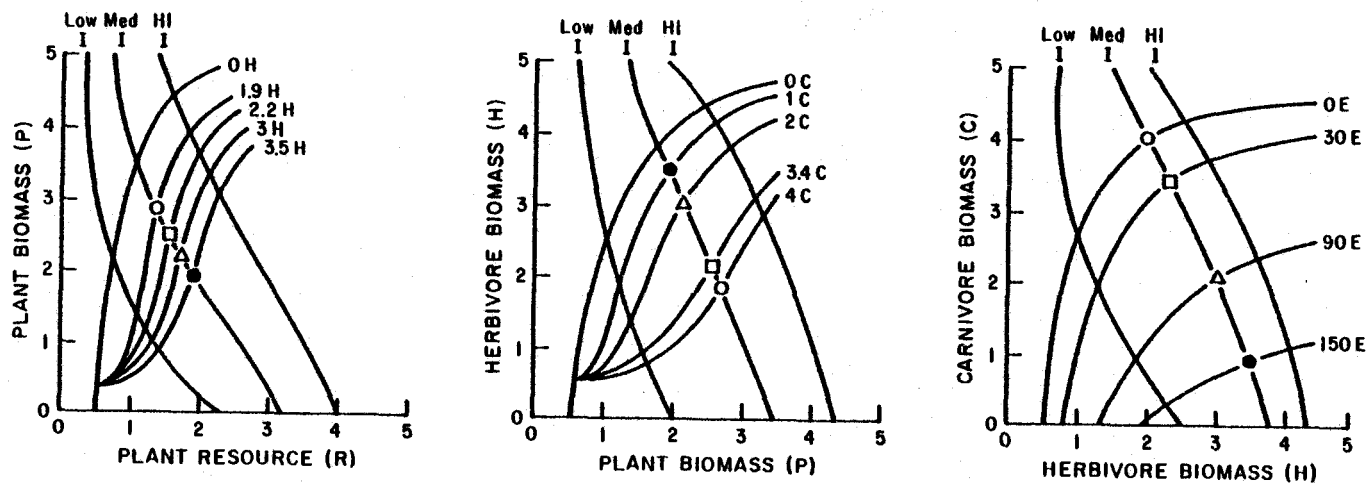are shown. Taken from Liss and Warren (in preparation).

Figure 4.

and nonpredatory losses. The forms of the response functions are based upon theoretical and empirical knowledge. Detailed discussions of the method of derivations of these isocline systems are given elsewhere (Booty 1975; Liss 1977; Warren and Liss 1977).

For each combination of values of environmental factors I and E, a single steady-state point exists on each phase plane. This set of steady-state points defines steady-state densities of C, H, P, and R, that is, the steady-state structure of the community. For example, the points that define the steady-state biomasses of C, H , P, and R at Med I and 0 E (open circles), 30 E (squares), 90 E (triangles), and 150 E (closed circles) are shown. This model represents communities as multi-steady-state systems.

RESULTS AND INTERPRETATION

Community Level Responses

The level of guppy exploitation had a direct effect on the
structure of the communities. Histograms of four representative
communities, one at each level of exploitation, illustrate the
differences observed in these systems (Figure 5). These histograms
represent mean community structures when amphipods and guppies
fluctuated near steady-state points. The most direct response to
exploitation was by the guppy population. The biomass of guppy
populations maintained in all sixteen communities decreased linearly
as the level of exploitation increased. The biomass of guppies in
System 3 at 0 percent exploitation was nearly eight times as large as
the biomass of guppies in System 1 at a 40 percent exploitation rate
(Figure 5). The system at 40 percent exploitation supported a much
larger biomass of amphipods than systems exploited at lower levels.
The amphipods were prey for the guppies and also competed with the
guppies for the alfalfa ration. The relationship between these
populations will be discussed in greater detail in a later section.

General trends in the responses of the nematode and protozoan
populations to exploitation of guppies are evident in the community
histograms. Nearly linear increases in nematode biomass occurred with
increased exploitation of guppies. The nematodes apparently served
as a source of prey for the guppies and thus responded positively to

Figure 5. Community structure in relation to exploitation. These

histograms represent community structure when amphipod

and guppy populations were near steady states. Mean

biomasses for the period of November 1977 through March

1978 were plotted for guppies(G), nematodes(N), protozoans

(P), rotifers(R), and amphipods(A). Prior to and during

this period, no environmental perturbation with the

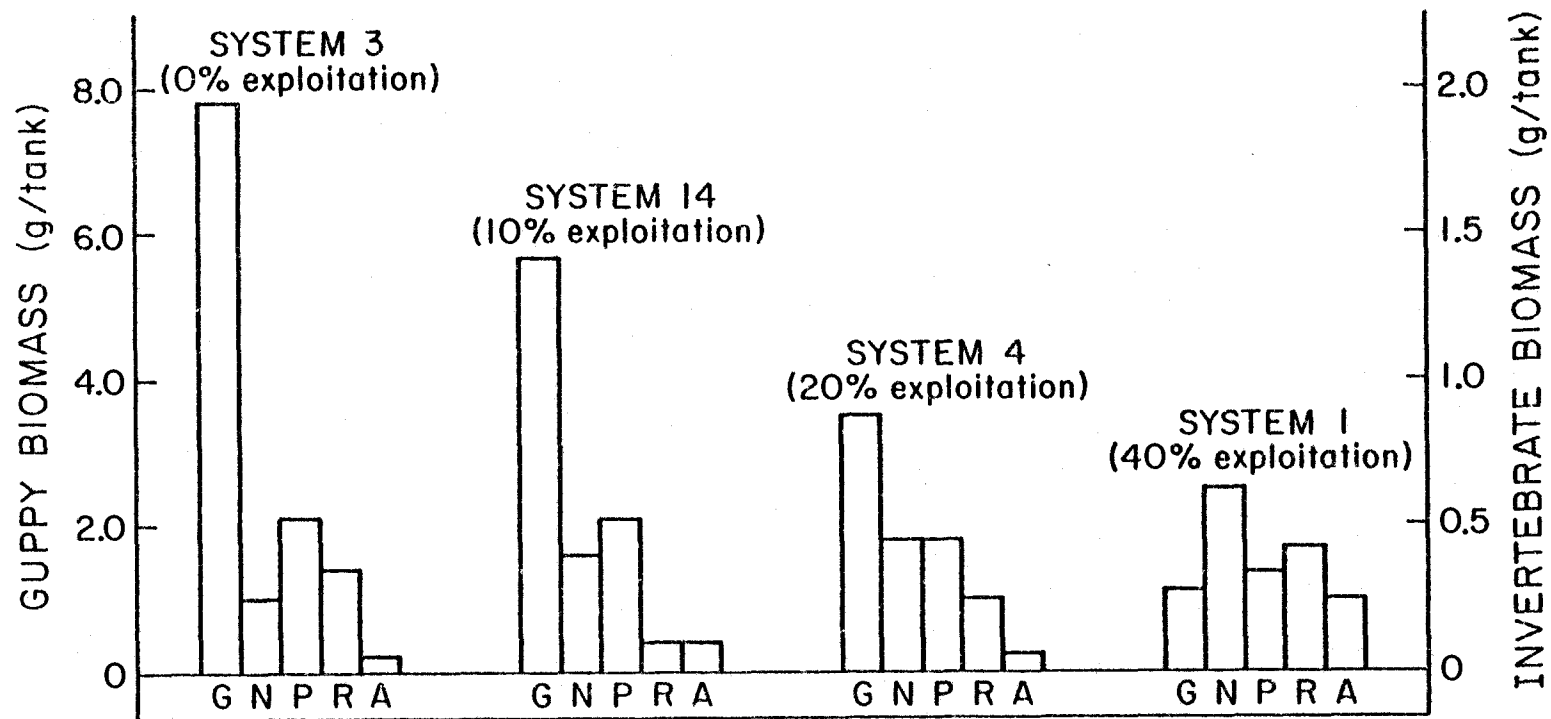exception of exploitation had been imposed on these

communities.

Figure 5.

increased guppy exploitation. Conversely, decreases in protozoan biomass were observed with increased guppy exploitation. The most apparent decreases were from 10 to 40 percent exploitation, with little difference occurring between the protozoan biomasses at 0 and 10 percent. This general decrease in protozoan biomass appears to have been an indirect effect of exploitation. The nematodes, which increased with exploitation on guppies, were apparently predators on the protozoans. Even though exploitation had no apparent effect on the species composition of the community, it obviously altered species abundances. The different forms of the four representative community histograms indicate the importance of exploitation in determining the structure of the communities.

In Figure 6, histograms of the same four communities, one at each exploitation rate, are shown before and after introduction of the toxicant, dieldrin. These histograms represent mean community structure when guppy and amphipod populations were at near steady states. The presence of dieldrin caused relatively little change in the basic forms of the communities. The direct negative impact of the toxicant was primarily on the populations of guppies. This tended to decrease predation on and competition with the amphipods. A decrease in guppy biomass coupled with an increase in amphipod biomass was thus observed at all levels of guppy exploitation. Previously discussed relationships between exploitation rate, guppy biomass, and amphipod biomass were not altered. No significant changes in the

Figure 6. Community structure at four different levels of guppy

exploitation before and after introduction of dieldrin.

Histograms for the pre-dieldrin period represent community

structure when amphipod and guppy populations were near

steady states (November 1977 through March 1978).

Histograms for the period when dieldrin was present

represent community structure when amphipod and guppy

populations were again near steady states (June 1978 through

January 1979), but over a less confined region in phase

space than before perturbation. Mean biomasses were

plotted for guppies(G), nematodes(N), protozoans(P),

rotifers(R), and amphipods(A).
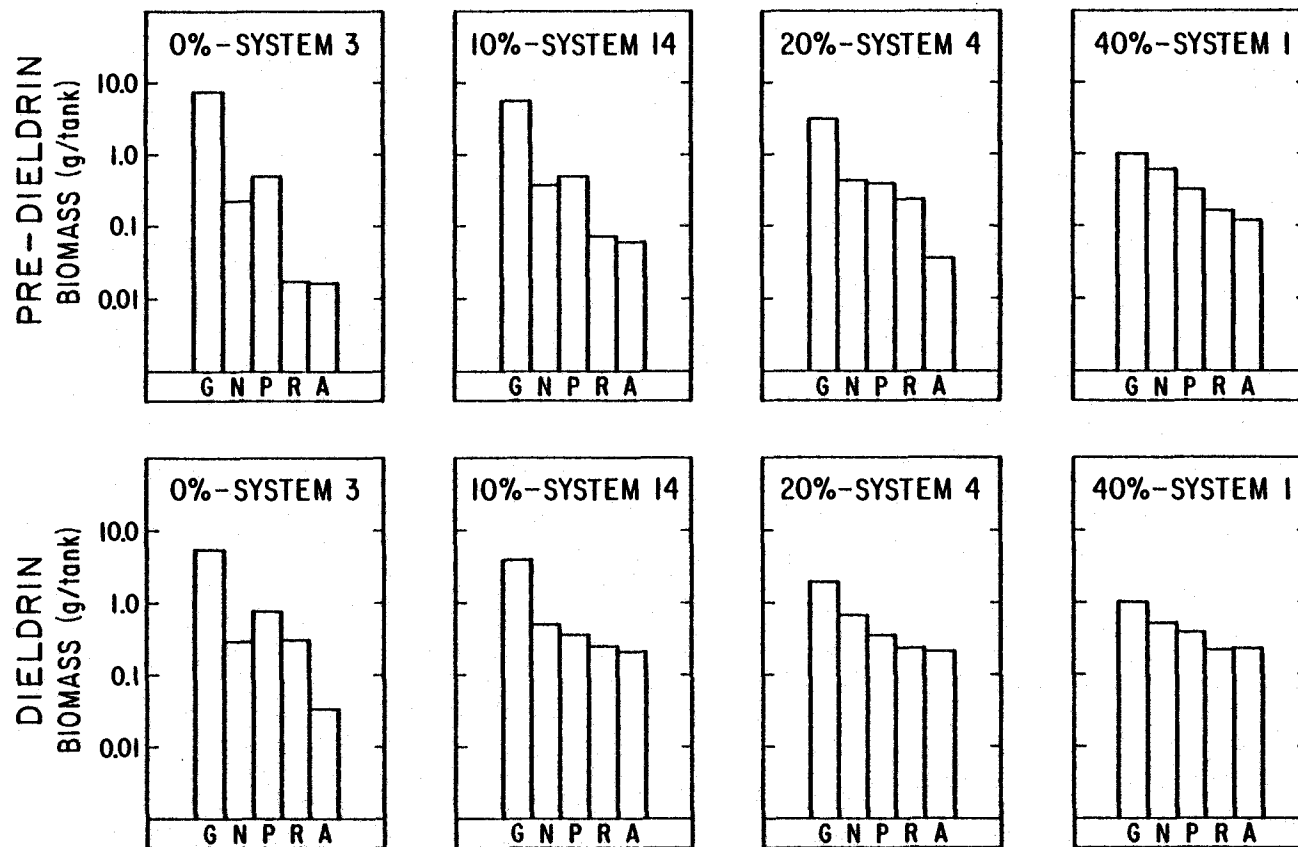
Figure 6.

biomasses of the microorganisms were apparent. With the exception of its relatively small direct effects on the biomasses of the guppy and indirect effects on the amphipod populations, dieldrin appears to have had little impact on community structure.

Contrastingly, structures of communities subjected to increases in habitat and nutrient availability were altered substantially. In these systems, the alfalfa ration was increased from 0.6 g/day to 4.0 g/day, and the rock substrate was increased to cover 95 percent of the tank bottoms. These alterations were initially intended to increase available food and cover for the invertebrate populations in order to increase their densities. However, the guppies also utilized the alfalfa ration. In Figure 7, a series of histograms from one community (System 15) illustrates the change in community structure with increased nutrient and habitat availability. Because both guppies and amphipods utilized the alfalfa as a nutrient source, an immediate increase in both populations occurred. This increase was observed in the seven other similarly treated communities (Appendix I). Decreases occurred in the biomasses of nematodes, protozoans, and rotifers in each of these eight communities. The additional alfalfa and the increased rock cover altered the character of the bottom sediments. Decreased water circulation, decreased light intensity to the sediments, and increased organic material caused anoxic conditions to develop in the sediments. This appears to have reduced habitat and nutrient materials available for the species of microinvertebrates

Figure 7. Community structure in relation to increased habitat and

nutrient availability. This series of histograms represents

community structure in System 15 (40 percent exploitation)

between November 1977 and October 1978. Both habitat and

nutrient input were increased in April 1978*. Monthly

biomasses are plotted for guppies(G), nematodes(N),

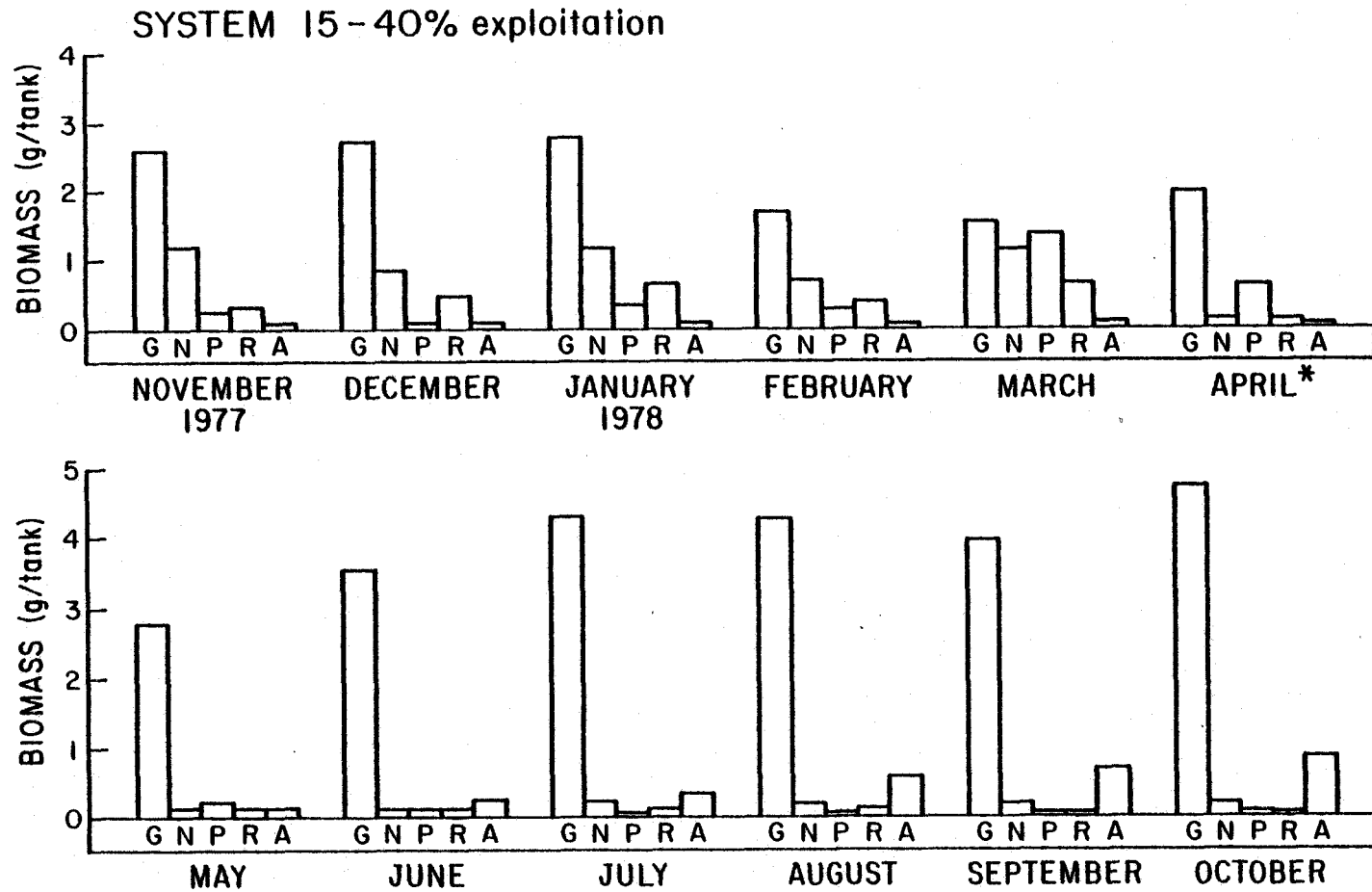protozoans(P), rotifers(R), and amphipods(A).

SYSTEM 15-40% exploitation

Figure 7.

previously most abundant. Table 2 shows the decreases in total

biomasses of microinvertebrates that occurred after changes in

substrate and organic input in these eight systems.

The response of the community to the increased habitat and

nutrient availability was thus a marked change in community structure.

This environmental perturbation decreased abundances of nematodes,

protozoans, and rotifers in the community. Continued development of

these systems eventually led to other species of microinvertebrates

becoming dominant.

Table 2. Total microinvertebrate mean biomasses 5 months before and 10
months after increase in habitat and nutrient availability.

SYSTEM NUMBER	Mean biomass before increase g/tank	Mean biomass after increase g/tank
2	1.40	0.36
8	1.33	0.36
9	1.77	0.57
10	1.54	0.58
11	1.24	0.33
13	1.66	0.42
15	2.07	0.40
16	1.23	0.21

Community Subsystems

A biological community can be viewed as an organization of hierarchically ordered subsystems. These subsystems and their level-specific environments may be incorporated and concordant one with another within the community. Earlier, community organization was taken to entail incorporation and concordance of community subsystems and their environments. This concept of community organization encompasses not only the performances of these subsystems but also their capacities. Because the environment leading to the performance of any subsystem includes all other subsystems incorporated in that community, the performance of any subsystem is in a very important sense determined by the community as a whole. If much understanding is to be achieved in the interpretation of the responses of systems of populations, emphasis must be placed on the community and the external environmental factors (I and E) that influence these responses.

Most natural communities can be viewed as having several major subsystems corresponding to major community subhabitats. Each major community subsystem may include several systems of populations that may, in turn, incorporate several to many populations. The sixteen aquatic microcosms in this study are perhaps best understood as having only one major habitat type, a benthic one, within which all populations were more or less closely associated. In this view, most of what follows directly treats the responses of and interactions within systems of populations including two or more populations.

Total biomass of all populations of microinvertebrates exhibited no response to exploitation on guppy populations. The four communities in Figure 8 supported similar biomasses of microinvertebrates, even though each of these four systems (1, 3, 4, and 14) was maintained at different levels of guppy exploitation. The synchrony of microinvertebrate biomasses in these four systems was unexplained, but it was not the result of the cyclic behavior of a single dominant microorganism. The relative abundances of individual microorganism populations varied within and between communities. The cyclic pattern of behavior of total microinvertebrate biomass appears not to have been altered by the introduction of dieldrin in April 1978. As noted earlier, microinvertebrate biomasses of the eight communities in which rock substrate and organic input were increased declined dramatically (Table 2). This appears to have been by alteration in bottom sediments and reduction of habitat and nutrient resources available to the microinvertebrate species being monitored.

Explanations of the responses and interactions of systems of two or more populations are important in that they provide an operational account of responses observed at higher levels of organization. One method for the interpretation of population system performances is isocline analysis. Phase plane representations of coordinate values of population biomasses were used in this study to represent population system responses. If the phase-space trajectories of coordinate population values were confined to a very limited region

Figure 8. Total microinvertebrate biomass for systems 1, 3, 4, and

14 from November 1977 through February 1979. A* represents

the time at which the dieldrin was introduced into each of

these four systems (April 1978).
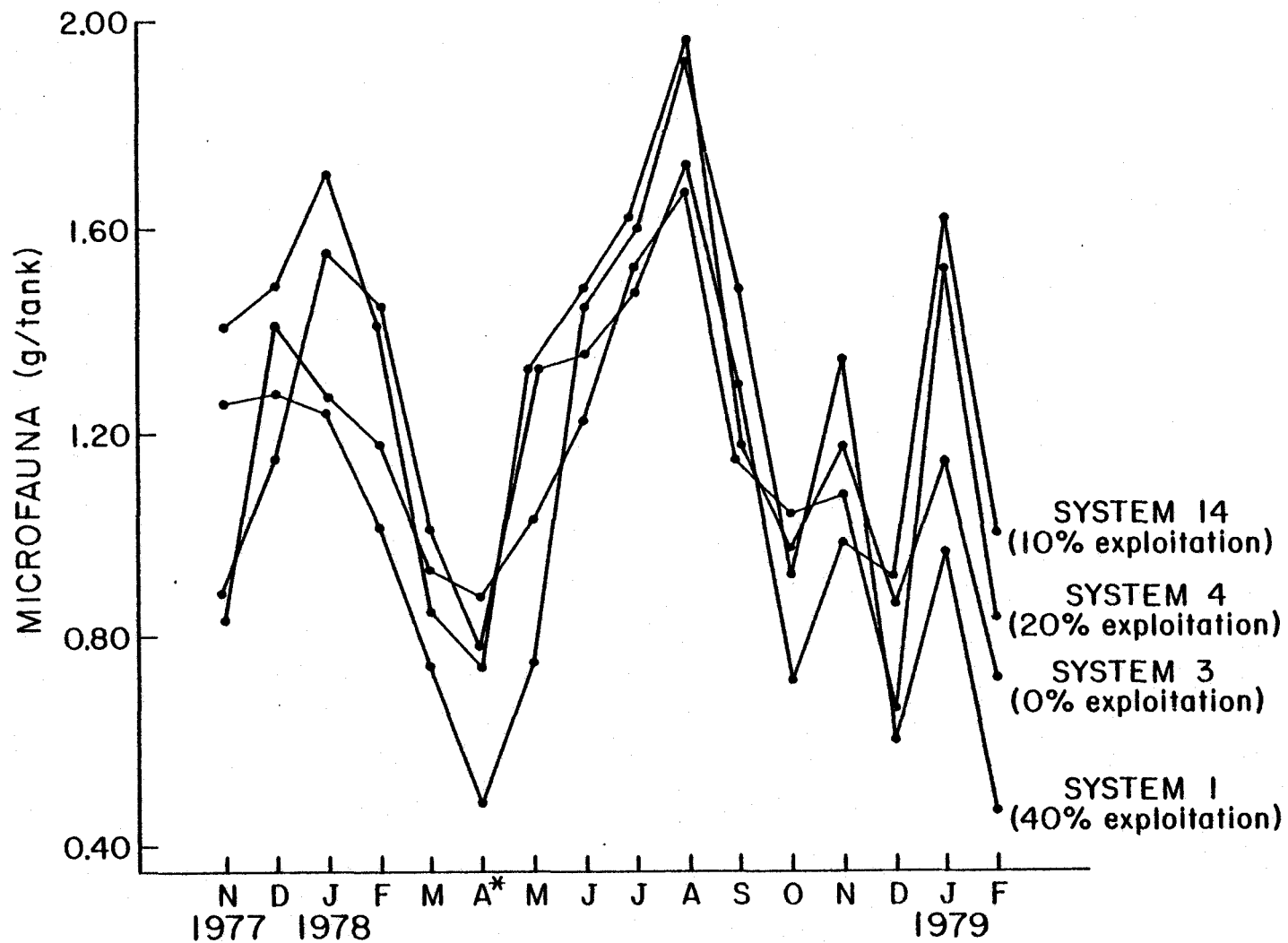
Figure 8.

of a phase plane over a relatively long period of time, the populations were assumed to be moving near to a steady-state point. The expression "near steady state" will be used here to refer to movement into a limited area in phase space within which repeated overlap of trajectories of population biomasses occurred. For example, the population biomasses of guppies and amphipods moved from an area in phase space occupied at the moment of introduction of the guppies to a different area in phase space determined, in part, by rate of exploitation of the guppy population. Movement to another near steady-state domain occurred after perturbation with the toxicant. Such factors as monthly differences in actual rate of exploitation in contrast to mean calculated rate of guppy exploitation as well as other factors influence the fluctuations of population biomasses that occur within the limited domain in phase space.

Because of the direct removal of individual guppies from the communities, the guppy population displayed the most direct response to exploitation. The communities maintained approximately 1 to 2 g of guppies at 40 percent exploitation, 3 to 5 g at 20 percent exploitation, 5 to 7 g at 10 percent exploitation, and 7 to 9 g at 0 percent exploitation before dieldrin introduction or increase in nutrient and habitat availability. The phase plane representation for four communities (Systems 1, 3, 4, and 14) in Figure 9 illustrates the distinct differences in near steady-state guppy biomasses that resulted from exploitation. Such discrete differences were apparent in all

Figure 9. Phase plane representation of the near steady-state

behavior of guppy and amphipod populations at four levels

of guppy exploitation. Each point represents the biomasses

of the guppy and amphipod populations for one month. The

direction of the trajectory is indicated by an arrow

following the first point. Points are plotted for the time

during which these systems were near steady states, prior

to the introduction of dieldrin or increased nutrient and

habitat availability.
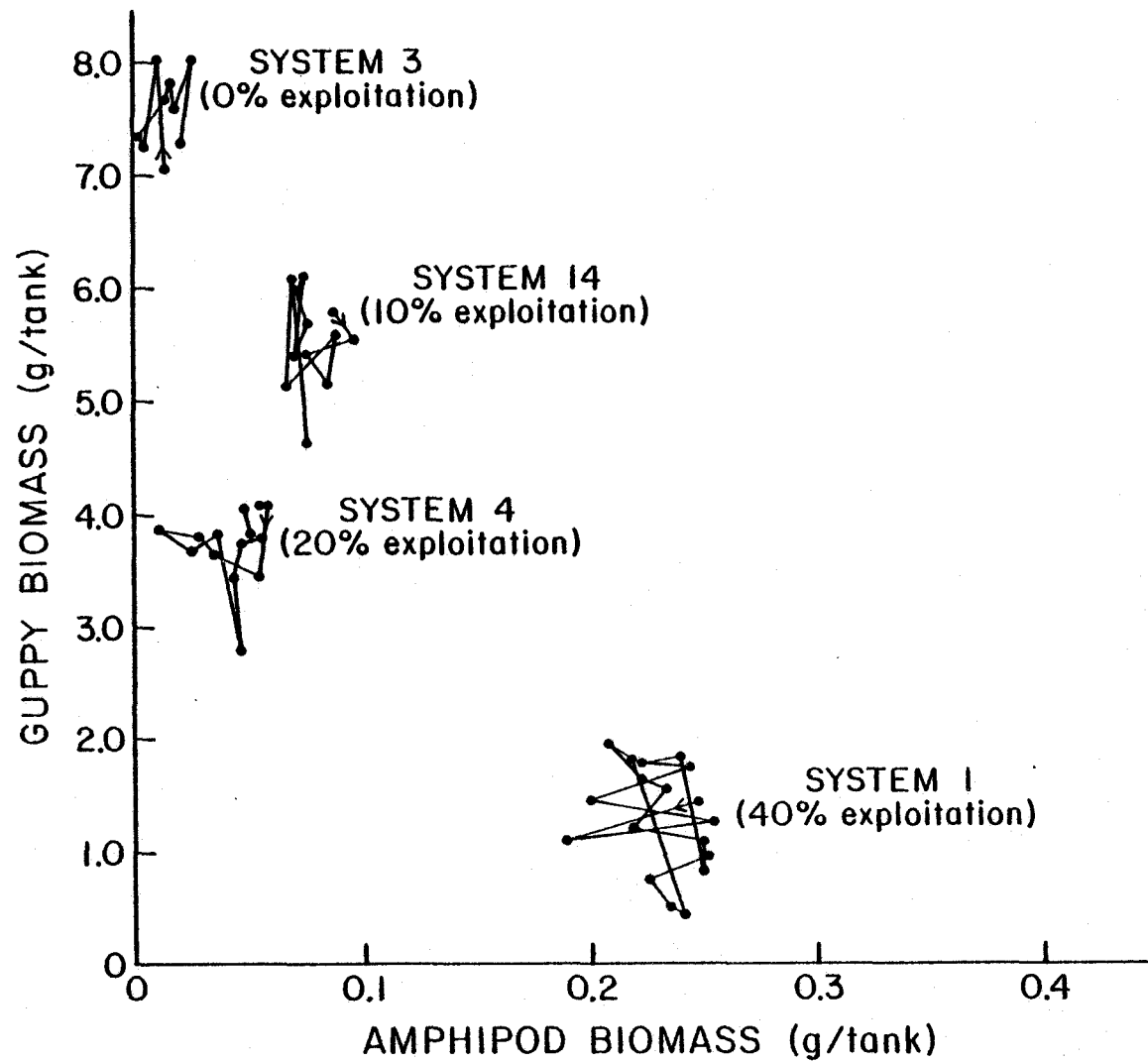
Figure 9.

the communities.

This phase plane (Figure 9) also shows a relationship between guppy and amphipod populations at different levels of exploitation. These four systems exhibited the clearest examples of near steady-state behavior of the guppy and amphipod populations. But, in all communities, a general increase in amphipod biomasses resulted from decreases in guppy biomasses. The relationship between guppy and amphipod populations was not simply one of predator and prey. Because the amphipods served as a prey for the guppies, the initial high densities of the amphipod populations were decreased dramatically in all sixteen systems following the introduction of the guppies (Table 3). After this decrease, amphipod biomasses remained extremely low (<0.3 g). This was too low for the amphipod to be a principal food source for the guppy. The major source of nutrient for both the guppy and amphipod populations was the alfalfa ration. Thus, the amphipod not only was preyed upon by the guppy but was also forced to compete with the guppy for the alfalfa. Predation and competition together were largely responsible for the low levels of amphipods observed in the communities.

Although amphipods were not a major food source for the guppies, the interrelationships between the two populations appear to have been important in maintaining community structure. The guppy and the alfalfa nutrient source were major girders interrelating the populations within the community. The alfalfa was utilized either

Table 3. Numerical densities of amphipod populations
before and after the introduction of guppies.

SYSTEM NUMBER	Amphipod density before guppy introduction	Amphipod density 1 month after guppy introduction	Amphipod density 3 months after guppy introduction
1	1112	307	158
2	740	298	115
3	575	215	60
4	3545	715	96
5	1107	374	290
6	735	360	56
7	875	615	205
8	575	195	120
9	500	180	101
10	2400	945	395
11	1305	333	96
12	2454	738	126
13	1995	575	72
14	930	385	90
15	650	200	115
16	655	235	78

directly or indirectly by every member of the community. The guppy,

a generalist species, consumed the alfalfa as well as amphipods,

nematodes, and other microinvertebrates. The nematode was the largest

member of the microinvertebrate subsystem. This probably made it a

more detectable prey organism for the guppy than were the smaller

microinvertebrates. Nematodes were substantially more abundant than

the amphipod in all sixteen microcosms. Biomass of nematodes

exhibited a general increase as guppy biomass decreased with

exploitation. Because both amphipods and nematodes served as prey

for the guppy population, their total monthly biomass was plotted

against guppy biomass on the phase plane in Figure 10. The communities

in Systems 1, 3, 4, and 14 were chosen for this phase plane because

of the near steady-state behavior of guppy and amphipod populations

that they exhibited (Figure 9). Unfortunately, because

microinvertebrate sampling was not begun until November 1977, only

five months of data on the nematode were available before these four

systems were perturbed with dieldrin. Nevertheless, trajectories

of the summed biomasses of amphipods and nematodes in relation to

guppy biomass during this brief period are very interesting in

relation to trajectories on the guppy-amphipod phase plane in Figure 9.

Nematodes increased the near steady-state biomasses of prey in each

system on the phase plane representation. In Figure 9, the amphipods

in System 4 (20 percent exploitation) reached a near steady-state

biomass that was slightly less than what one might have anticipated

Figure 10. Phase plane representation of the near steady-state

behavior of guppy, amphipod, and nematode populations

at four levels of guppy exploitation. Each point

represents the biomass of the guppy and the combined

biomasses of the amphipod and nematode populations for

one month. The direction of the trajectory is indicated

by an arrow following the first point. Points are

plotted from November 1977 through March 1978, prior to

introduction of dieldrin or increased nutrient and

habitat availability.
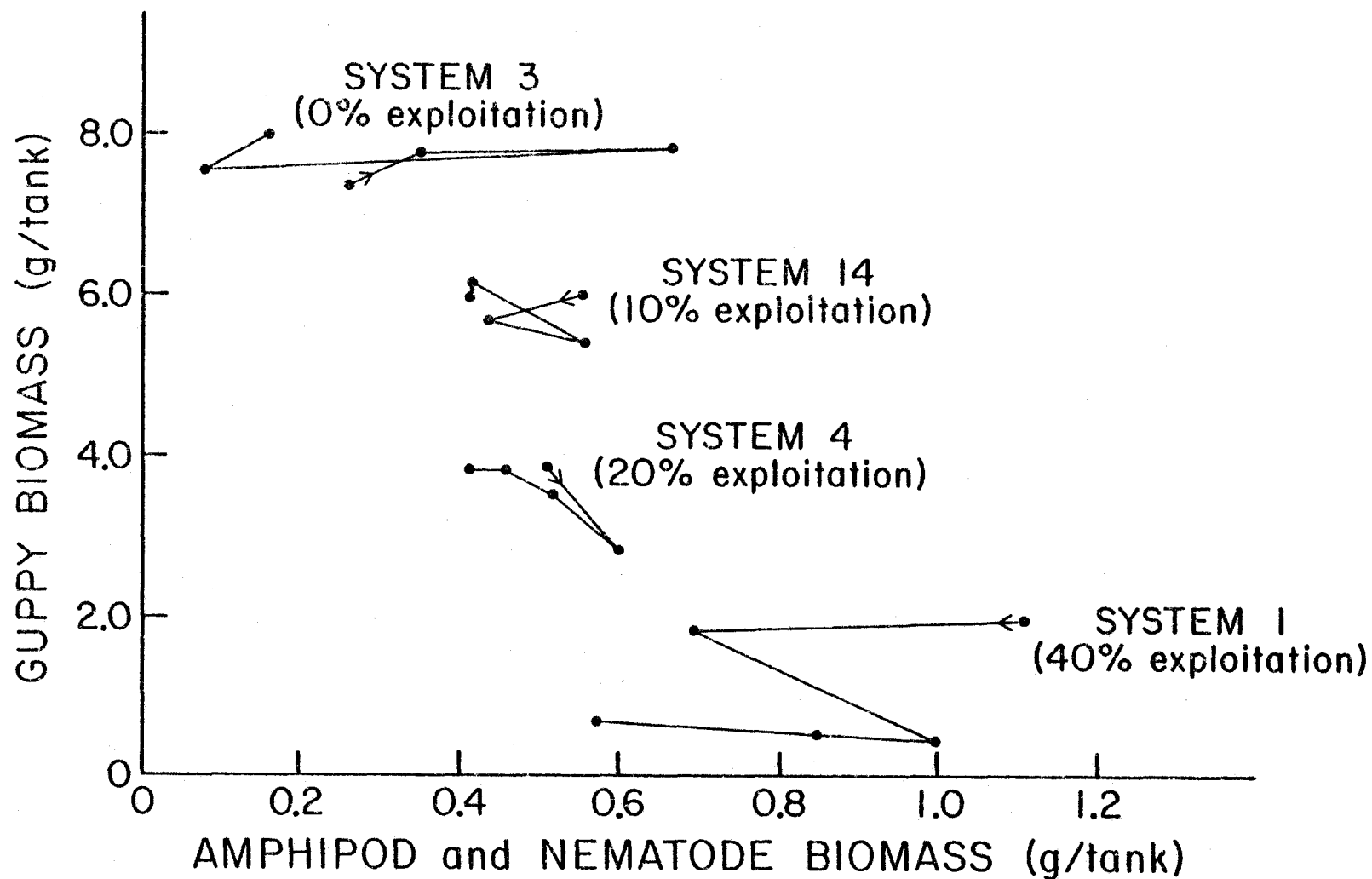
Figure 10.

considering the positions in phase space of the near steady states of the other systems (1, 3, and 14). The combination of amphipod and nematode biomass moved the near steady-state biomasses of System 4 to the right (Figure 10). On the guppy-nematode-amphipod phase plane, System 4 now appeared to be on the same prey isocline as Systems 1, 3, and 14. Undetected environmental differences may have allowed System 4 to support fewer amphipods and more nematodes at steady state than the other three systems.

The nematodes provided an important link between the guppies and the other microinvertebrates. The nematodes, which were prey for the guppies, were predators on other microinvertebrate populations. The protozoans appear to have been the major source of prey for the nematodes. The phase plane in Figure 11 illustrates a quite variable relationship between the nematode and protozoan populations. Even though much overlap occurred between regions occupied in phase space, a general increase in protozoan biomass and decrease in nematode biomass occurred with increase in exploitation on the guppies. Decreases in predation intensity on nematodes caused by increases in exploitation on the guppies apparently resulted in increased nematode abundance. Increase in nematode populations appears to have reduced protozoan populations. The roles of the rotifers, gastrotrichs, and flagellates in these communities remained undetermined.

Although the amphipod and nematode were not the most important nutrient sources available to the guppy (alfalfa being most important),

Figure 11. Phase plane representation of the domains of behavior for

nematode and protozoan populations in System 1 (40 percent

guppy exploitation), System 4 (20 percent guppy

exploitation), System 14 (10 percent guppy exploitation),

and System 3 (0 percent guppy exploitation). The

outlined domains of behavior include the biomasses of

nematodes and protozoans prior to as well as during the

presence of dieldrin (November 1977 through January 1979)

because no response of the microinvertebrate populations

to dieldrin was apparent.
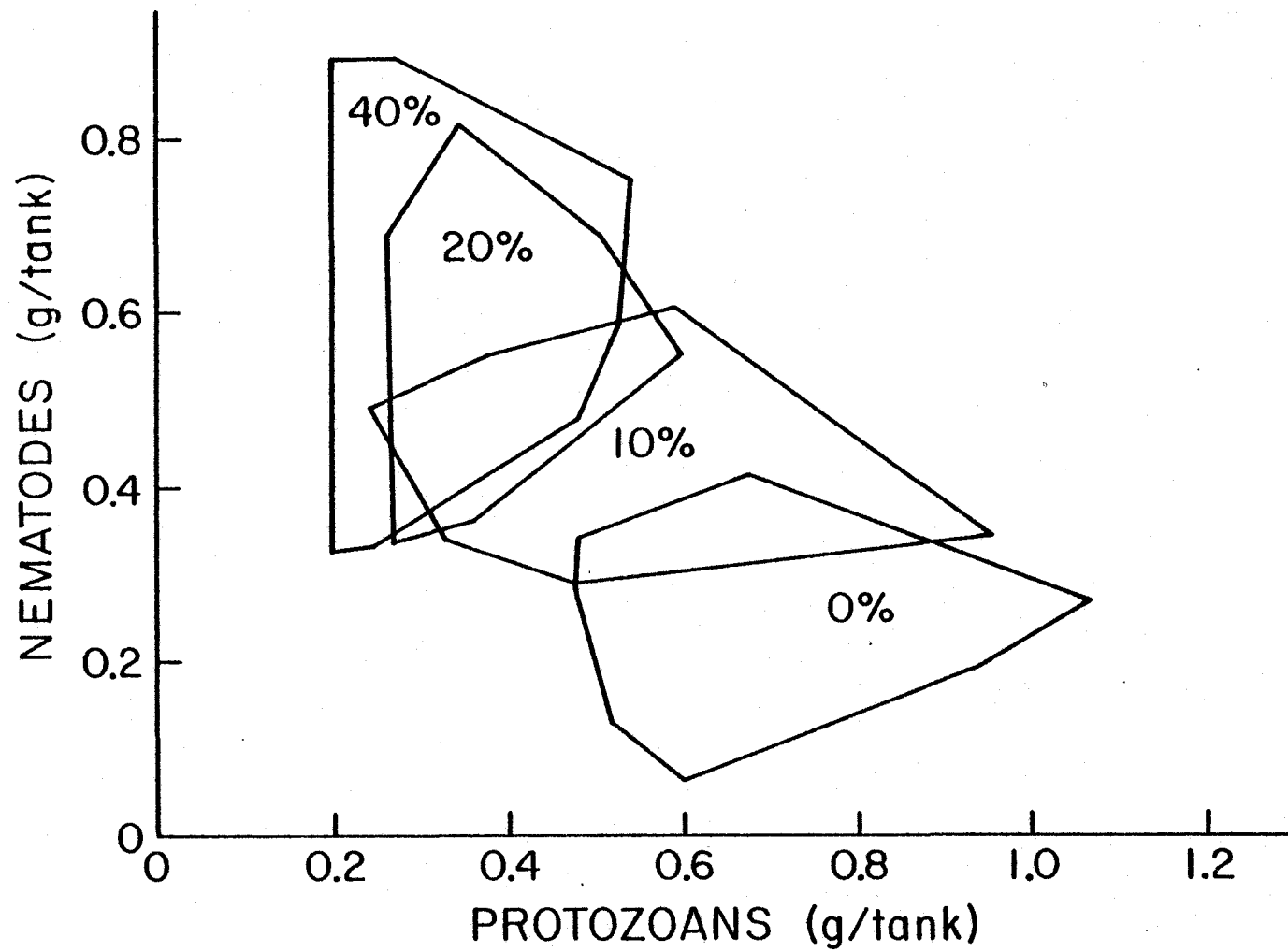
Figure 11.

the relationships illustrated on the guppy-amphipod and guppy-nematode-amphipod phase planes most clearly exemplified steady-state behavior of populations. One effect of a persistent and major perturbation of a system would be to shift the location of steady-state behavior of its populations in phase space. Such was the case with dieldrin. System 3 at 0 percent exploitation, System 14 at 10 percent exploitation, System 4 at 20 percent exploitation, and System 1 at 40 percent exploitation were perturbed with the toxicant dieldrin. The major direct effects of this toxicant appear to have been on the populations of guppies. However, as prey of the guppies, the amphipods were indirectly influenced. The guppy-amphipod and guppy-nematode-amphipod phase planes illustrate the immediate response of the populations to dieldrin (Figures 12 and 13). Dieldrin acts on the nervous system and possibly inhibited the predation efficiency of the guppy. With the exception of System 1 at 40 percent exploitation, a general decrease in guppy biomass was observed in every system. Subsequently, as the intensity of predation as well as competition decreased, amphipod biomass increased (Figure 12). The apparent lack of guppy response at 40 percent exploitation could be related to the condition of the fish. In System 1 at 40 percent, there was more food per individual fish than in the systems at lower levels of exploitation. The guppies at 40 percent exploitation were in better condition and showed no immediate response to the dieldrin. The remaining systems were perturbed away from their previous steady-state region or domain

Figure 12. Phase plane representation of the near steady-state

behavior of guppy and amphipod populations at four levels

of exploitation before and after the introduction of

dieldrin. Each point represents the biomasses of the

guppy and amphipod populations for one month. The

direction of the trajectory is indicated by an arrow

following the first point.
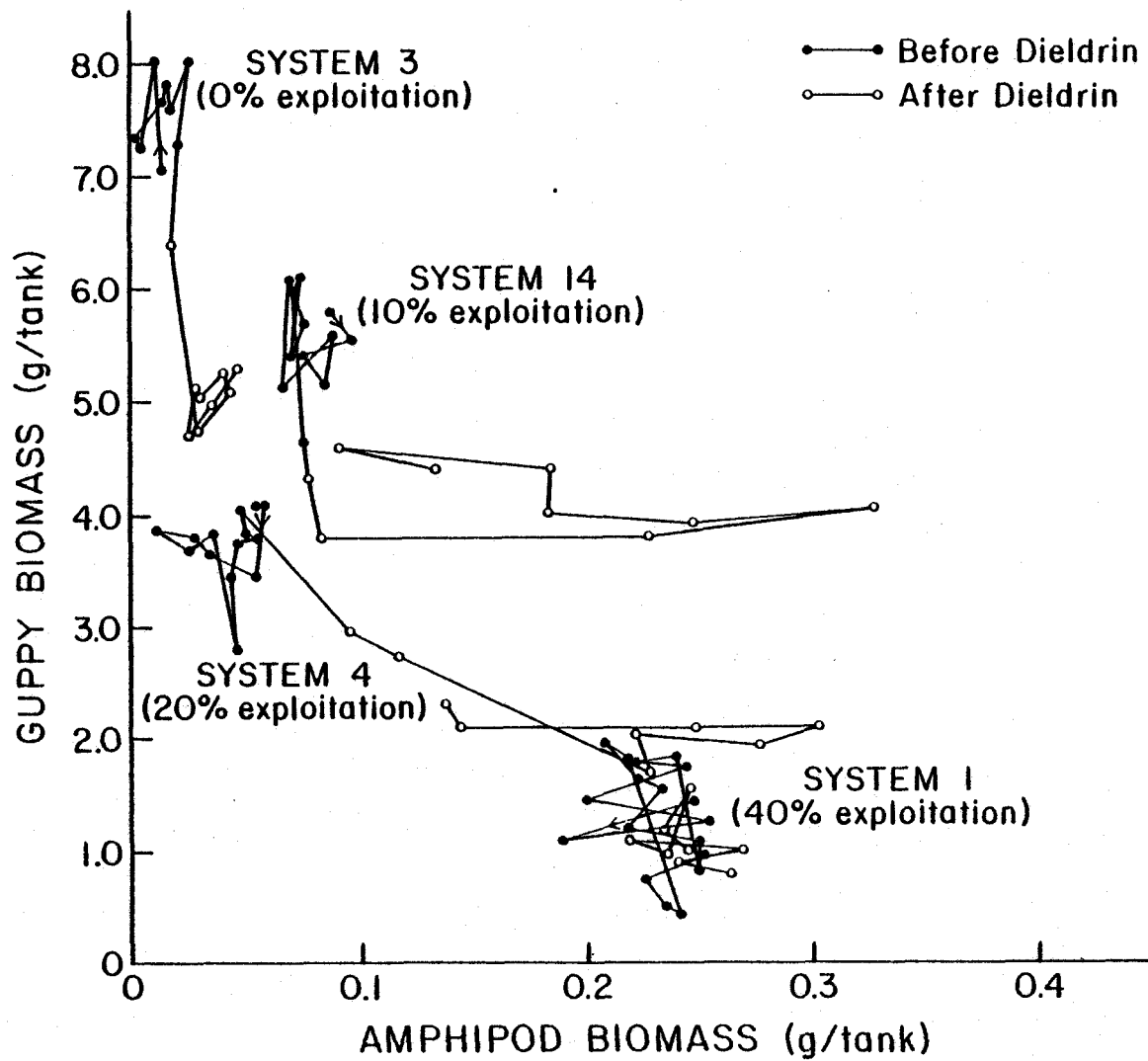
Figure 12.

Figure 13. Phase plane representation of the near steady-state

behavior of guppy, amphipod, and nematode populations

at four levels of guppy exploitation before and after

the introduction of dieldrin. Each point represents

the biomass of the guppy and the combined biomasses of

the amphipod and nematode populations for one month.
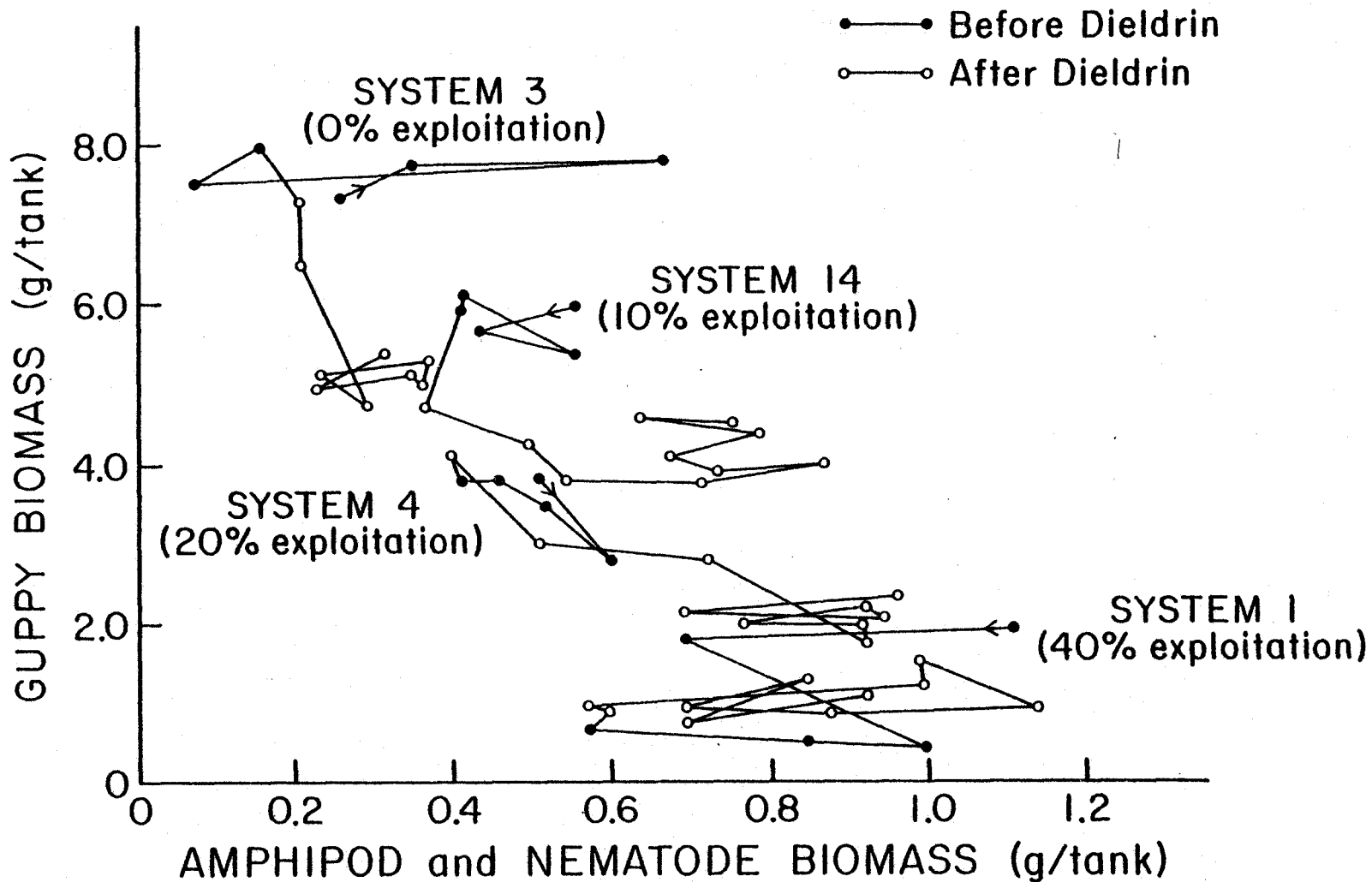
Figure 13.

of behavior toward some new domain. The guppy and amphipod populations in System 3 were the first to reach new steady-state biomasses (Figure 12). Although the nematodes appeared not to respond directly to the dieldrin, shifts in the domains of steady-state behavior after the perturbation were apparent on the guppy-nematode-amphipod phase plane (Figure 13).

The increase in rock substrate and organic input resulted in major perturbations in the eight systems altered. Figure 14 shows the response of two of these systems at 0 percent exploitation on a guppy-amphipod phase plane. Systems at 10 percent, 20 percent, and 40 percent exploitation responded in similar manners. The increased nutrient and habitat availability caused an immediate increase in guppy and amphipod biomass. The trajectories of both systems moved up and to the right in phase space. The paths of the similar trajectories suggest that these two systems had very similar realized capacities. By the end of this phase of the study, new steady-state biomasses had not been attained.

Figure 14. Phase plane representation of the response of guppy and

amphipod populations in two near steady-state systems to

an increase in nutrient and habitat availability. Prior

to perturbation, approximate steady states for 0 percent

guppy exploitation occurred from 7.0 to 9.0 g guppy

biomass and 0.01 to 0.05 g amphipod biomass for over a

year. Increased nutrient and habitat availability in

April 1978 caused trajectories to move up and to the

right in phase space. Each point represents the biomasses

of guppy and amphipod populations for one month. New

steady-state biomasses have not been reached.
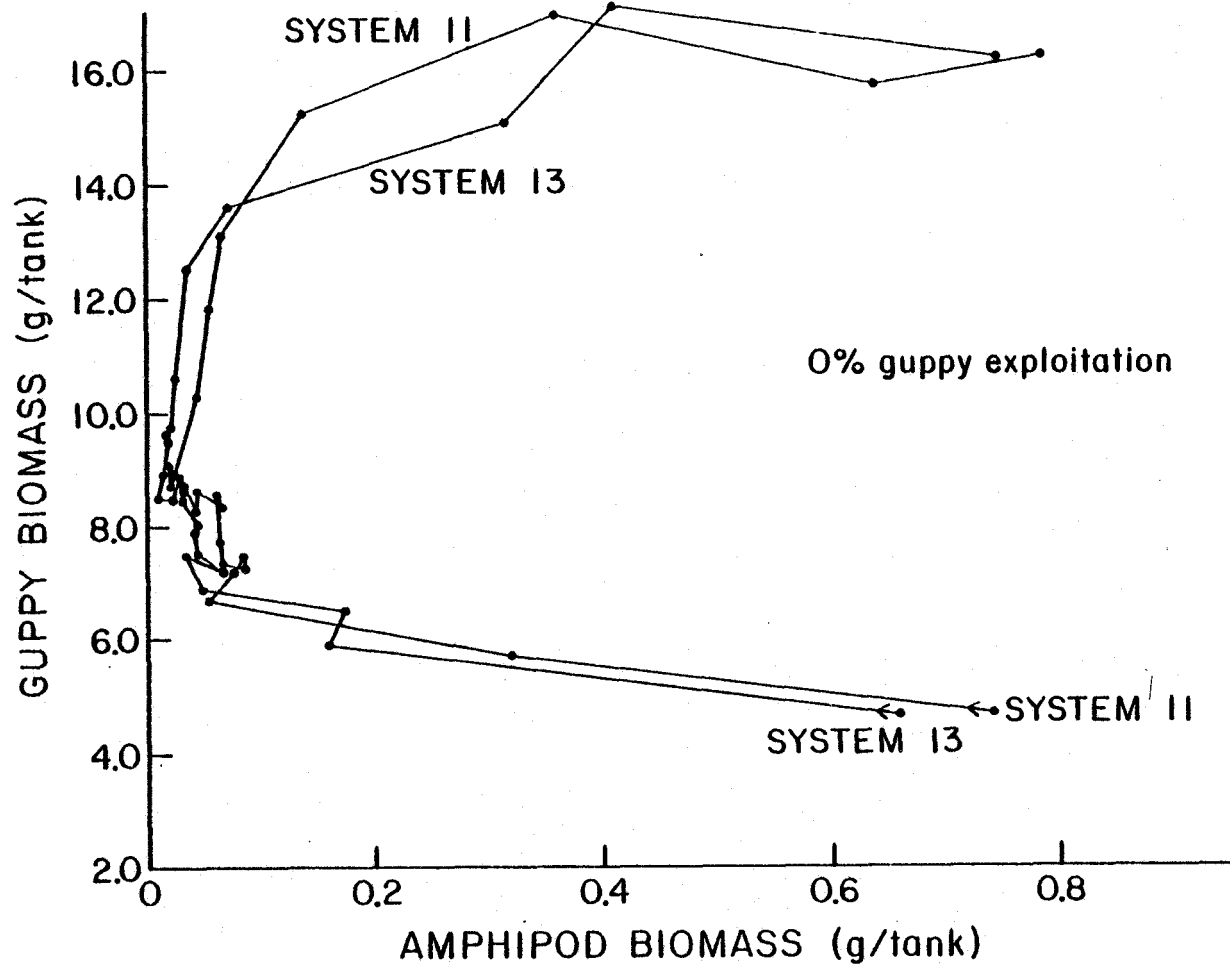
Figure 14.

DISCUSSION

Early in this thesis, in the section entitled Conceptual

Foundation, a conceptual framework for organismic systems and an

isocline theory for analysis of dynamic behavior of systems were

presented. This was done because of their importance in the design

of these microcosm experiments and in understanding the results. The

biological communities in the microcosms can be understood to be

different expressions, under different environmental conditions, of

some common potential capacity that resides in the species pool from

which the communities were colonized (Figure 3). The different

communities developing under treatments of low and high organic input,

low and high rock habitat availability, different exploitation rates

on guppies, and presence or absence of dieldrin developed somewhat

different structures and can be understood to have had somewhat

different realized capacities. Such capacities can only indirectly

and partially be represented by performances such as structure and

dynamic behavior of the communities and their component populations.

The potential capacity of these communities can be only

partially represented as the domains of phase space that might be

occupied by the communities under different environmental conditions.

At any point in this phase space, a community has a unique realized

capacity, which changes as the structure of the community changes with

movement in phase space. All of these realized capacities together

can be understood to be a partial representation of the common

potential capacity of all communities, each particular community

realizing only some part of the potential capacity of this class of

communities. The dynamic and near steady-state behavior as well as

the structure of these communities can to some extent be analyzed by

means of isocline theory. The system of isoclines shown earlier in

Figure 4 were deduced from systems of curves theoretically

representing population responses. Only in the most general way can

such theoretical understanding be applied in interpreting the phase

space behavior of these laboratory communities. In particular, the

theoretical derivations provide some notion of the forms of predator

and prey isoclines, of the identities that parameterize them, and of

their positions relative one to another. For given empirical results,

isocline locations in phase space can to some extent be inferred

from population behaviors taken to be near steady states. In

Systems 1, 3, 4, and 14, both before and after introduction of

dieldrin, near steady states were achieved. In Systems 2, 8, 9, 10,

11, 13, 15, and 16, after increase in organic input and rock habitat

availability, new steady states were not achieved, although something

of their probable locations can be inferred. In any case, as will be

shown, all the dynamic and near steady state behavior and all the

consequent structures partially map one aspect of the potential

capacity of these communities in phase space.

In Figure 15 A, the seven encircled areas on the guppy-nematode-amphipod phase plane represent near steady-state regions in phase space occupied by Systems 1, 3, 4, and 14 before and after the introduction of dieldrin. The near steady-state biomass of System 1 at 40 percent guppy exploitation exhibited no immediate response to the dieldrin and is thus shown to occupy the same region in phase space before and after the perturbation. The near steady-state biomasses of these four systems can be explained by a system of intersecting isoclines (Figure 15 B). The six ascending predator isoclines on the phase plane are parameterized by level of guppy exploitation and presence or absence of dieldrin. These six isoclines are shown to intersect a family of descending prey isoclines, which are parameterized by a low level of energy input. In this study, Low I would include a low level of organic input and a low level of rock habitat availability. Other identities also involved in determining the position of the prey isoclines are light level, temperature, other aspects of the physical and chemical environment, and other organisms such as snails that compete for the alfalfa nutrient material. Each intersection of a predator isocline with this prey isocline defines a possible steady-state point for the populations represented on the phase plane in 15 A. That the near steady-state regions for the different systems cannot be fitted by a single isocline could indicate the theoretical existence of a family of prey isoclines, each member of which could, for example, be parameterized

Figure 15 A.   General regions in phase space occupied by four systems

on a guppy-nematode-amphipod phase plane before and after

introduction of dieldrin. The shaded circles labeled

with "D" are the near steady-state biomasses of the

systems after the introduction of dieldrin. System 1

exhibited no immediate response to dieldrin and thus

occupies the same region in phase space before and after

the toxicant perturbation.

15 B.   An isocline representation of the probable effects of a

toxicant, T, on the possible steady-state biomasses of

carnivore, C, and a herbivore, H, under different levels

of competition for the herbivore, Cmp, (Adapted from

Warren and Liss 1977).
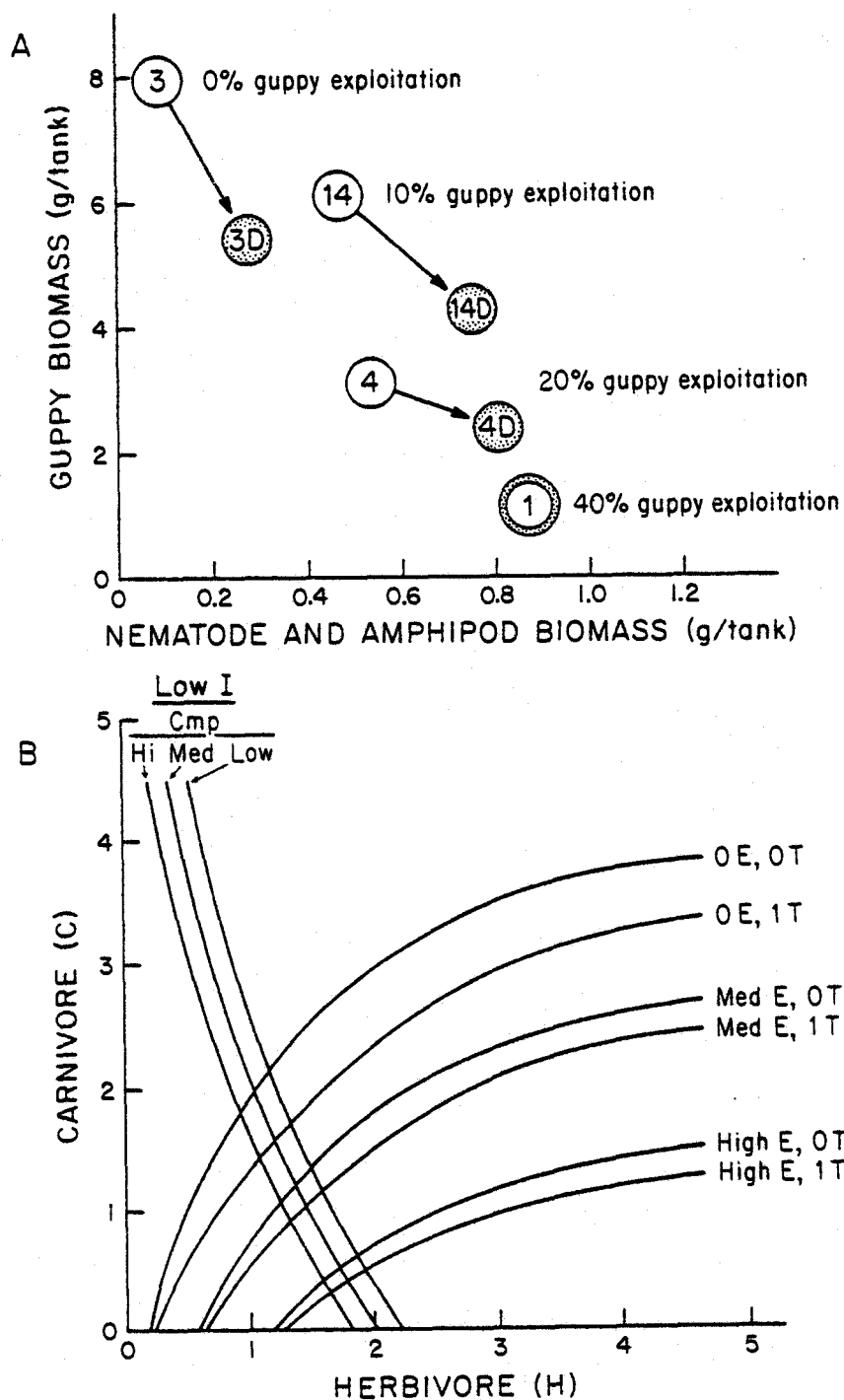
Figure 15.

by a different density of a competitor of the herbivore (i.e., snails). A high density of such a competitor would lower the steady-state biomasses for both the prey and the predator populations. A similar system of intersecting isoclines can be used to explain the responses of four systems (10, 13, 15, and 16) to an increase in nutrient and habitat availability (Figure 16). The encircled areas in Figure 16 A represent the general positions of the systems in phase space before and after this environmental alteration. A movement upward and to the right occurred, but the systems had not come to new steady states after the perturbation. The systems of isoclines shown in 16 B illustrate the theoretical existence of a new family of prey isoclines at High I. In this study, High I would include the increase in nutrient and habitat availability.

The near steady-state and dynamic behavior of these systems before and after dieldrin introduction suggest that dieldrin may not have substantially altered the position of the respective prey isoclines. The toxicant did apparently cause a reduction in the near steady-state biomasses of guppies at 0 percent, 10 percent, and 20 percent exploitation (Figure 15). This led to increases in near steady-state biomasses of amphipods and nematodes. These populations apparently responded to dieldrin only indirectly through changes in predation and competition. The total region in phase space occupied by Systems 1, 3, 4, and 14 after perturbation with the toxicant dieldrin is represented by the shaded area in Figure 17. The shaded

Figure 16 A. General regions in phase space occupied by four systems

on a guppy-nematode-amphipod phase plane before and

after the increase in nutrient and habitat availability.

The shaded circles are nonsteady-state biomasses of

the systems after perturbation. These indicate a

definite movement of the systems up and to the right

in phase space.

  16 B. An isocline representation of theoretically possible

steady states of a carnivore population, C, and a

herbivore population, H, at two levels of energy input

with different levels of carnivore exploitation and

different levels of competition for the herbivore

(Adapted from Liss 1977).
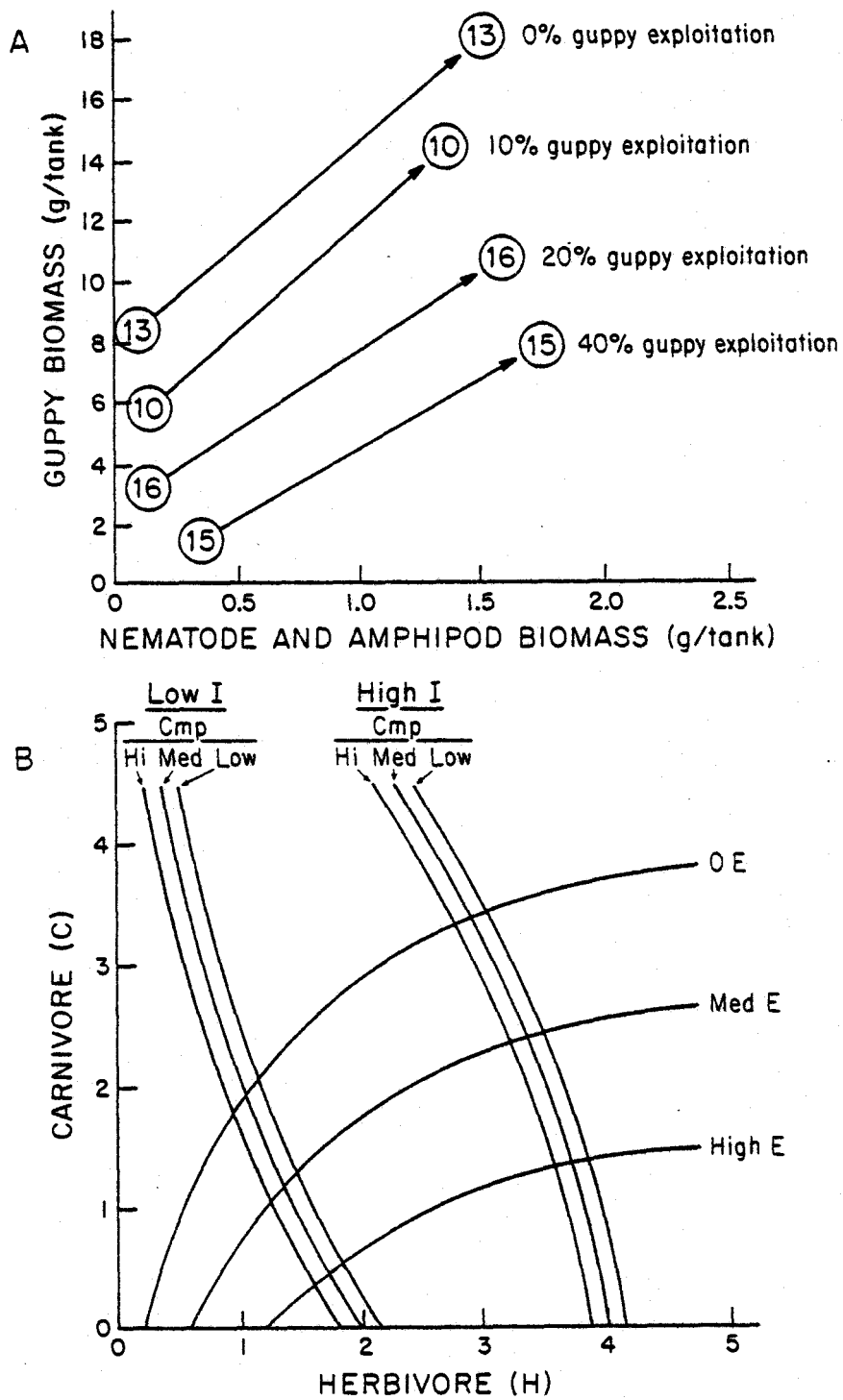
Figure 16.

Figure 17. Domains of behavior for the aquatic systems before the
introduction of dieldrin or increase in nutrient and
habitat availability (A), after the introduction of
dieldrin (shaded area), and after the increase in
nutrient and habitat availability (B).
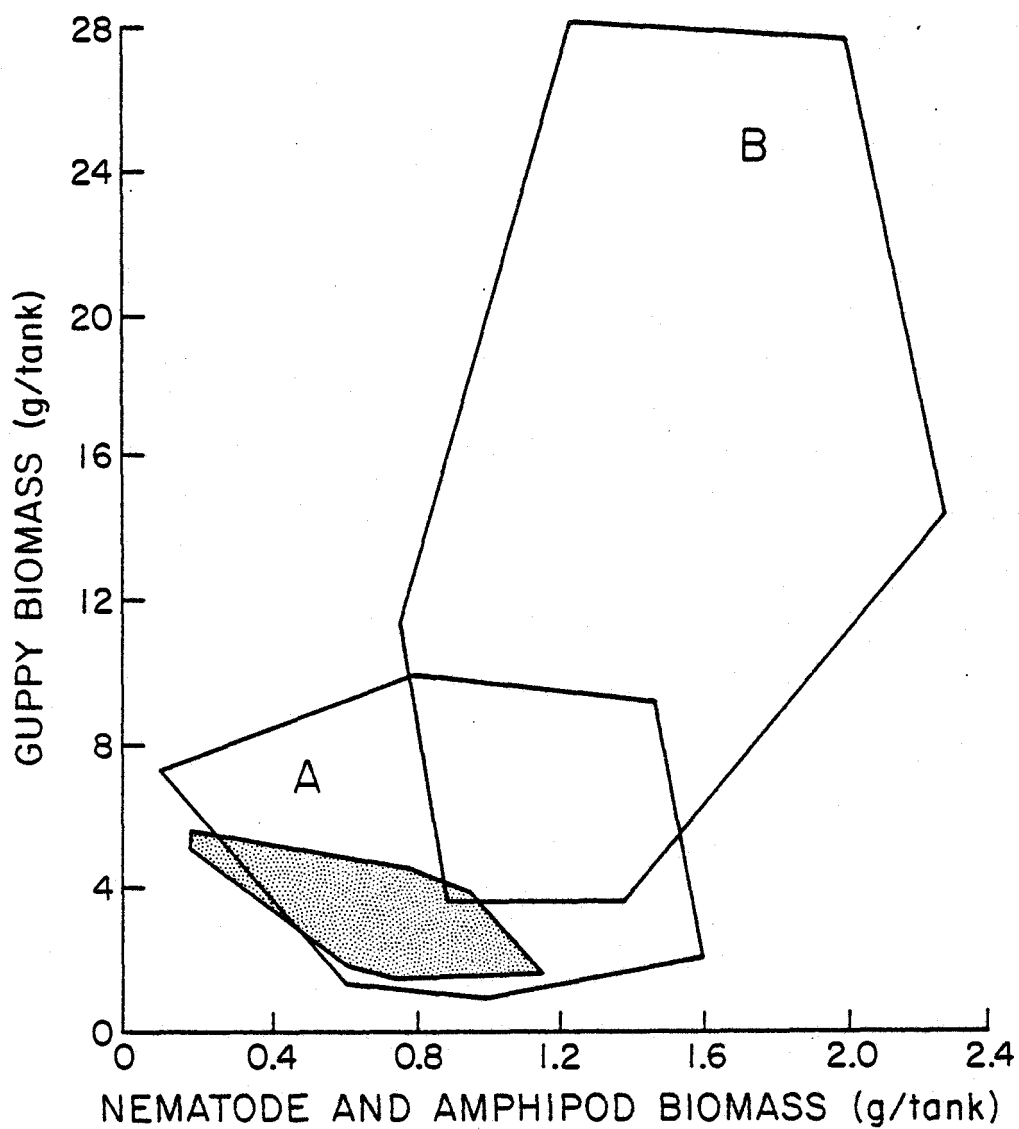
Figure 17.

area falls within a larger area, A, which encompasses the domain of behavior of all the microcosm communities prior to either introduction of dieldrin or increased nutrient and habitat availability.

Area B encompasses the nonsteady-state responses of the guppy, nematode, and amphipod populations to the increase in nutrient and habitat availability, through March 1980. Without steady-state behavior, the approximate locations of predator and prey isoclines cannot be located. Strictly speaking, with the habitat change, the predator isoclines would probably not be simple extentions of the ones theoretically existing before the changes. Steady-state behavior would occur upward and to the right of the region occupied by the area of A.

The domains of behavior for Systems 1, 3, 4, and 14 before and after the introduction of dieldrin are represented on a nematode-protozoan phase plane by the shaded area in Figure 18. There were no apparent direct effects of the dieldrin on these populations. This shaded area falls within a larger area, A, which encompasses the domain of behavior of all the remaining microcosm communities prior to any nutrient or habitat increase. Area B encompasses the domains of behavior for these systems after nutrient and habitat availability were increased. The dramatic decrease in nematodes and protozoans is clearly illustrated. A set of isoclines similar to those shown in Figures 15 B and 16 B could be used to explain population responses on a nematode-protozoan phase plane. Because the increased rock

Figure 18. Domains of behavior of the nematode-protozoan subsystem
before and after the introduction of dieldrin (shaded
area), before the increase in nutrient and habitat
availability (A), and after the increase in nutrient
and habitat availability (B).
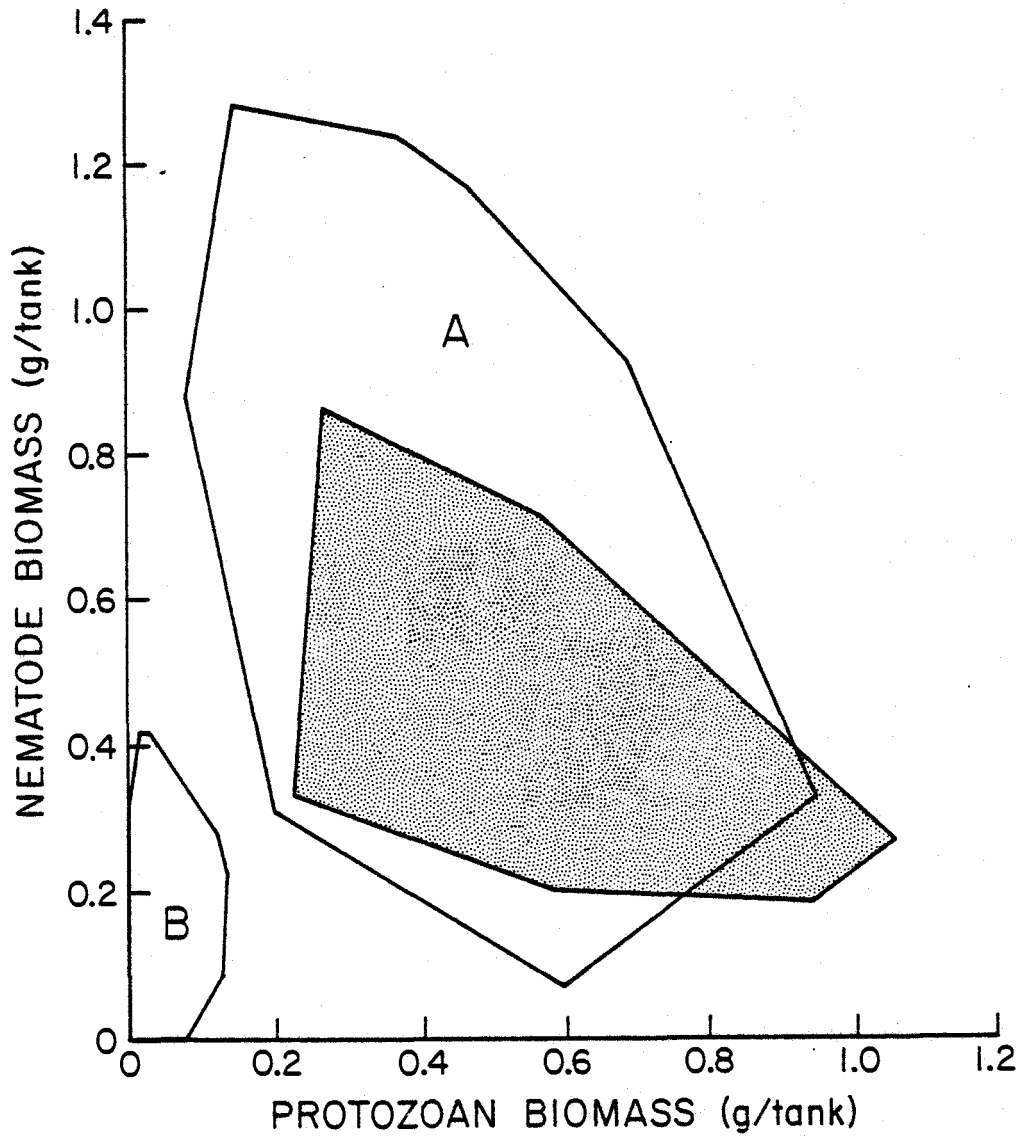
Figure 18.

cover and additional nutrient input caused oxygen depletion and thus

decreases in habitat availability for the nematode and protozoan

phase plane for High I would intersect the predator isoclines at a

lower level than those for Low I.

In both Figures 17 and 18, the combined areas of A and B can be

taken as representative of the demonstrated part of the potential

capacity of the microcosm communities. The combined areas encompass

observed performances of the communities with and without toxicant at

two levels of nutrient and habitat availability with different rates

of exploitation on the guppy. By examining areas A and B on these two

phase planes, one can visually assess the impact of the two

environmental perturbations. The increase in nutrient and habitat

appears to have had a dramatic effect on the community. In both

figures, Area B represents the domain of behavior occupied by the

populations after habitat and nutrient were increased, and in both

figures, this area is quite different from area A. Dramatic changes

occurred in the biomasses of every population on these phase planes.

Guppies and amphipods increased sharply. Nematodes and protozoans

along with other previously abundant species of microorganisms

decreased dramatically. This decrease in microinvertebrate biomass

that was occurring in January 1979 eventually led to a new group of

microinvertebrates becoming most abundant. The shaded area on Figures

17 and 18 represent the four systems into which dieldrin was

introduced. Addition of dieldrin did not much alter the domain of

behavior of these populations and had a minimal impact on the community as a whole. This study, however, involved the response to dieldrin for only 10 months and observed responses can be considered as immediate and short term effects. A longer term study (Woltering, in preparation) has revealed a return of System 3 at 0 percent exploitation to its near steady-state biomass prior to dieldrin introduction. In System 1, which was exploited at 40 percent, the guppy population eventually went extinct, this having substantial effects on the other members of the community.

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APPENDIX

Appendix I. Histogram representation for community structures
from November 1977 through January 1979 for
Systems 1 - 16.
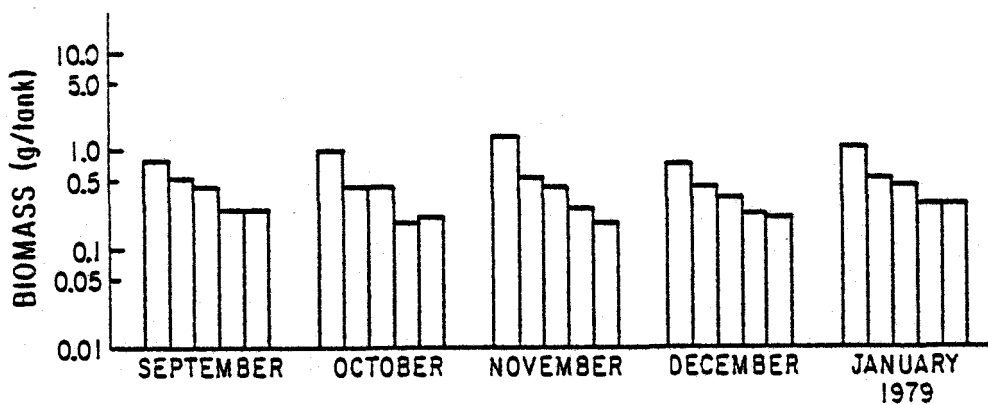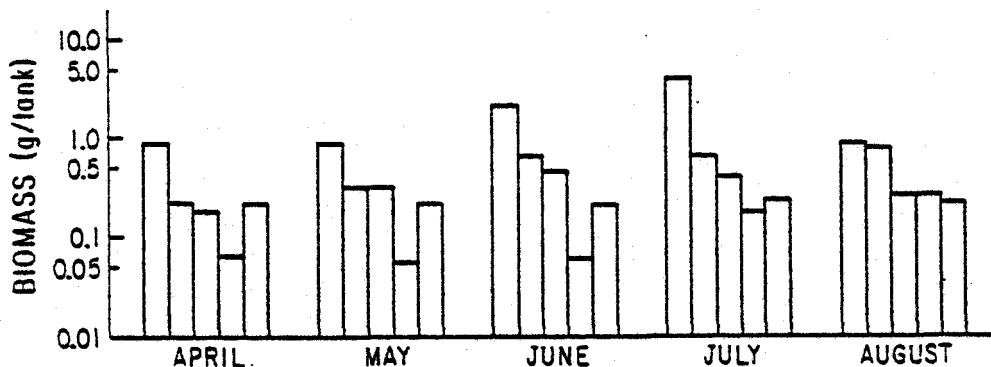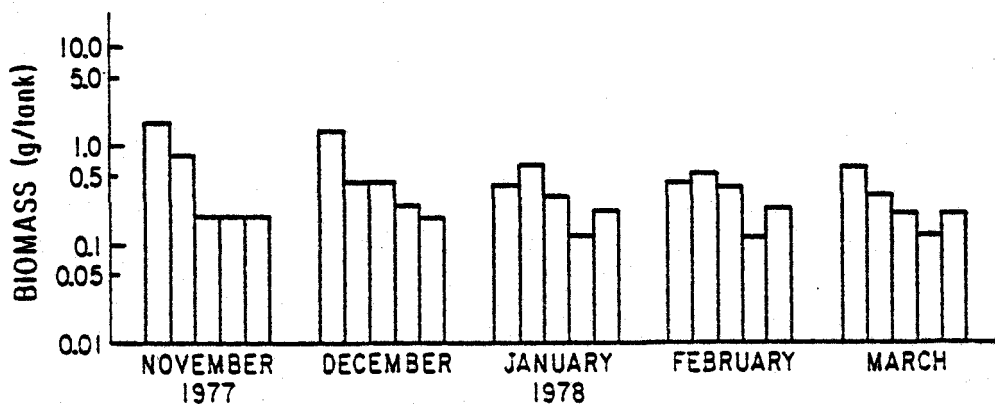
Community structures for System 1 (40 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
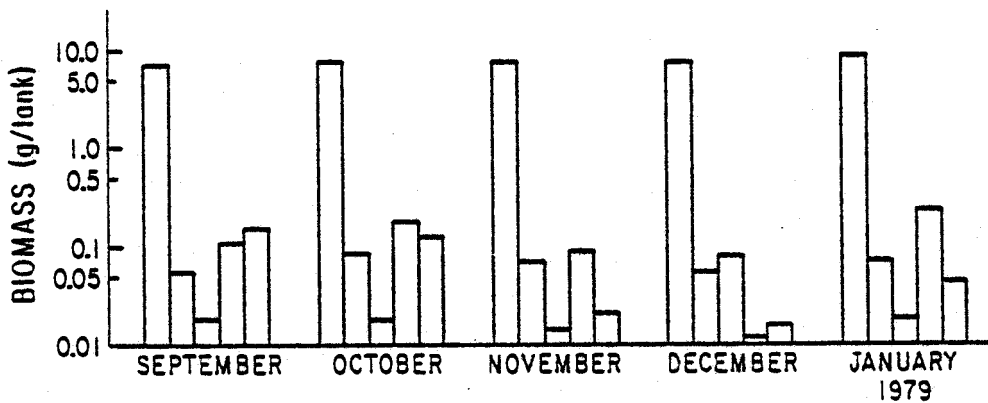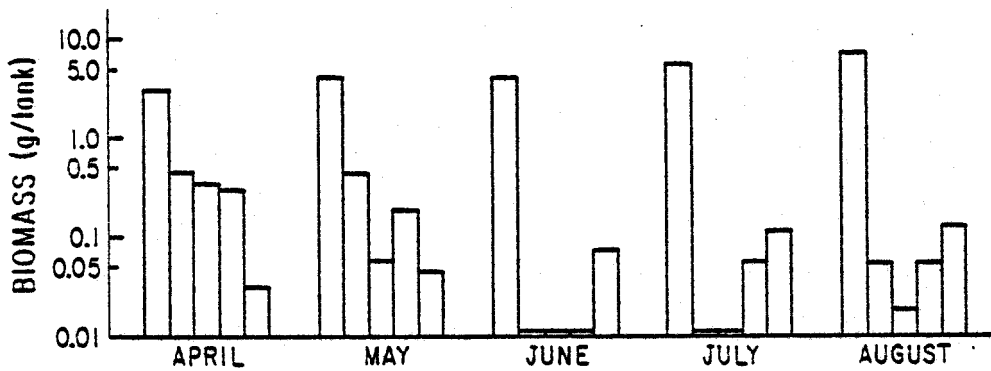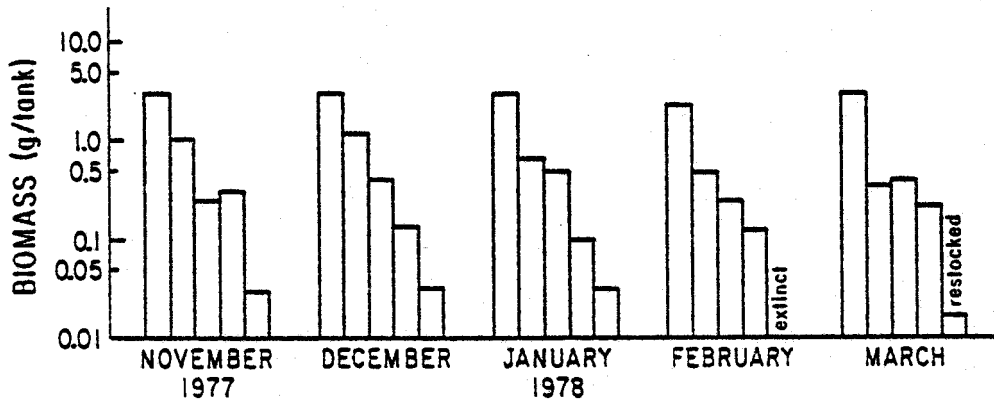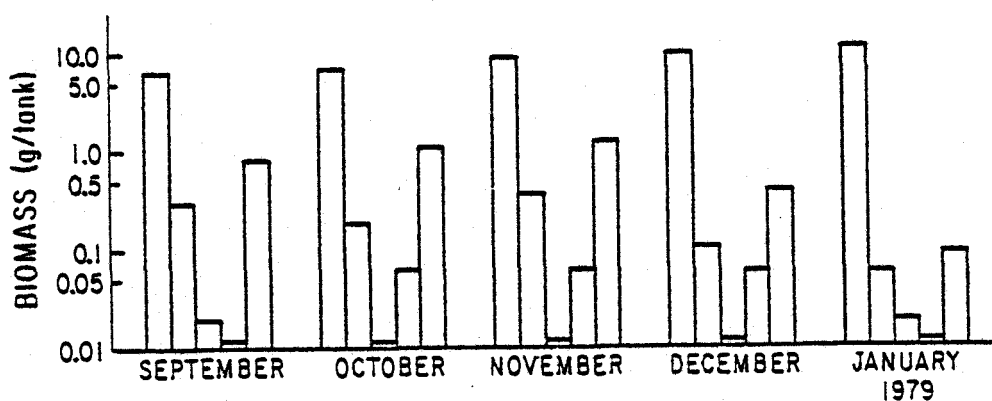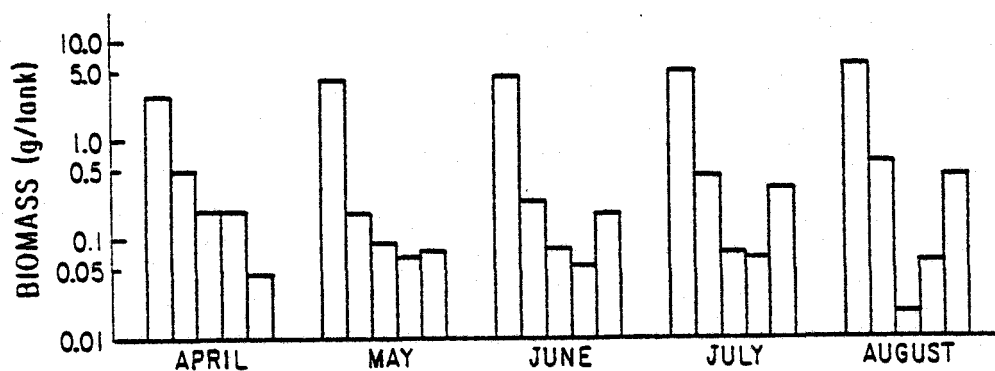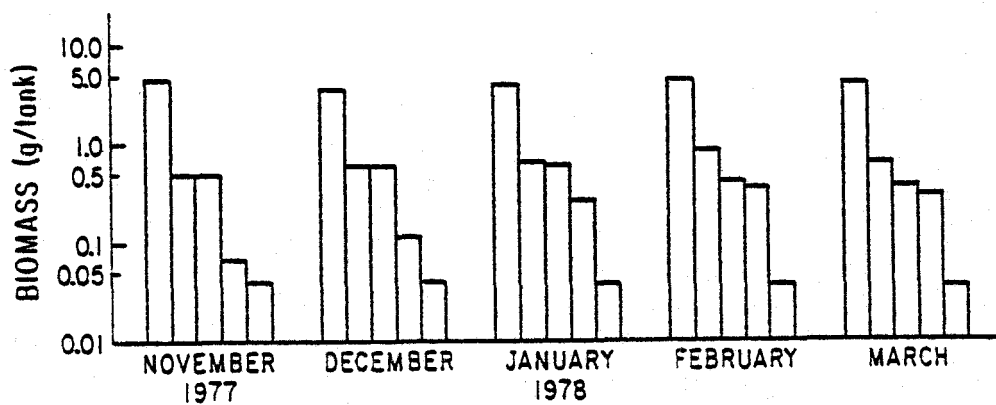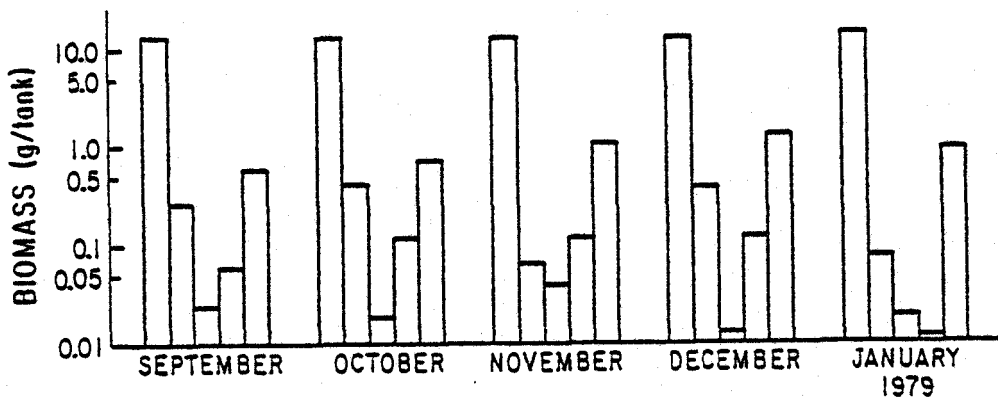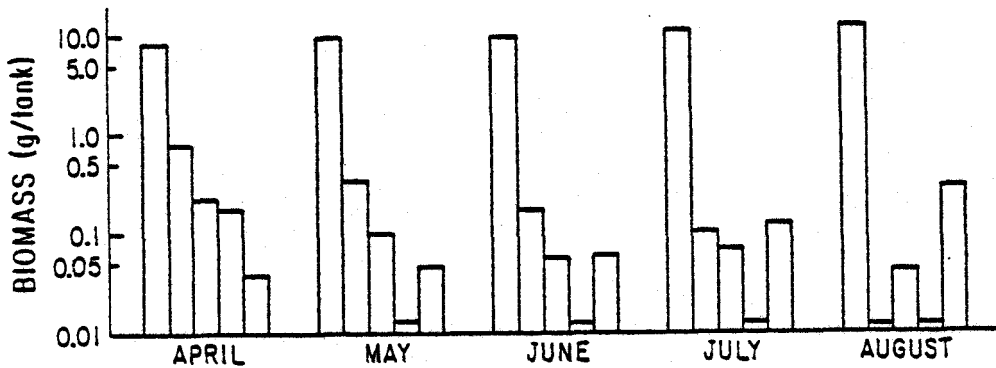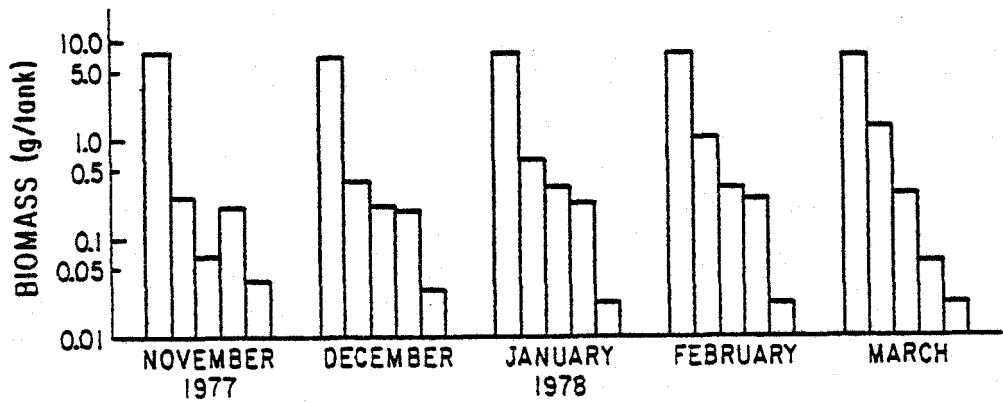
Community structures for System 2 (20 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
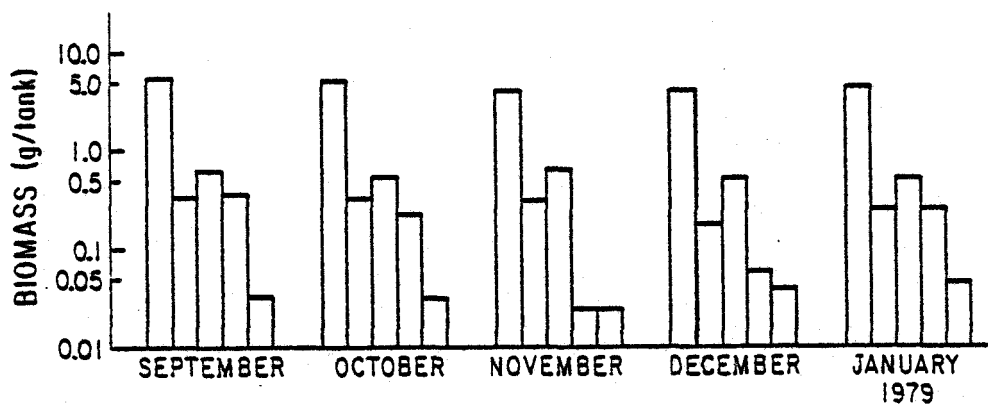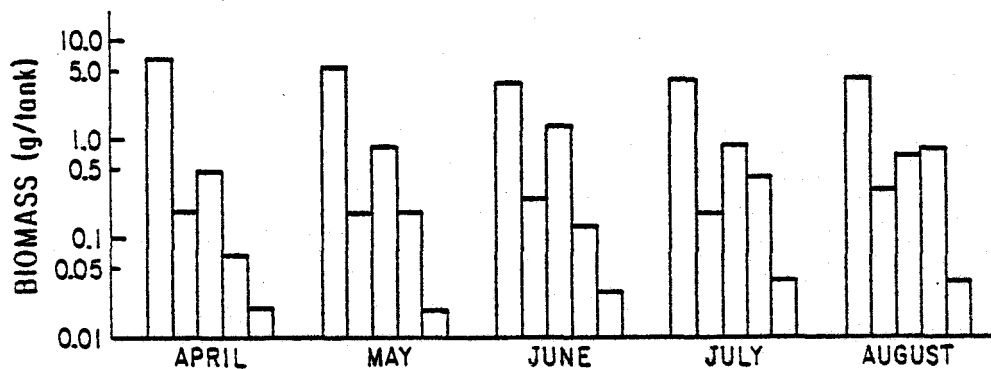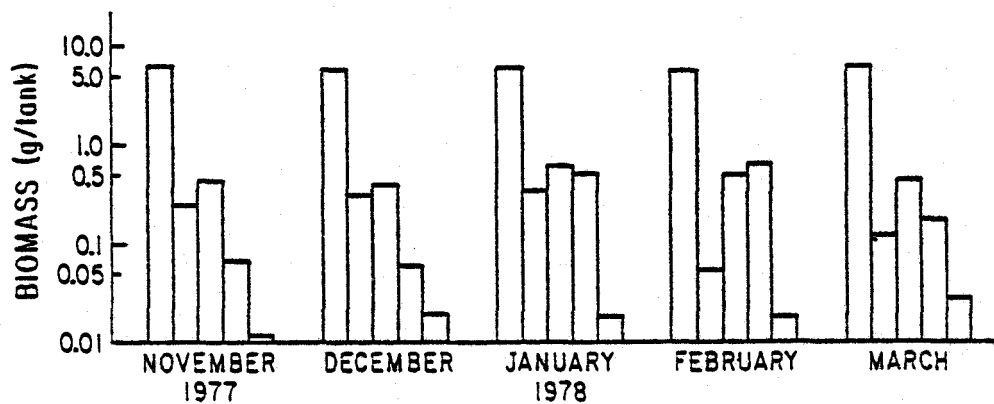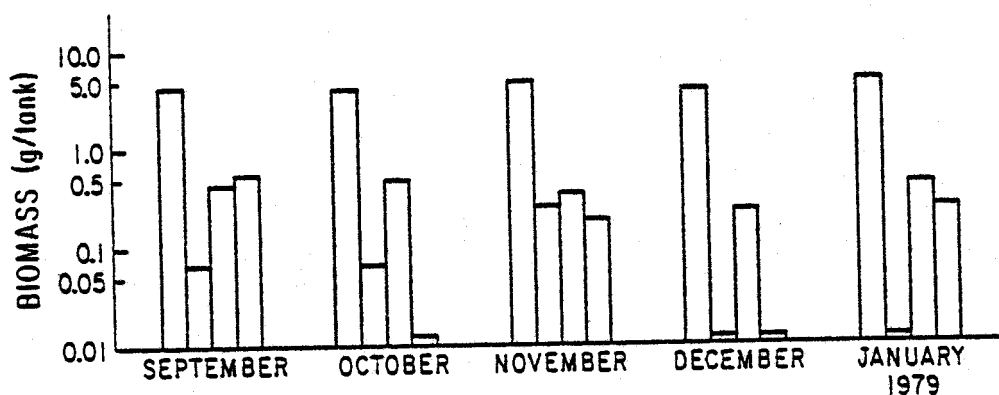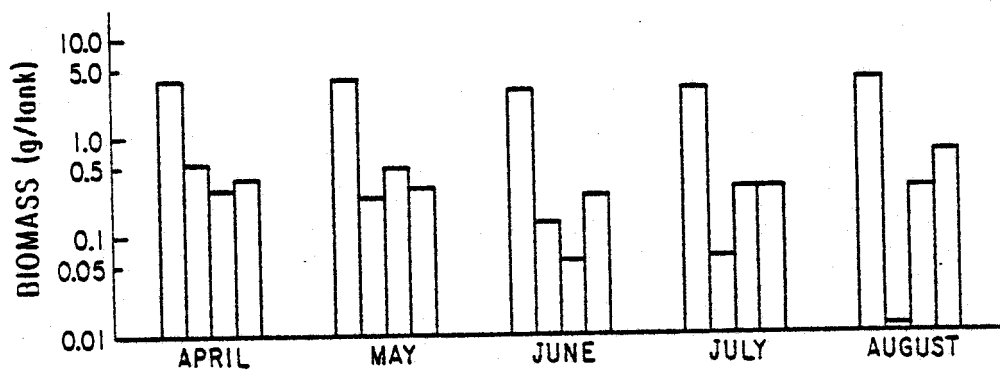
Community structures for System 3 (0 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
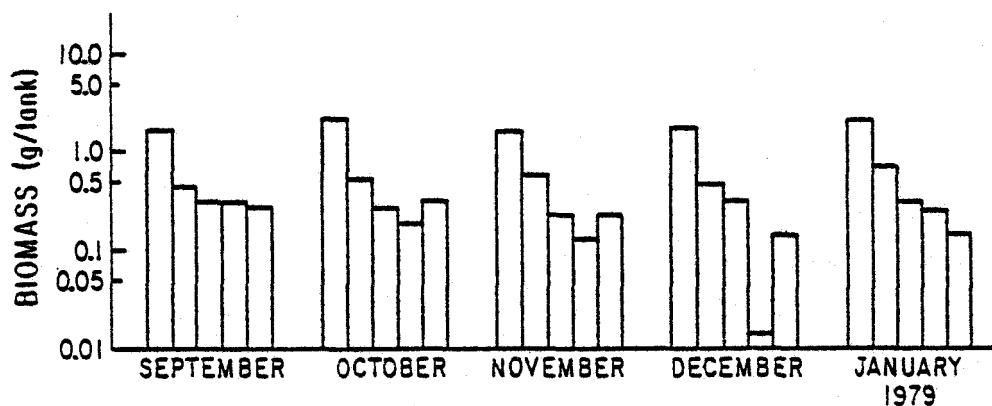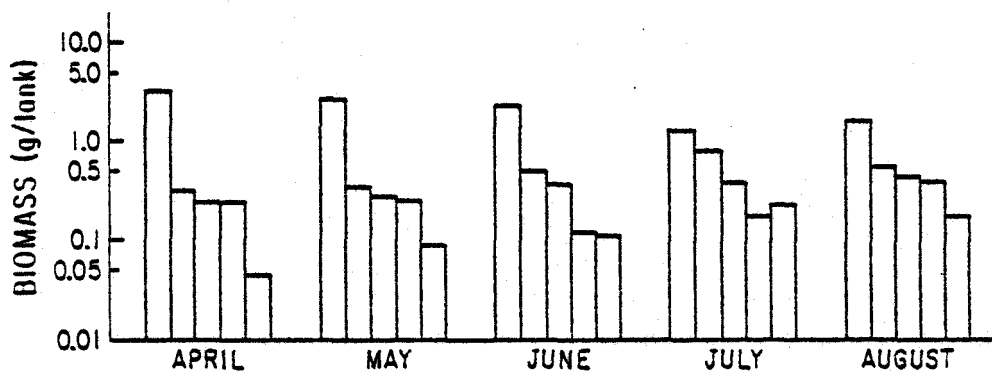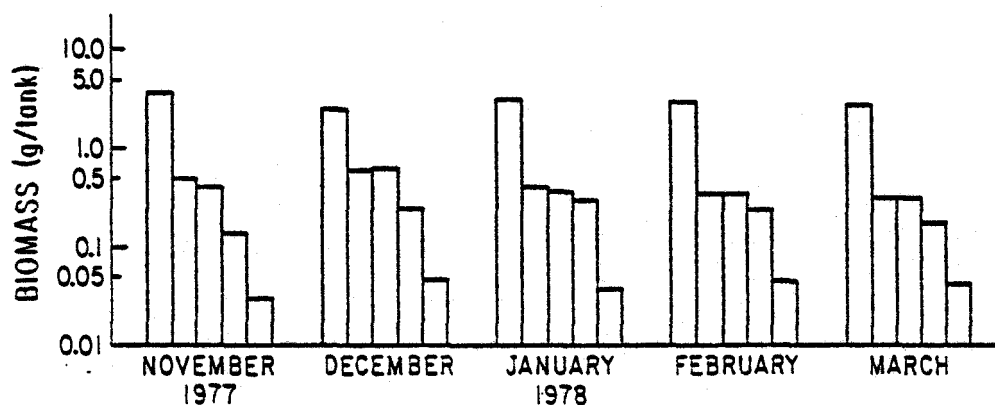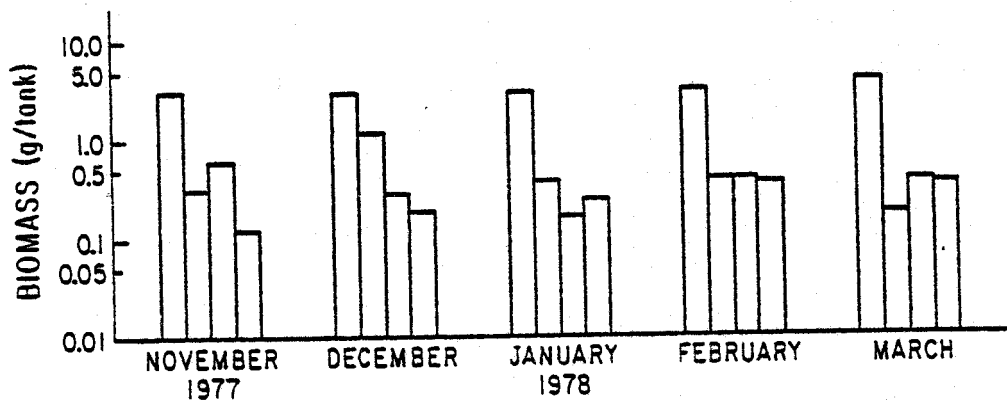
Community structures for System 4 (20 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
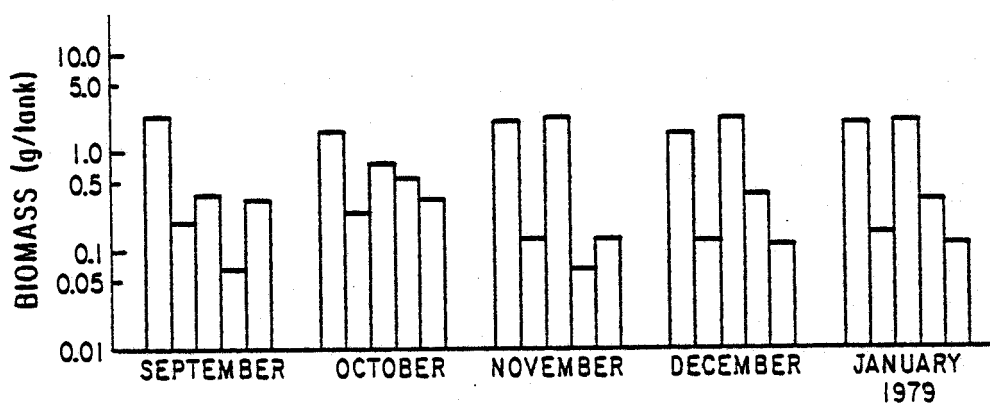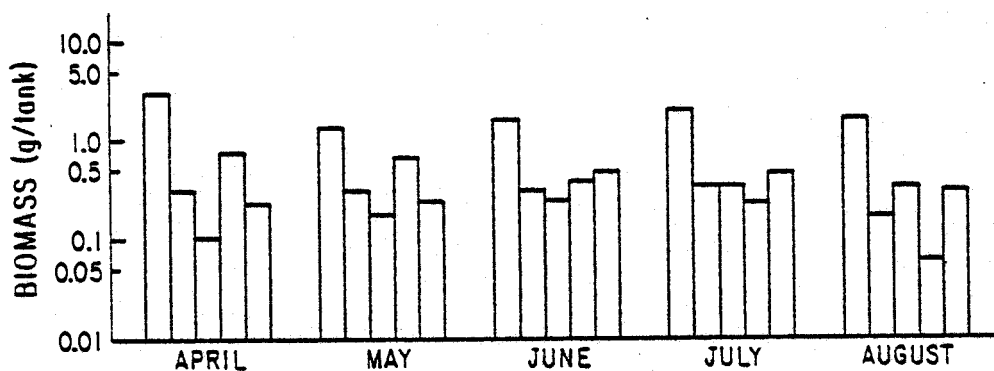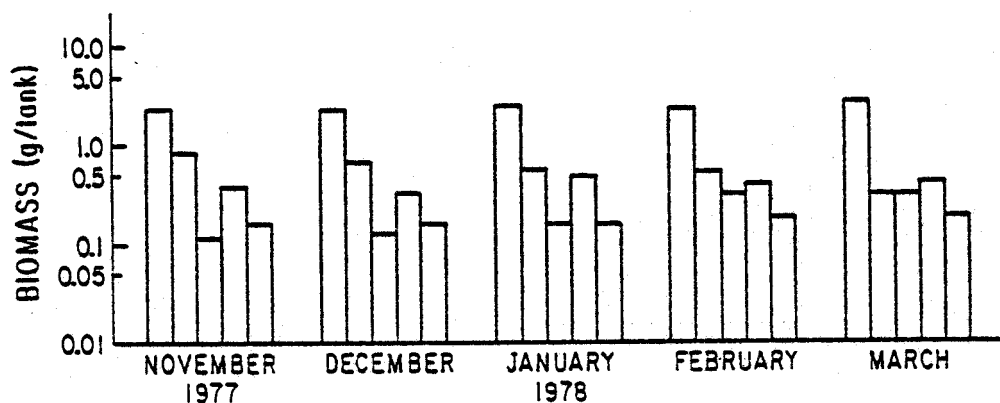
Community structures for System 5 (20 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
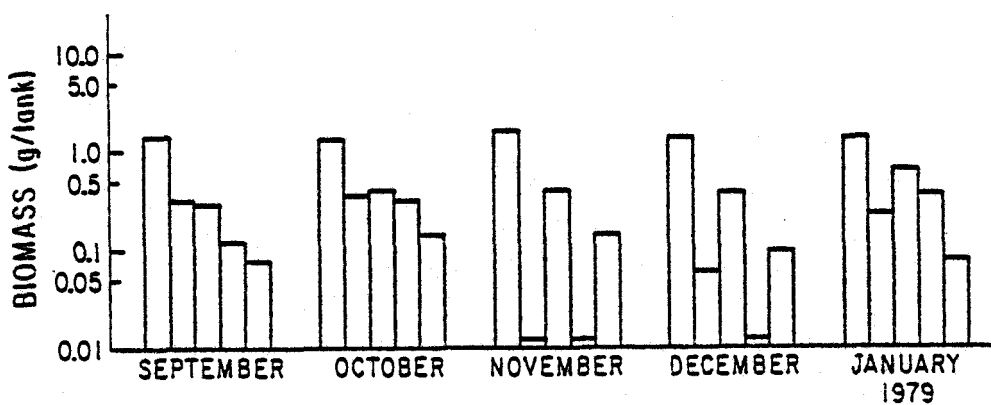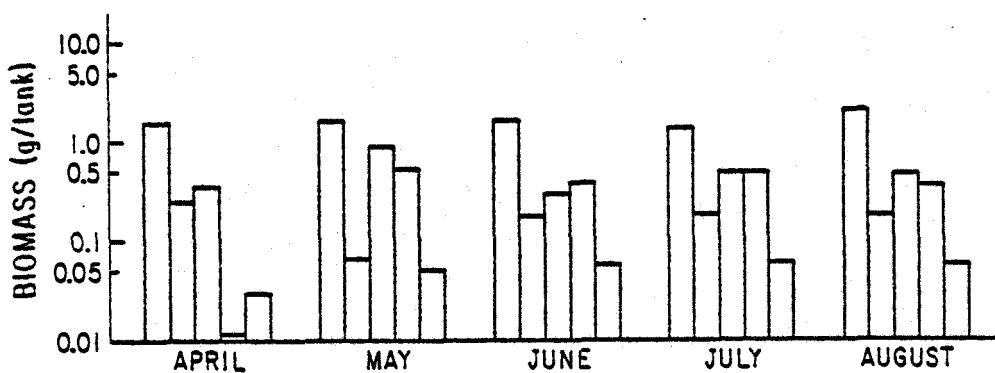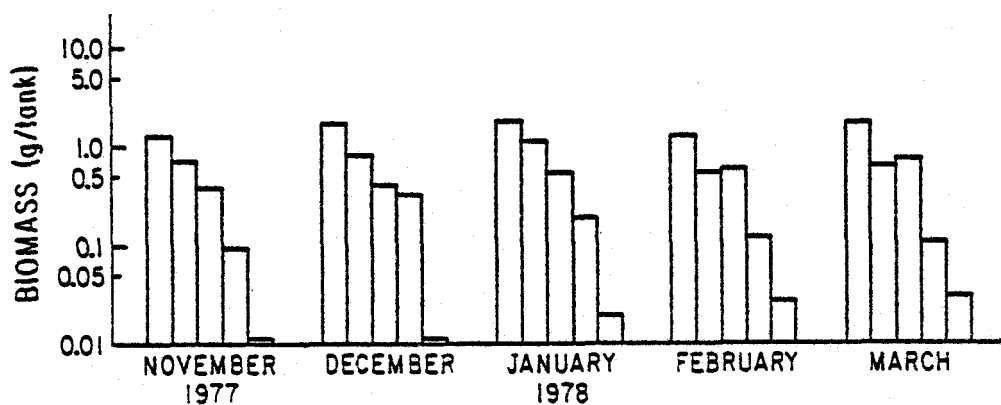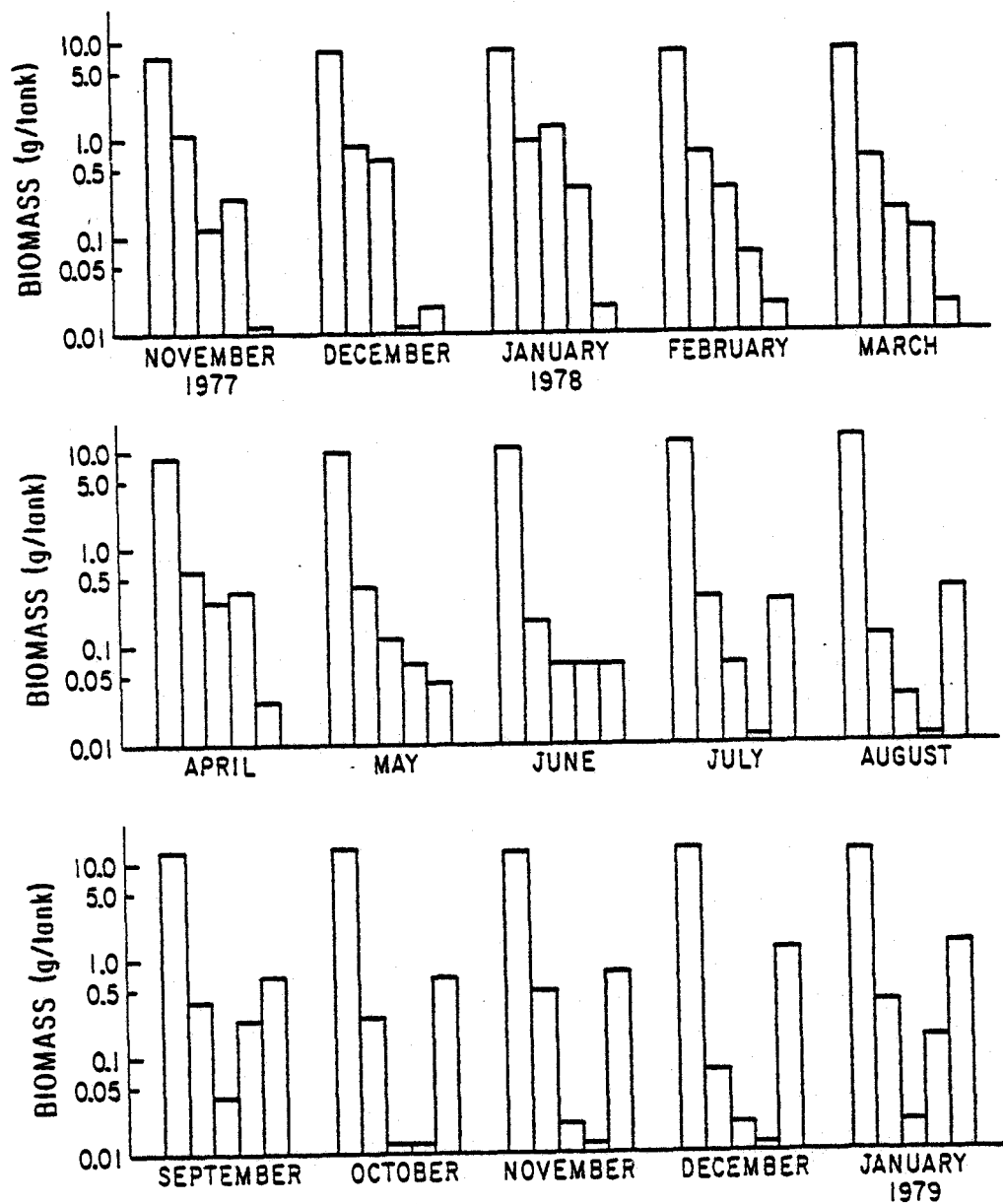
Community structures for System 6 (40 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
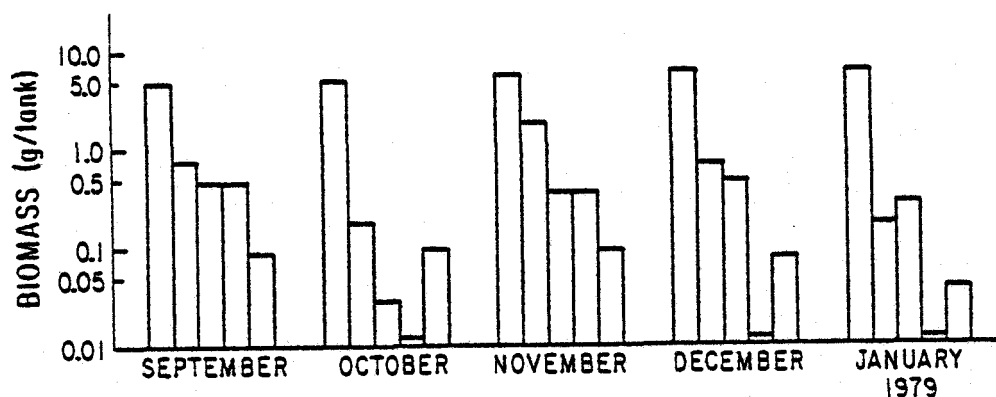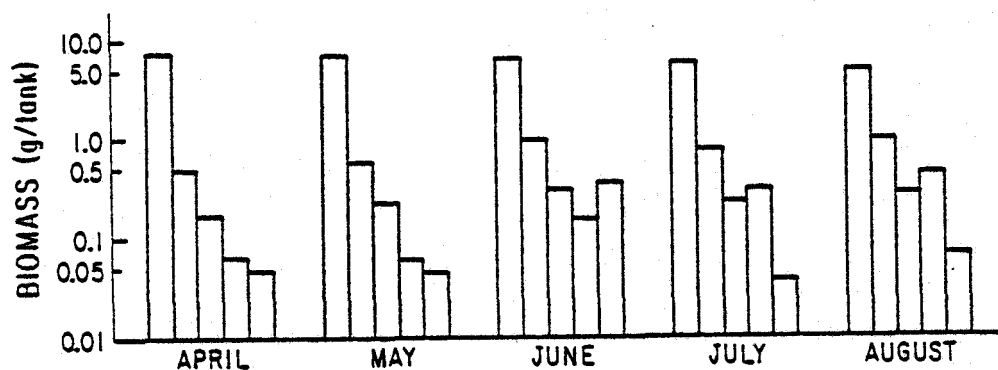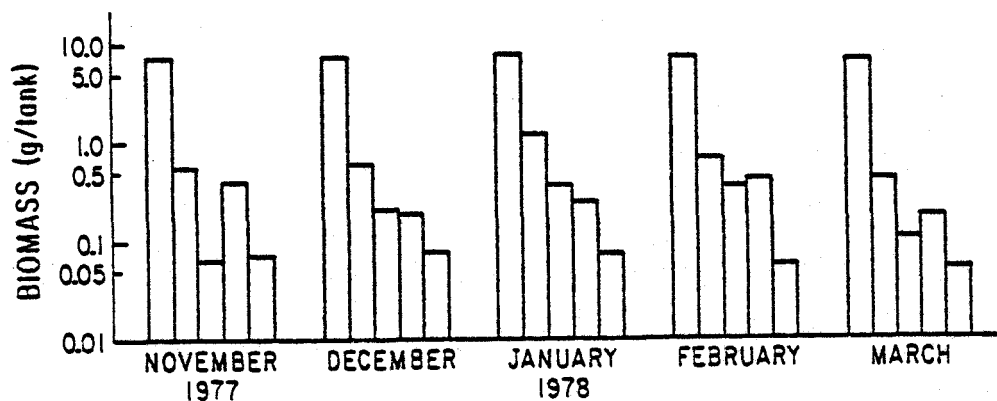
Community structures for System 7 (0 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
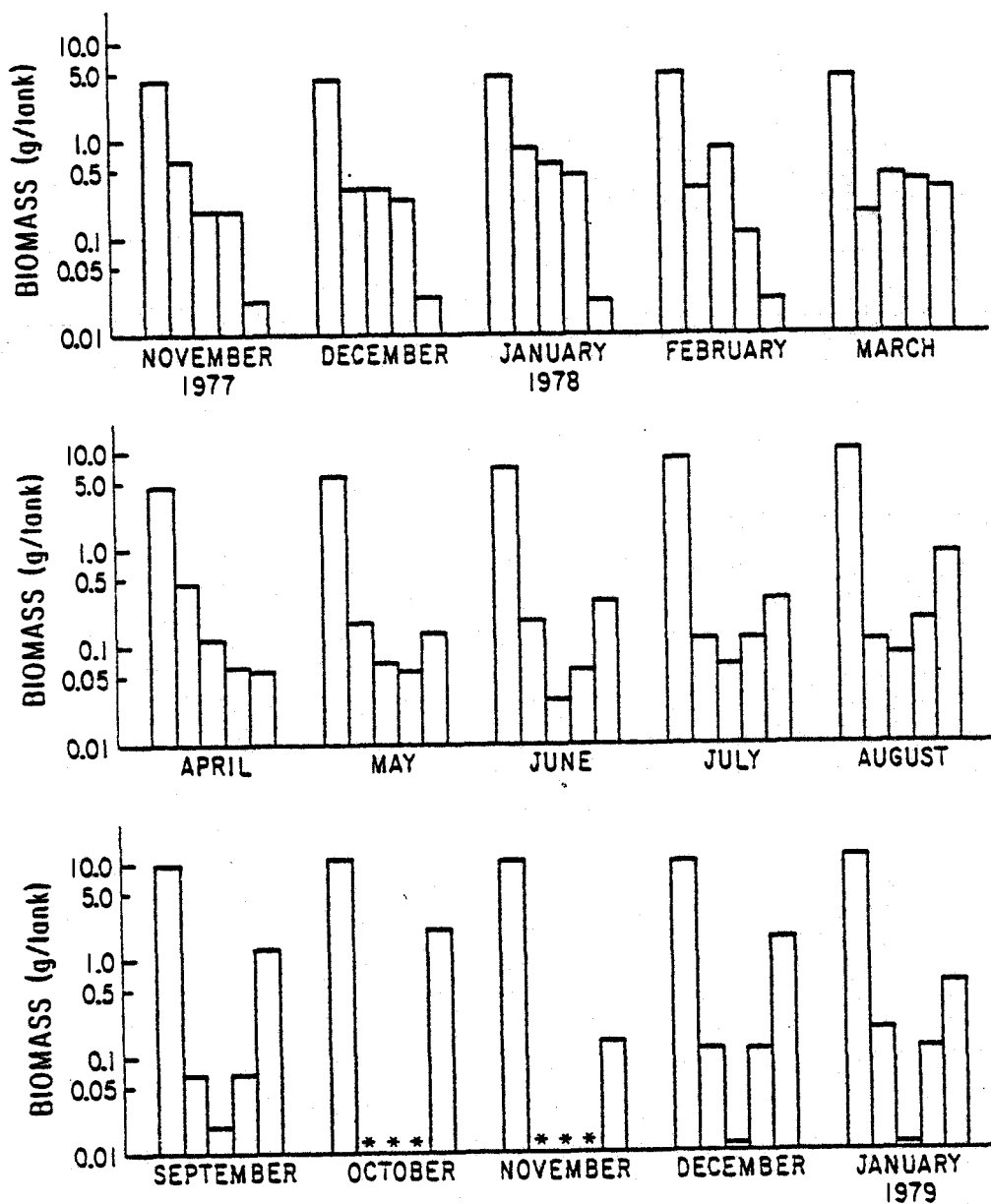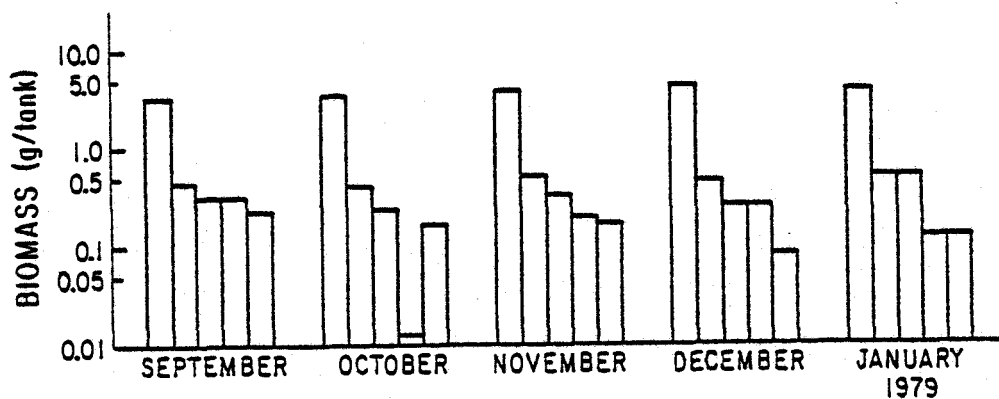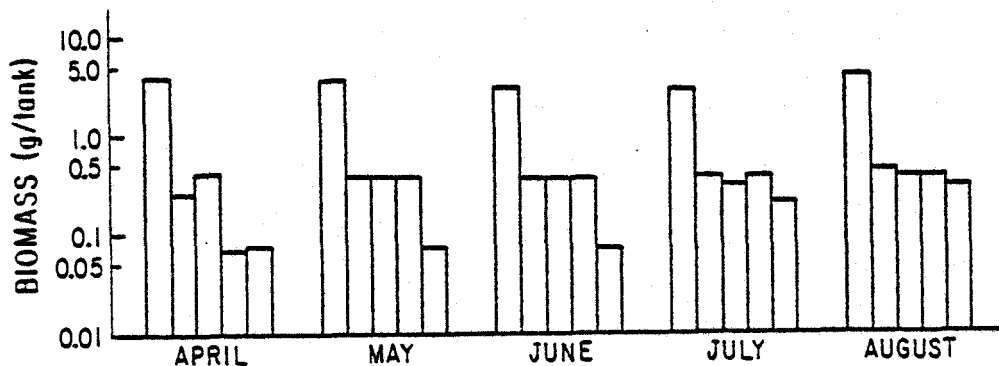
Community structures for System 8 (10 percent guppy exploitation)
during each month of the study. The order in which populations
appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN -
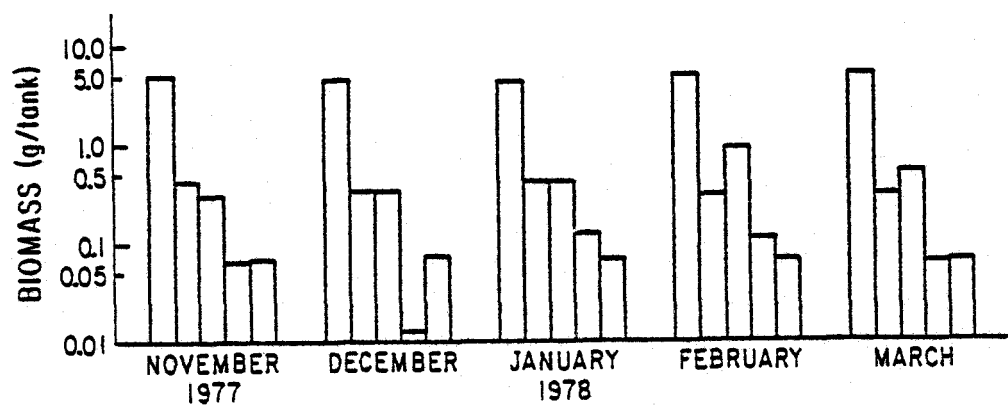ROTIFER - AMPHIPOD. *Samples not available for this period.
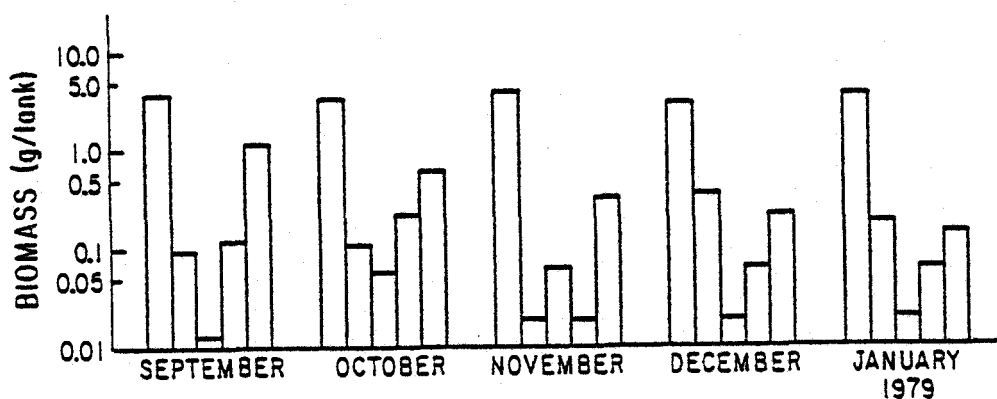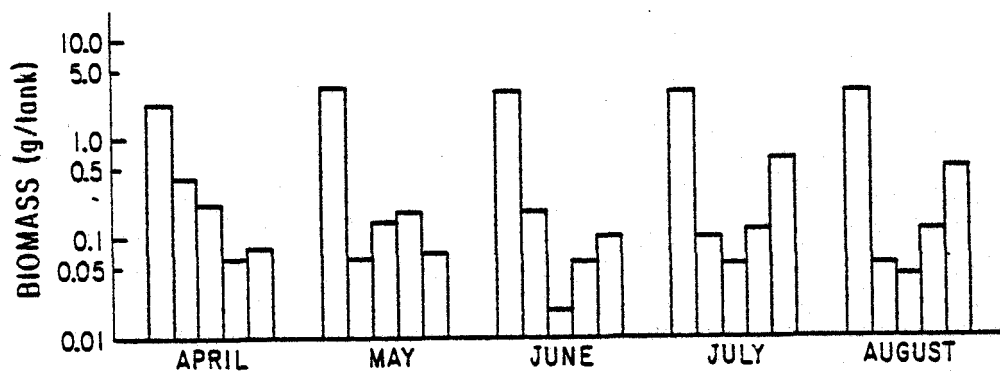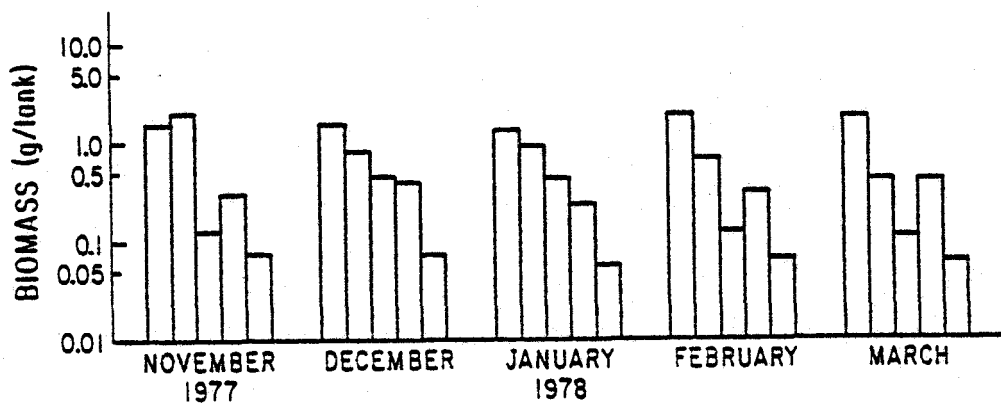
Community structures for System 9 (40 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
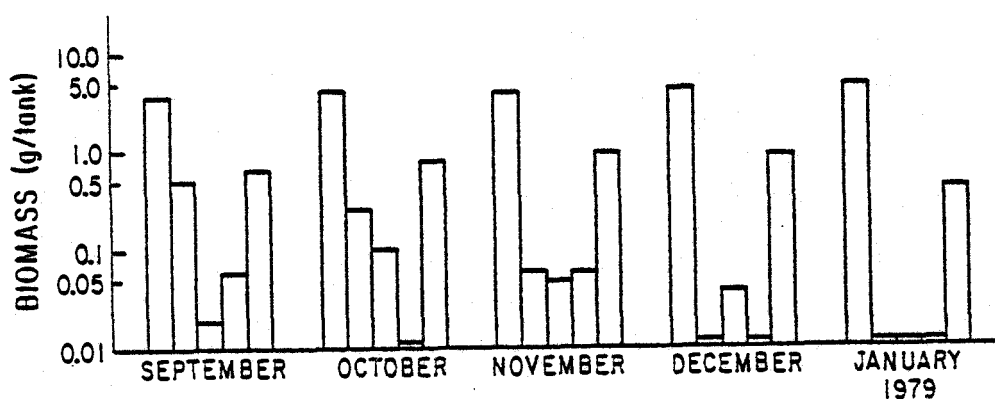
Community structures for System 10 (10 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
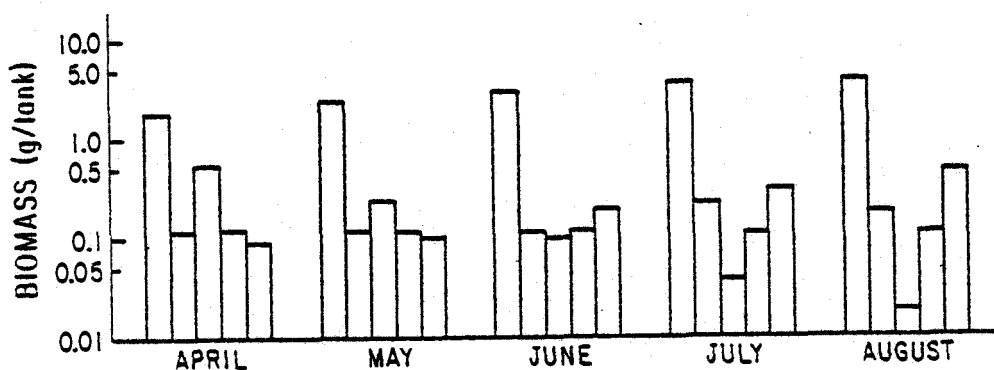
Community structures for System 11 (0 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.
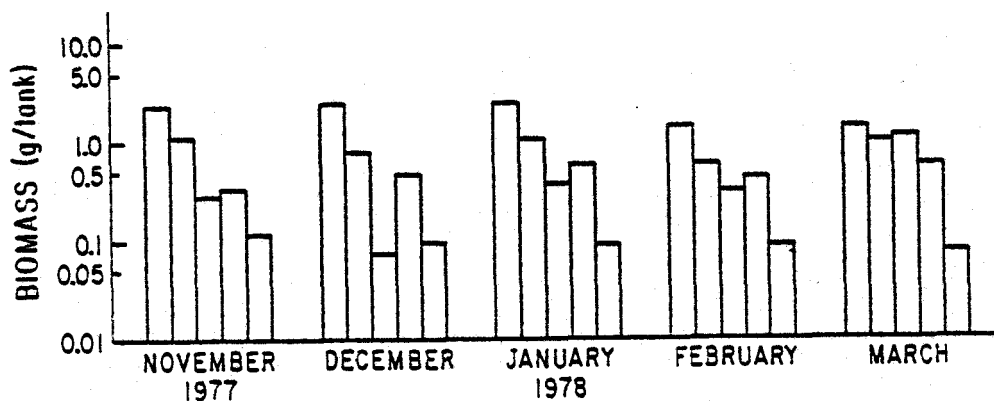
Community structures for System 12 (10 percent guppy exploitation)
during each month of the study. The order in which populations
appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN -
ROTIFER. (Amphipods do not appear in this system because they
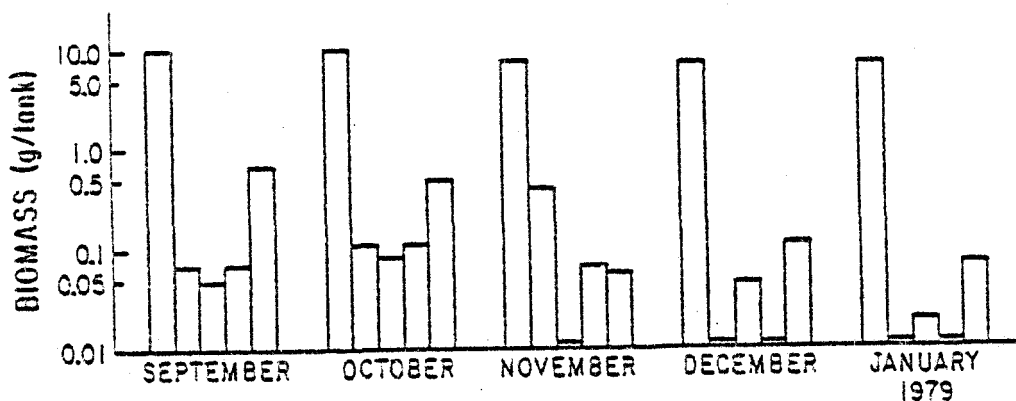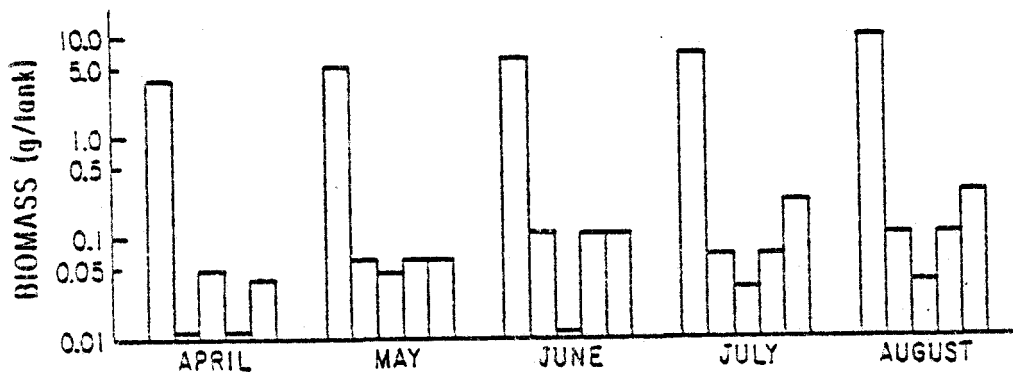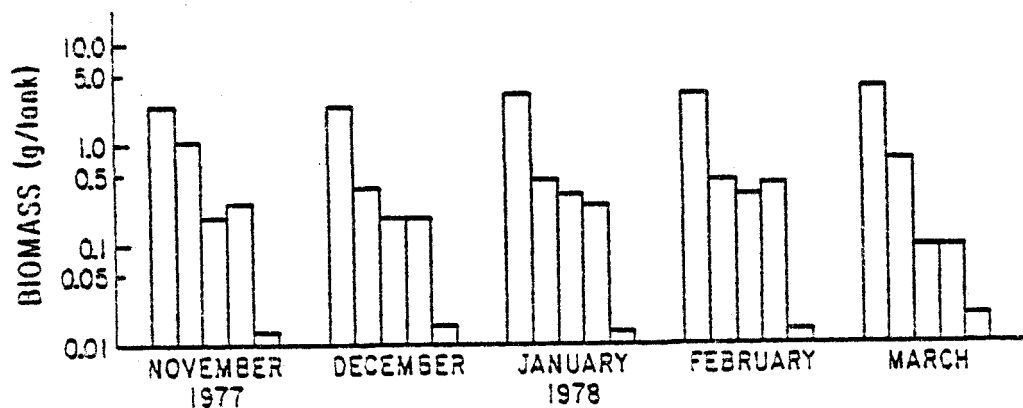went extinct before November 1977.

Community structures for System 13 (0 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.

Community structures for System 14 (10 percent guppy exploitation)
during each month of the study. The order in which populations
appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN -
ROTIFER - AMPHIPOD.

Community structures for System 15 (40 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.

Community structures for System 16 (20 percent guppy exploitation) during each month of the study. The order in which populations appear in the histograms is: GUPPY - NEMATODE - PROTOZOAN - ROTIFER - AMPHIPOD.

Appendix II. Contents of alfalfa ration.

Alfalfa	60.0 %
Gelatin	8.7 %
Dextrin	15.6 %
Mineral Mix	4.0 %
Methy Cellulose Gum	1.0 %
∝ cell	2.7 %
Choline chloride	1.0 %
Vil mix	2.0 %
Salmon oil	5.0 %