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STRUCTURE AND ORGANIZATION OF PERSISTENT AQUATIC LABORATORY COMMUNITIES EXPOSED TO THE INSECTICIDE DIELDRIN

by

William J. Liss, Becky L. McClurken-Lilley and
Douglas S. Lee

Oak Creek Laboratory of Biology
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331

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Steven F. Hedtke

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16. ABSTRACT

Sixteen aquatic communities composed of persistent populations of guppies (Poecilia reticulata), amphipods (Gammarus fasciatus), snails (family Planorbidae), planaria (Dugesia sp.), and various microinvertebrates were established under laboratory conditions. Eight of these communities received low energy input with low habitat availability while the remaining eight communities had high habitat availability and received high energy input. At each level of input, guppy populations in two systems were exploited at either 0, 10, 20, or 40 percent of the population biomass each month. Macroinvertebrates were also sampled monthly for population counts and biomass measurements. After each system reached near steady-state conditions, 1 µg/l of dieldrin was introduced into one system of each treatment. These systems were allowed to reach new steady-state conditions.

The response of the systems was dependent upon both the energy input/habitat and exploitation levels. The low energy input/habitat systems were more sensitive to dieldrin particularly at higher levels of exploitation. The influence of organization and environment on population persistence and system structure are explored theoretically with isocline models and the implications for aquatic ecology and environmental management strategies are discussed.

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INTRODUCTION

Management of toxic substances must be based upon good understanding of their effects not only on individual organisms but also on populations and communities. Accomplishing this presupposes some theoretical perspective for understanding populations and communities. In this report we present our perspective, apply it in understanding the structure and organization of laboratory communities exposed to a toxicant in relation to the environments of the communities, and explore some of the broader implications of this perspective for understanding and control of toxic substances. Much of the report deals with research conducted as a part of a 5 year project supported by USEPA. The goal of the project was to advance understanding of the capacities and performances of individual organisms, populations, and simple communities exposed to toxicants. The first three years of this work, supported by a research grant, was reported by Liss et al. (1980). The work reported here deals with research conducted over the last two years of the project.

The objectives of that research were:

1. Determine and explain, under different sets of environmental conditions, the effect of the insecticide dieldrin on the persistence, structure and organization of laboratory communities, including the ability of the systems to recover from toxicant perturbation. Environmental conditions include different levels of habitat availability and rates of energy and material resource input and different rates of population exploitation.
2. In ancillary experiments, determine and explain, under different sets of environmental conditions, the effects of dieldrin on the

persistence, structure and organization of systems that are of simpler organization and shorter duration than the laboratory communities, yet still capable of representing population and simple community responses. The response to toxicants of these simpler systems will be compared to toxicant response in the more complex systems to determine the extent to which simple models can provide some understanding of toxicant effects in complex systems.

Some of the results from the first three years work must necessarily be included here to provide continuity and background for interpretation of the last two years of research.

We view the perspectives for understanding populations and communities and any possible utility they may provide as a way of thinking about toxic substance effects in relation to system structure and organization, system dynamics, and system environment as being more important than the particular empirical results reported here. In essence, the laboratory community research was designed, conducted, and interpreted according to our perspective. The empirical research is useful for evaluating the utility of the perspective for understanding systems and its conformity with observational experience. The more complex laboratory communities discussed here are not necessarily intended as tools for testing toxic substance behavior and effects.

The performance of a system is anything the system does as a whole. Performances include structure or state, change in structure, yield, and persistence. The performance of a system at a particular time can be understood as being jointly determined by the capacity of the system and conditions in its environment at that time (Warren et al. 1979). A system with a given

capacity will exhibit different performances (or different magnitudes of a given kind of performance) under different sets of environmental conditions. In this sense, the capacity of a system can be understood to be all of its possible performances in all possible environments. The performance of a system will change if either its capacity or its environment changes.

The way that a system is organized determines its capacity to perform. Thus any performance of a system, including its response to a toxicant, can be understood to be jointly determined by the organization (capacity) of the system and conditions in the environment of the system. As individual organisms, populations, communites or any other natural system develop or evolve, their organization and thus their capacity to perform changes. Exposure to toxicants, exploitation, and other affects of man on natural systems may substantially alter the capacity of the systems. These are the most profound effects that man's activities may have on natural systems for if capacity is significantly altered, man's effects on natural systems may be largely irreversible (Warren et al. 1983). Thus, a system whose capacity has been fundamentally changed may not be able to recover or return to its original or previous state(s) even if its environment were returned to its previous state(s).

System organization we take to be a theoretical concept entailing incorporation, concordance, and interpenetration of the capacities and performances of the subsystems and their environments (Warren et al. 1983). Structure--the apparent form of the system as a whole--we take to be a more empirical, observable performance than organization. For relatively simple systems, such as we will deal with here, structure can entail the kinds of species composing the system and their distribution and abundance in space

and time. We will deal theoretically and empirically with both steady-state and dynamic system structure. Organization of such simple systems can entail the ways in which the species are incorporated or unified into a system, with emphasis on their capacities in relation to the capacity of the system as a whole, the concordant or harmonious, rule-like relations between the species that integrate or link them together to form a system, and the interpenetration, permeation, or interspersion of species populations, emphasizing that interactions between different species consist of interactions between individuals or groups of individuals of the different species. Population interactions such as predation and competition play an important role in organizing the laboratory communities.

Mathematical models can be used to symbolize, partially articulate, and provide a perspective on system structure and organization. The following generalizations pertaining to system structure and dynamics in relation to system environment will be illustrated with isocline models and demonstrated empirically in the laboratory communities:

1. Under different states of the environment of a natural system, the system will come to have different steady-state structures and organizations and thus can be understood to be a multisteady-state system.
2. Dynamics or changes in structure of an n-dimensional system 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 as a result of changes in the state of the environment of the system.

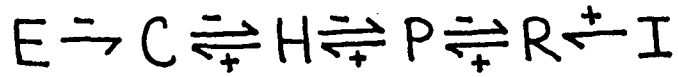
Isocline models of the kind to be discussed here provide one of the principle bases for both illustrations of these generalizations and interpretation of the laboratory community results. More detailed information concerning model derivation can be found in Booty (1976), Liss (1977), and Thompson (1981).

Isoclines and phase planes representing a simple predation system is shown in Figure 1. Systems with somewhat more complex organization than that shown in Figure 1 can also be represented with systems of isoclines on phase planes, but the predation system will suffice to illustrate the generalizations.

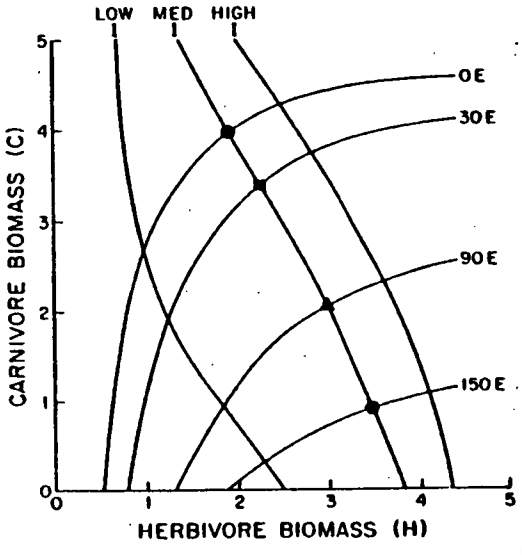
The intersecting isoclines define systems of steady-state relationships between the populations composing the system. The position and form of the isoclines is determined by systems of graphs or equations representing the rates of change in biomass of the populations composing the system (Booty 1976, Liss 1977, Thompson 1981). A complete set of isoclines on all phase planes provides at least a partial view of the structure and organization of a system in relation to environmental conditions.

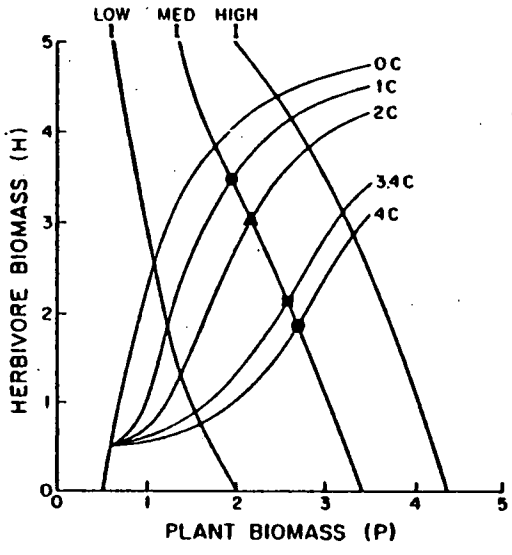
The structures of systems are in continuous developmental and evolutionary change. Even so, these systems can be understood ideally as being multisteady-state systems. For a system to be understood as being a multisteady-state system it is necessary only to be able to conceive of the environment of the system as having different states. In the example shown here (Fig. 1), for each set of environmental conditions I and E, that is, for each state of the environment of the system, there exists a single steady-state point on each phase plane, each of these points being a two-dimensional projection of a single, multidimensional system steady-state point in phase space. The set of these two-dimensional points defines the

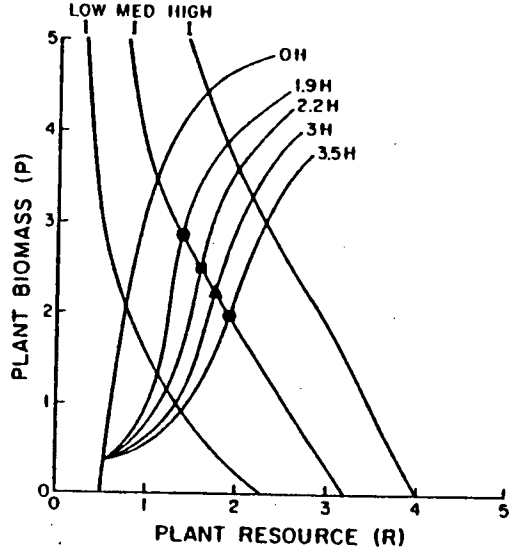
Figure 1. Phase planes and isocline systems representing the interrelationships between populations in a system represented as



where C,H,P, and R comprise the system and E, units of harvesting effort, and I, rate of input of plant resources, are factors in the environment of the 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. Each prey isocline is defined as a set of biomasses of predator and prey where the rate of change of prey biomass with time is zero. The ascending lines on each phase plane are predator isoclines. Each predator isocline is defined as a set of biomasses of predator and prey where the rate of change of predator biomass with time is zero. 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 positions and forms of the isoclines can be deduced from equations or sets of graphs representing the rates of gain and loss of each of the populations (Booty, 1976; Liss, 1977). 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,R at Med I and 0E (circles), 30E (squares), 90E (triangles) and 150E (hexagons) are shown. In this simple system, at each input rate, increased E brings about reduction in steady-state biomass of C, increases in H, reductions in P, and increases in R. Increases in I shift the steady-state relationships between predator and prey to the right on each phase plane, essentially increasing the biomasses of C,H,P, and R. After Liss and Warren (1980).


LOW MED HIGH
0E
30E
90E
150E
CARNIVORE BIOMASS (C)
HERBIVORE BIOMASS (H)
0
1
2
3
4
5


LOW MED HIGH
0C
1C
2C
3.4C
4C
HERBIVORE BIOMASS (H)
PLANT BIOMASS (P)
0
1
2
3
4
5

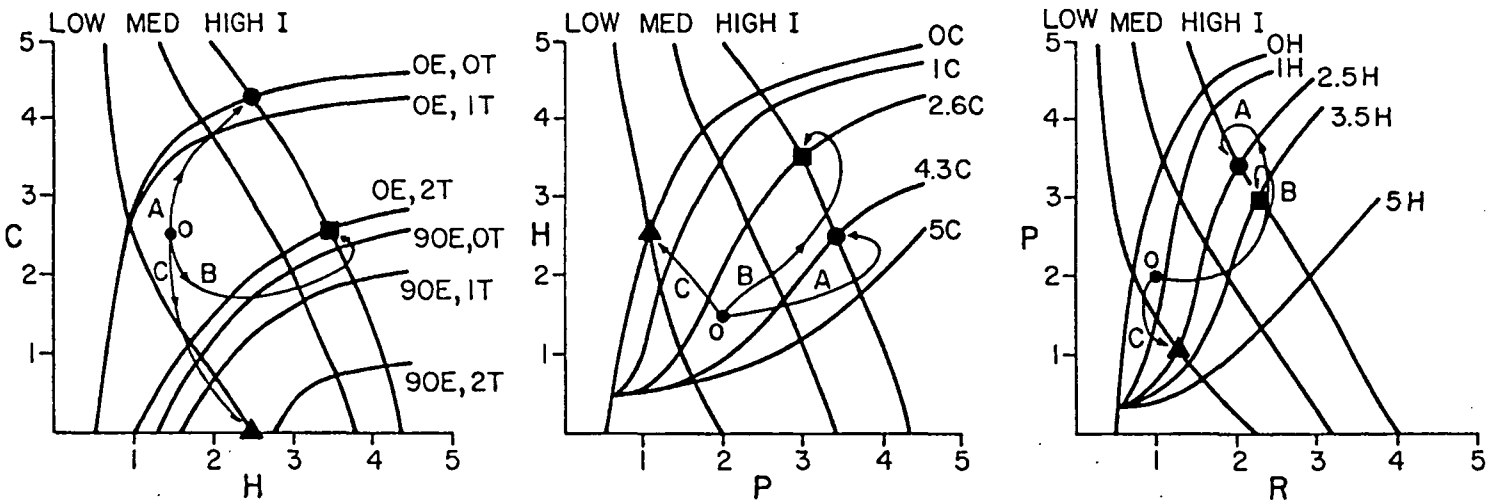

LOW MED HIGH
0H
1.9H
2.2H
3H
3.5H
PLANT BIOMASS (P)
PLANT RESOURCE (R)
0
1
2
3
4
5

steady-state structure of the system for a given set of environmental conditions. Changing the state of the system's environment (for example, from Med I, 0E to Med I, 30E or Med I, 150E) brings about a change in the steady-state structure of the system. A system may have an infinite number of possible steady-state structures.

In the predation system shown here, a single system steady-state point exists for each environmental state. Systems represented with different sets of equations or with different values for the constants in the equations may have more than one potential system steady-state point at some or all environmental states. That is, isoclines need not have the uniform, monotonically increasing or decreasing shapes shown in Figure 1. They may be bowed or looped (e.g. Rozenzweig, 1968), thus creating the possibilities for multiple intersections for a given set of environmental conditions. For the most part, this will not affect the general conclusions we wish to draw and these conclusions can be most clearly illustrated with systems having single system steady-states for a given set of environmental conditions.

On each phase plane, trajectories represent the changes through time in biomasses of the populations composing the system. If environmental conditions are fixed, trajectories on each phase plane will converge upon the steady-state points locating the steady-state structure of the system under those conditions (Fig. 2). In natural systems, environmental conditions are rarely constant for long enough periods of time to permit systems to reach steady-states. Thus, trajectories are in constant pursuit of a steady-state point whose location in phase space is continuously being shifted as a result of changes in environmental conditions. For an n-dimensional system, the trajectory on each phase plane is a two-dimensional projection of an n-dimensional trajectory in phase space.

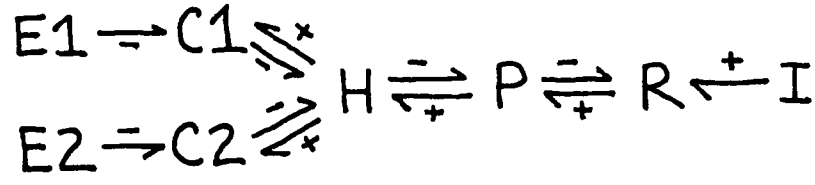
Figure 2. Phase planes and isocline systems illustrating a possible effect of different concentrations of a toxicant (T) on the structure of a simple community. In this example the toxicant directly affects only the carnivore population. The presence of the toxicant lowers the predator isocline at each E, the extent to which it is lowered depending upon the effect of the particular toxicant concentration on carnivore growth, reproduction, and survival. Steady-state structure at HIGH I, OE, OT (circles); HIGH I, OE, 2T (squares); LOW I, 90E, 2T (triangles) is shown. Trajectories of biomasses of carnivore (C), herbivore (H), plant (P), and plant resource (R) originating at point O are shown to converge on each of these steady-states under each particular set of environmental conditions. Introduction of toxicant at a concentration of 2T reduced carnivore biomass, increased herbivore biomass, reduced plant biomass and increased plant resource at each combination of levels of I and E (for example, compare circles and squares at HIGH I, OE on all phase planes). After Warren and Liss (1977).


LOW MED HIGH I
0E, 0T
0E, 1T
0E, 2T
90E, 0T
90E, 1T
90E, 2T
A
O
C
B
C
H
1
2
3
4
5
LOW MED HIGH I
0C
1C
2.6C
4.3C
5C
H
P
LOW MED HIGH I
OH
1H
2.5H
3.5H
5H
P
R

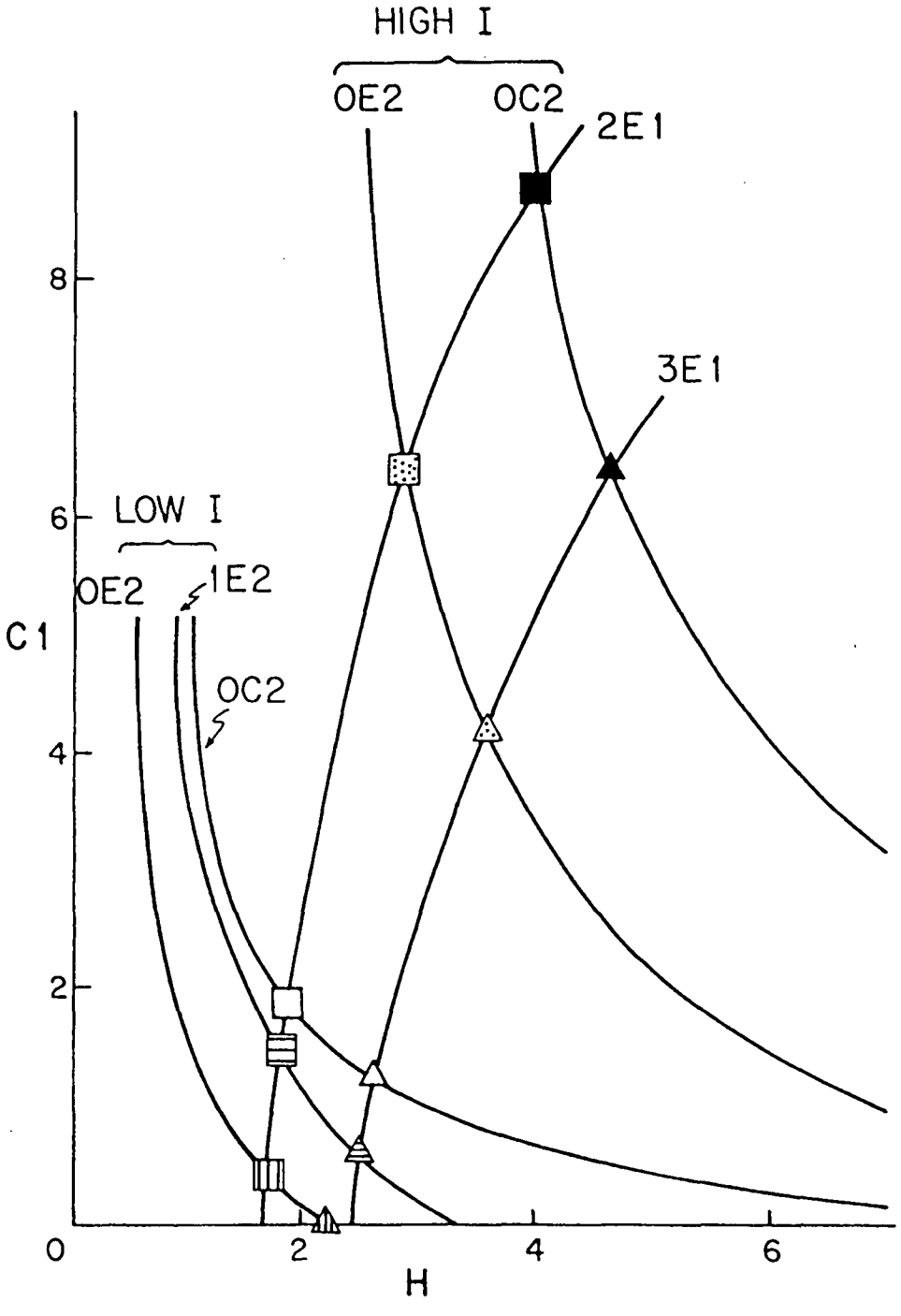
Introduction of toxic substances can alter the structure and organization of systems (Fig. 2). The response of systems to toxic substances is affected by their organization and conditions in their environments such as I and E (Warren and Liss, 1977). For example, in Figure 2, the carnivore population is able to persist at LOW I when it is heavily exploited (90E) if a toxic substance (T) is not present (the predator isocline identified by 90E, 0T intersects the prey isocline identified by LOW I). But, under these same environmental conditions at a toxicant concentration of 2T, the carnivore population is driven to extinction (the prey isocline identified by LOW I does not intersect the predator isocline identified by 90E, 2T; C trajectory). Under different sets of environmental conditions the carnivore is able to persist, although at reduced biomass, at a toxicant concentration of 2T. Persistence at 2T is possible at LOW I when the carnivore is unexploited (0E), or at MED I and HIGH I when C is heavily exploited (90E). The laboratory communities provide an empirical demonstration of the importance of system organization and system environment in determining response to toxicants.

Both predation and competition are important in organizing the laboratory communities and determining their response to a toxicant. If an exploited competitor C2 utilizing prey species H were added to a system such as that shown in Figure 1, the prey isoclines at each I would, in effect, "explode" into an infinite family of prey isoclines (Booty 1976, Liss 1977, Thompson 1981), each parameterized by a particular level of harvesting effort on the competitor (Fig. 3). In this particular example, addition of a competitor shifted to the left the prey isoclines defining the steady-state relationships between C1 and H at each I, so altering steady-state C1 and H densities and consequently the densities of other

Figure 3. Phase plane and isocline systems showing the steady-state relationships between a carnivore C1 and its prey H in the system



C2 is a competitor of C1 for H and is exploited by E2. E1 and E2 are different harvesting systems. Prey isoclines become parameterized not only by I but also by E2, the number of units of effort harvesting C2. When C2 is not present (0C2), steady-state densities of C1 and H are indicated at LOW I, 2E1 (open square), LOW I, 3E1 (open triangle), HIGH I, 2E1 (solid square, and HIGH I, 3E1 (solid triangle). Addition of C2 shifts the prey isoclines to the left at each I lowering the steady-state biomasses of C1 and H at each E1 (for example, compare biomasses of C1 and H at LOW I, 2E1, 0C2--the open square--with the biomasses of these populations when C2 is present and unharvested at LOW I, 2E1, 0E2--the vertically-barred square). The greater the intensity of harvesting of C2 (the lower its biomass is maintained) the less the prey isocline is shifted to the left at each I. This example illustrates the particular effect of introducing a competitor into a system such as that shown in Figure 1. The impact of introduction of a competitor may vary considerably depending upon the organization of the system into which the competitor is introduced. Isoclines on this phase plane were generated through computer iteration using the simulation command control language SIMCON (Worden 1976, Thompson 1981). (We appreciate the assistance of Grant Thompson, Oak Creek Laboratory of Biology, in generating this phase plane.) After Lee (1983).


HIGH I
OE2
OC2
2E1
3E1
LOW I
OE2
1E2
OC2
C1
8
6
4
2
0
2
4
6
H

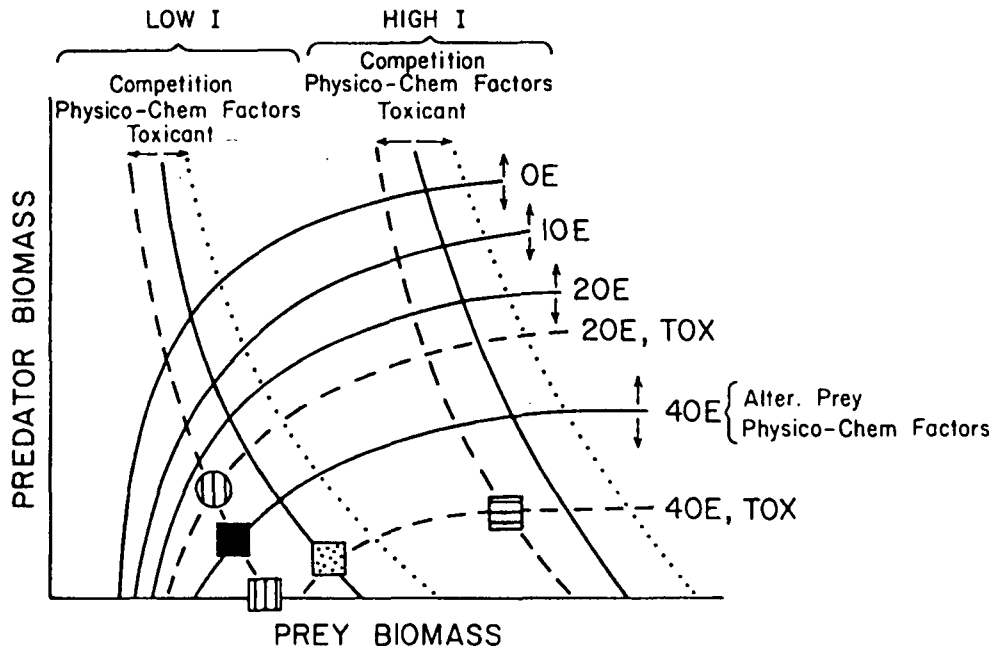
species in the system. Note that the prey isocline identified by LOW I, 0E2 does not intersect the predator isocline identified by 3E1. Under these conditions C1 and C2 cannot coexist, C1 being driven to extinction by the presence of an unharvested competitor (vertically-barred triangle). C1 and C2 can coexist if environmental conditions change in such a way that predator and prey isoclines intersect in positive phase space. This can occur if 1) E1 is reduced from 3E1 to 2E1 (vertically-barred triangle to vertically-barred square), 2) E2 is increased from 0E2 to 1E2 (vertically-barred triangle to horizontally-barred triangle), and 3) I is increased from LOW I to HIGH I (vertically-barred triangle to stippled triangle). Thus competitive coexistence is dependent upon the levels of I and E.

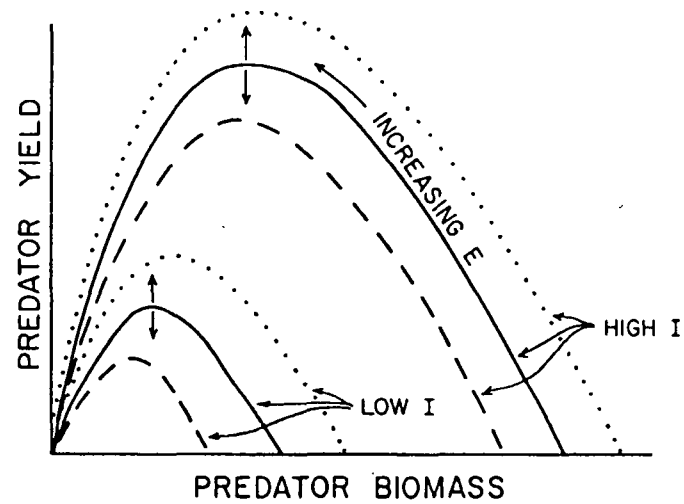
A generalized isocline model summarizing some possible effects of changes in system environment and organization on steady-state relationships between a predator and its prey is shown in Figure 4. Changes in the levels of any of the factors identifying the predator and prey isoclines can alter the position and form of the isoclines and so shift the location of the steady-state point in phase space, thus altering system steady-state structure.

Not only the presence of a competitor of the predator, as is shown in Figure 3, but also the presence of competitors of the prey or trophic levels leading to the prey can alter the position of the prey isoclines at each I (Booty, 1976). Physico-chemical factors (temperature, oxygen, etc.) affecting the prey or trophic levels leading to the prey can also bring about shifts in the prey isoclines at each I. Physico-chemical factors directly affecting the recruitment, growth, or survival of the predator can alter the position and form of the predator isoclines. Species that are prey of the predator but do not compete with other prey can also bring about shifts in the predator

Figure 4. A. Generalized phase plane and isocline systems representing the interaction between predator and prey, and some possible effects of energy and material input rate (I), competition, physico-chemical factors, toxic substances, exploitation (E), and alternative prey. Steady-state points are indicated at the intersections of predator and prey isoclines. At each I, presence of a competitor, toxic substances, or physico-chemical factors affecting the prey can shift the prey isocline on the phase plane. For example, the presence of a competitor or a toxic substance affecting the prey may shift the prey isocline to the left at each I (solid prey isocline to dashed prey isocline). Physico-chemical conditions more favorable to the prey may shift the prey isocline to the right at each I (solid prey isocline to dotted prey isocline). At each E, presence of alternative prey and toxic substances directly affecting the predator can shift the predator isocline. For example, the presence of a toxic substance directly affecting the predator may shift the predator isocline downward at each E (solid predator isocline to dashed predator isocline at 20E and 40E). This is the response shown in Figure 2. Physico-chemical conditions more favorable to the predator may shift the predator isocline upward at each E.

B. Predator steady-state yield curves and how the magnitudes of these curves can be affected by changes in I, competition, toxicants, physico-chemical factors, and alternative prey. Each curve is derived from a prey isocline on the predator-prey phase plane. After Liss (1977).


LOW I
HIGH I
Competition
Physico-Chem Factors
Toxicant
Competition
Physico-Chem Factors
Toxicant
PREDATOR BIOMASS
0E
10E
20E
20E, TOX
40E
Alter. Prey
Physico-Chem Factors
40E, TOX
PREY BIOMASS


PREDATOR YIELD
INCREASING E
HIGH I
LOW I
PREDATOR BIOMASS

isoclines. A toxic substance affecting the prey or lower trophic levels leading to the prey can alter the prey isoclines at each I. A toxicant directly affecting predator survival, growth, or reproduction can bring about shifts in the position and form of the predator isoclines at each E, as shown in Figure 2.

From each prey isocline a steady-state predator yield curve can be derived as shown in Figure 4 (Liss 1977, Thompson 1981). Changes in the magnitude of factors parameterizing prey isoclines (I, competition, etc.) shift the location of the prey isoclines and so lead to changes in the magnitude of the yield curves. Changes in the magnitude of factors parameterizing predator isoclines can also lead to changes in the magnitude of the yield curves if, at each E, they alter the location of the steady-state point on a particular prey isocline and thus alter the steady-state biomass and yield the population is able to maintain at that particular E. Toxic substances directly affecting a predator and/or affecting its prey or trophic levels leading to the prey can bring about changes in the magnitude of predator yield curves.

The phase planes and isocline system in Figure 4 depict some of the kinds of factors that bring about shifts in the location of predator and prey isoclines and so affect system structure. However, with this model or any other, it is not possible to generalize about the particular effect of any factor on system structure. For example, we cannot conclude that the addition of a competitor will, in all kinds of systems, shift prey isoclines to the left and reduce steady-state predator and prey densities, although this may be an intuitive result. The particular effect on system structure of the addition of a competitor or other parameterizing factor,

as indicated by the magnitude and direction of shift of predator and prey isoclines, depends upon the organization of the system, that is, upon the other kinds of species composing the system and the nature of the interactions or interrelationships between them (Thompson 1981).

MATERIALS AND METHODS

Laboratory Community Experiments

Sixteen aquatic communities were established, each composed of persistent populations of guppies (Poecilia reticulata), amphipods (Gammarus fasciatus), snails (family Planorbidae), planaria (Dugesia sp.), and benthic microinvertebrates including flagellates, rotifers, nematodes, gastrotrichs, and protozoans (Liss et al. 1980). Green and blue-green algae and diatoms were present. Habitat and escape cover for invertebrates was provided by a substrate of 1.5 cm quartzite gravel four cm. deep. A gelatinous mixture of 60 percent alfalfa and 40 percent Oregon Test Diet (Sinnhuber et al. 1977) served as primary energy and material input in the laboratory communities. The nitrogen content of the alfalfa ration was 3.0 percent.

Each laboratory system was maintained in a fiberglass tank measuring 1.2m x 1.1m x 0.4m and holding 560 liters of water. This was continuously exchanged by a 600 milliliter per minute flow of heated well water. Water temperature (21 ± 1°C), dissolved oxygen (8.2 ± 0.5 ppm), and pH (7.8 ± 0.1) were maintained at nearly constant levels. Light was provided by fluorescent lights placed above each tank. Intensities ranged from 15 to 23 foot-candles at the surface of the water. Light was maintained at this low level to prevent blue-green algae blooms. Photoperiod was controlled by a timer set for 14 hours light and 10 hours darkness.

Initially all 16 laboratory systems were established with three circular nests of quartzite gravel covering 20 percent of the bottom area of each tank and each received a 0.6 gram per tank daily alfalfa-OTD ration. This treatment is identified as low energy and material input and low habitat availability, or LOW I. In April 1975, 200 amphipods were stocked in each system, with

the size distribution of amphipods introduced into each system being similar. Sediment accumulation and development of a benthic microflora and microfauna ensued. Snails and planaria inadvertently colonized all the systems and became major components of some of the communities. By November 1976, groups of 37 guppies (4.5 grams), each with a similar size distribution and sex ratio, had been stocked in all systems. Four guppy populations were exploited at one of four rates, 0, 10, 20, or 40 percent of the biomass of the population present at the time of sampling (0E, 10E, 20E and 40E, respectively). The systems were sampled every 28 days.

In March 1978, eight of the laboratory systems (two at each guppy exploitation rate) were modified to establish a higher level of energy and material input and habitat availability. The gravel habitat and escape cover was increased to cover 95 percent of each tank bottom. Energy and material input was increased to 4.0 grams of alfalfa-OTD ration daily. This treatment will be identified as HIGH I. Planaria are extremely effective predators on amphipods and were capable of driving amphipod populations to extinction if left uncontrolled. At HIGH I, planaria became abundant and in four of these systems, one at each guppy exploitation rate, planaria control was instituted by manually removing planaria during sampling. This proved to be an effective means of planaria control. Planaria were either absent or maintained at low densities in planaria-controlled systems (Table 2).

In April 1978, when four of the systems at LOW I (one at each guppy exploitation rate) established near steady-states, continuous introduction of one ppb of the organochlorine insecticide dieldrin was begun (Liss et al. 1980). Near steady-state (NSS) structure for the laboratory systems under each set of environmental conditions (I and E) was assumed when the trajectories of biomasses of the interacting populations in the system fluctuated

in a very restricted region of phase space relative to previous fluctuations. When the systems established NSS's, 10 to 18 monthly measurements of structure were necessary to adequately define the domain of NSS behavior. Dieldrin introduction into these systems was terminated in October 1979 and recovery of the systems from dieldrin perturbation was observed through September 1981.

Continuous introduction of one ppb of dieldrin into the four systems at HIGH I in which planaria were controlled began when these systems established NSS's. Dieldrin introduction into the systems whose guppy populations were exploited at 0E and 10E began in September 1981. Dieldrin was introduced into the remaining two systems (20E and 40E) in January 1982. Dieldrin was continuously introduced into all of these systems through September 1982, when the experiment was terminated.

Leeches and the amphipod Hyallela azteca inadvertently colonized several of the systems. Leeches prey on young snails and if they reach high densities they can reduce snail biomass. They increased in abundance in several systems in late 1980 and, in early 1981, leech control was instituted. Control was very effective in most systems, eliminating leeches entirely or severely reducing their abundance (Table 2). Hyallela began to colonize the systems in late 1979 and early 1980. This species became abundant in several systems and appears to have had an impact on system recovery at LOW I and on NSS structure at HIGH I.

Organisms in each laboratory system were censused and its guppy population exploited every 28 days. Guppies were netted from the tanks. Individual length and weight measurements were taken for immature guppies (standard length of 10 to 14 millimeters) and for mature females (standard length greater than 14 millimeters). Total number and weight were recorded for mature males and for newborns (standard length less than 10 millimeters).

The method of exploitation was similar to that employed by Liss (1974). A systematic exploitation schedule was developed for each exploitation rate. The schedule provided for the removal of a proportion of the population corresponding to the exploitation rate. At each exploitation rate, all sizes of fish were exploited with the same intensity.

Monthly exploitation of the guppy populations simulated the impact of harvesting by man or natural mortality. Heavy exploitation resulted in size distributions occasionally having up to 80 percent of a population's biomass residing in one large female. More or less than the intended percentage of biomass was thus often exploited in any one month. This led to some fluctuations in population biomass; over many months, however, mean exploitation rates were near the intended percentages.

Population number, biomass and yield (i.e. the biomass of the catch at a given sampling date) was determined for each guppy population. Size-specific fecundity of exploited females was also determined.

Sampling procedures also included the temporary removal of all benthic invertebrate populations, sediment, and gravel substrate. Individuals of all macroinvertebrate populations (snails, amphipods, planaria) were sized and the number and biomass of each size group was determined. From this, population number, biomass, and size structure were determined. All amphipods, snails, sediments, and unexploited fish were returned to the tanks after sampling.

The insecticide dilution and delivery system was similar to the continuous flow dilution apparatus described by Chadwick et al. (1972). A solution having a constant toxicant concentration was produced by passing water through a column of 1.5 cm quartzite gravel coated with technical grade dieldrin.

Concentrations of dieldrin in the water were determined weekly. Following standard extraction procedures, dieldrin analysis was done using a Varianaerograph 2000 gas chromatograph equipped with an electron capture detector.

The work to which the objectives stated in the Introduction pertained was originally proposed to span a three year period. During the second year funding was reduced. At the end of the second year, the Cooperative Agreement was terminated due to lack of funds. Due to reduction in funding and early termination, analysis of the concentrations of dieldrin in the tissues of organisms was not possible.

Ancillary Experiments with Laboratory Communities of Simple Design

The laboratory communities used in these experiments were intended to serve, in some sense, as "microcosms of microcosms", that is, as systems that are simpler in design than the larger, more complex laboratory systems, but still capable of representing population and simple community behavior and response to toxicants. Toxicant behavior and effects in these simpler systems were then to be compared to the behavior and effects of the toxicant in the more complex laboratory systems. The comparison was to be made in order to determine the extent to which simpler models of complex systems could provide some understanding and prediction of toxicant behavior and effects in the complex systems.

Systems composed of only guppy populations, only snail populations, and guppy and snail populations together were established (Table 1; Lee 1983). Guppies and snails were the most abundant populations in the more complex laboratory systems and were competitors for the alfalfa ration. Energy and material input into these systems was in the form of an alfalfa-OTD ration, which was introduced at rates that were the same as the rates of introduction

Table 1. Laboratory ecosystems designed for ancillary experiments. After Lee 1983.

System	Number of Tanks	Input Rate[1]	Exploitation Rate[2]
snail-alfalfa	2	4.0	-
	2	0.6	-
guppy-alfalfa	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	2	0.6	0
	2	0.6	25
	2	0.6	40
	2	4.0	0
	2	4.0	25
	2	4.0	40

1) gms alfalfa day^{-1}

2) % biomass removed $month^{-1}$

into the more complex laboratory systems. Guppy populations were exploited. Water temperature, light intensity, and light-dark cycle in the ancillary experiments were the same as in the more complex laboratory systems.

Each system resided in a 40 liter glass aquarium that had been adapted for flow-through usage. Each aquarium received 200 ml min^{-1} of well water at 21°C ± 0.5°C and was exposed to a 14/10 hour light-dark cycle. The systems received light intensities of 25 foot-candles. Each tank had approximately 3,450 cm^3 of cover available to newborn guppies and snails in the form of floating plastic plants.

Fourteen of the systems received a low rate of energy and material input in the form of an alfalfa ration (60% alfalfa and 40% Oregon Test Diet) and the other fourteen systems received a high rate of energy and material input (Table 1). These treatments will be identified as LOW I and HIGH I, respectively.

Twelve of the systems, six at LOW I and six at HIGH I, had only guppy and algae populations, with guppy populations in two systems in each subgroup of six being exploited at 0 percent, 25 percent, or 40 percent of the population biomass present at the time of sampling (0E, 25E, and 40E). Twelve systems were composed of guppy, snail, and algae populations with six systems at LOW I and six at HIGH I. Again, guppy populations in two systems in each subgroup were exploited at 0E, 25E, and 40E. The remaining four systems, two at LOW I and two at HIGH I, were maintained with only snail and algal populations.

Each system was sampled every 28 days. The length, weight, and numbers of all individuals in the guppy and snail populations were recorded. Guppy populations in these systems were exploited in the same way as the populations

in the more complex laboratory systems. In order to keep micro-invertebrates to a minimal level, each tank had accumulated sediments siphoned out every four days. Twice a month, for each system, the sediment samples were saved and dry weights were determined in order to keep track of changes in relative sediment densities through time.

The procedure for conducting these ancillary experiments was intended to be similar to that employed in conduct of the more complex laboratory community experiments; to allow the systems to establish NSS's and to adequately define the regions of NSS behavior prior to toxicant introduction. It was hoped that the simpler laboratory systems would establish NSS's more rapidly than the more complex systems and so the experiments would be of shorter duration while still being capable of representing population and simple community performances. Such systems would be useful microcosms.

The time required for the simpler systems to establish NSS's and for their NSS domains to be defined was nearly as long as that required in the more complex laboratory systems. The simpler systems required 9 to 15 months to establish NSS's, depending upon the levels of E and I. Several months were then required to adequately define the NSS domain of system behavior. Thus, because of the time needed for establishment and documentation of NSS's and the shortened funding period of the Cooperative Agreement, toxicant had not been introduced prior to preparation of this report. The experiment is being continued with funding from other sources and toxicant eventually will be introduced.

RESULTS AND INTERPRETATION

Trophic Organization of the More Complex Laboratory Communities

Trophic organization entails that aspect of community organization based on interactions between species populations for food resources. Figure 5 represents the inferred major trophic relations in the laboratory systems.

Organic sediments including the alfalfa-OTD ration and microorganisms were the common prey for three of the major populations: guppies, amphipods, and snails. The microorganism component included nematodes, flagellates, rotifers, gastrotrichs, and protozoans (Finger, 1980). Differences in alfalfa input, 0.6 or 4.0 grams per day, were the major source of differences in sediment densities between systems at LOW I and HIGH I.

Guppies are omnivorous, live-bearing, cannibalistic fish. Adult females (up to 42 mm and 2.0 grams) and mature males (up to 20 mm and 0.1 grams) were observed consuming the alfalfa-OTD ration, sediments, and amphipods. Stomach samples showed the presence of materials and micoorganisms identified in the sediments, plus amphipod parts. Newborn guppies were observed eating alfalfa and picking through the sediments.

The amphipods in these laboratory systems were herbivorous crustaceans that ranged in size from 0.5 to 15.0 millimeters (0.04-4.0 mg). They were observed feeding in the sediments and on the alfalfa-OTD ration. Amphipods moved freely throughout the tank and were found among the rocks and on the sides of the tanks when guppies were absent or at low densities. Their movement was usually limited to among the rocks and the sediment when guppies were present. Amphipods were prey of the guppy populations, although probably not as preferred a prey as the alfalfa ration. Amphipods were also competitors of the guppies for the alfalfa-OTD ration.

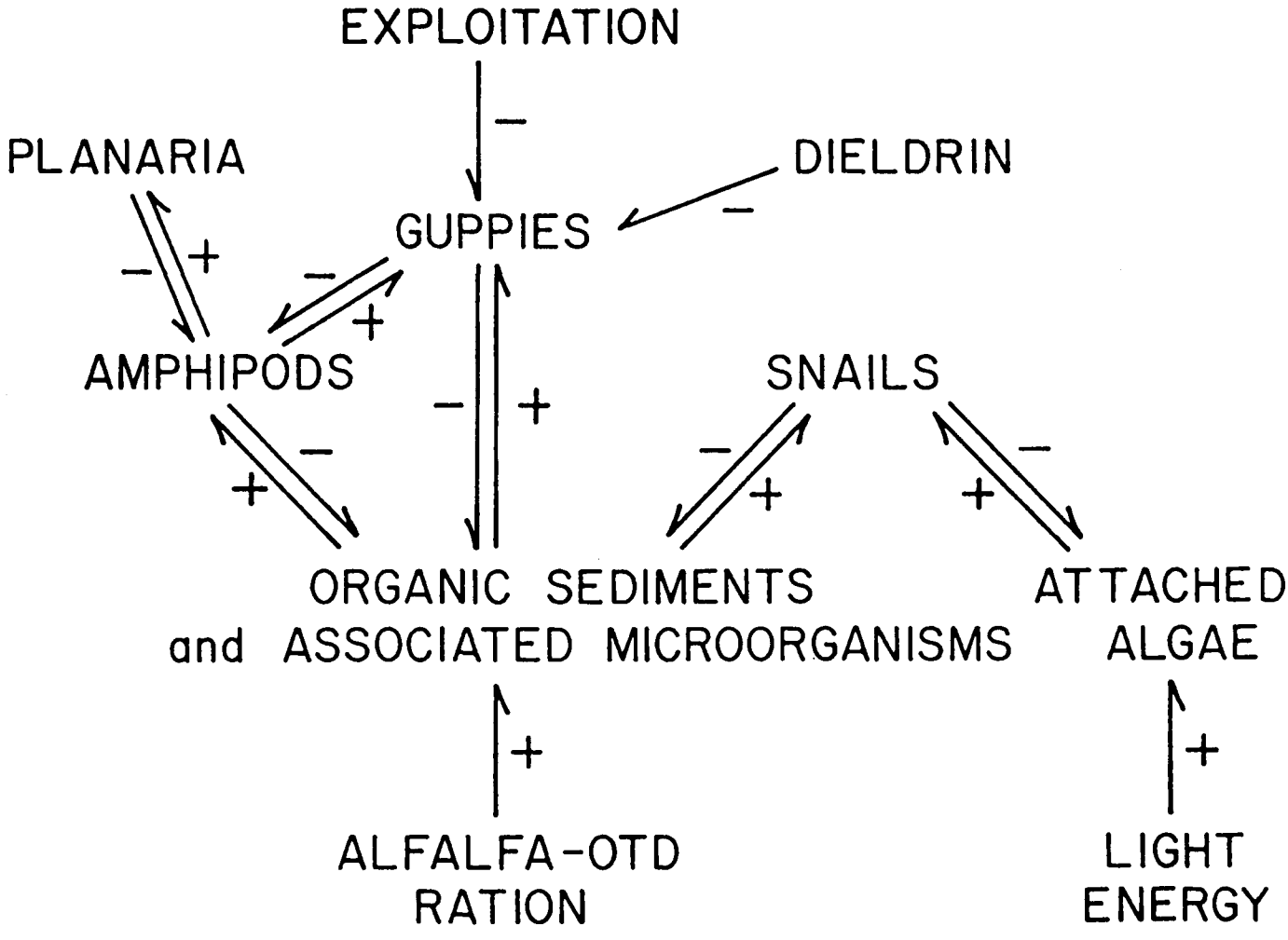


Figure 5. Kinetic diagram representing inferred trophic interrelations in the laboratory communities.

Snails were introduced as eggs attached to aquatic plants. Snails were observed eating attached algae on the sides and bottom of the tanks as well as feeding in the sediments. They were competitors of both guppy and amphipod populations for the alfalfa-OTD ration. Increased I brought about dramatic increases in snail biomasses. Censusing of snail populations in both HIGH I and LOW I systems was initiated about this time.

Planaria were inadvertently introduced and were more effective predators on amphipods than were guppies, the amphipods being unable to escape from planaria in the rock substrate. Planaria were observed in all systems at low densities (i.e., 1 to 30 individuals) as early as October 1977. Following the increase in energy and material input and substrate cover in eight systems, amphipod populations increased up to 15 times in biomass. Planaria populations increased following the increase in amphipods, and this led to drastic declines in amphipod populations. Intensive planaria control in four HIGH I systems allowed the amphipods to again increase. Planaria were not controlled in the remaining four systems at HIGH I and they eventually eliminated all the amphipods.

Attached algae included a mixture of blue-green and green algae and diatoms. These algae and associated microorganisms were a food resource for snails and probably other species in the laboratory systems.

Multisteady-state Structure and Organization Prior to Dieldrin Introduction

Habitat availability and energy and material input rate (I) and exploitation (E) were defined as components of the environment of the laboratory communities. Different environmental states were obtained by fixing I and E at different levels. We did not expect any system to establish

a perfect steady-state, for this is a theoretical concept. Rather we expected that system behavior would be localized to a region in phase space (a near steady-state) and, further, that the region or localized domain of behavior would be different under different sets of environmental conditions.

NSS structures of the laboratory communities prior to dieldrin introduction are represented on guppy-amphipod and guppy-snail phase planes shown in Figures 6A, 7, 8, and 9. NSS relations between amphipods and snails can be inferred from these relations. Mean NSS biomasses of the species composing the systems are given in Table 2. In the four systems at LOW I that were exposed to dieldrin, snail biomasses prior to dieldrin introduction were not determined.

At LOW I, increased E brought about reductions in NSS guppy biomasses and increases in NSS amphipod biomasses (Fig. 6). Increased amphipod biomasses apparently resulted from reduction in intensity of predation and possibly competition by guppies owing to reduction in guppy biomass.

Prior to introduction of guppies into the laboratory systems, amphipod populations reached maximum biomasses of 7.5 grams, the range at the time of guppy introduction being 0.5 to 5.0 grams. Introduction of guppies resulted in establishment of NSS amphipod biomasses that were much lower than the biomasses that existed prior to guppy introduction.

At HIGH I, NSS relationships between populations were shifted to the right on each phase plane, resulting in increased NSS biomasses of guppies, amphipods, and snails at each E (Figs. 8, 9, Table 2). This broadly conforms to the responses to increased I shown in Figures 1 and 3.

At HIGH I in systems in which planaria were controlled (open symbols, Fig. 9), the relationship between guppy and snail biomasses was an inverse

Figure 6. Guppy-amphipod phase plane at LOW I. A. Near steady-state behavior prior to toxicant introduction. B. Behavior of the systems during toxicant introduction. C. Behavior during recovery from toxicant introduction. Fish were restocked twice at 40E during recovery. Areas encircling open symbols in B and C represent near steady-state behavior prior to toxicant introduction. (After Woltering et al., in prep.)

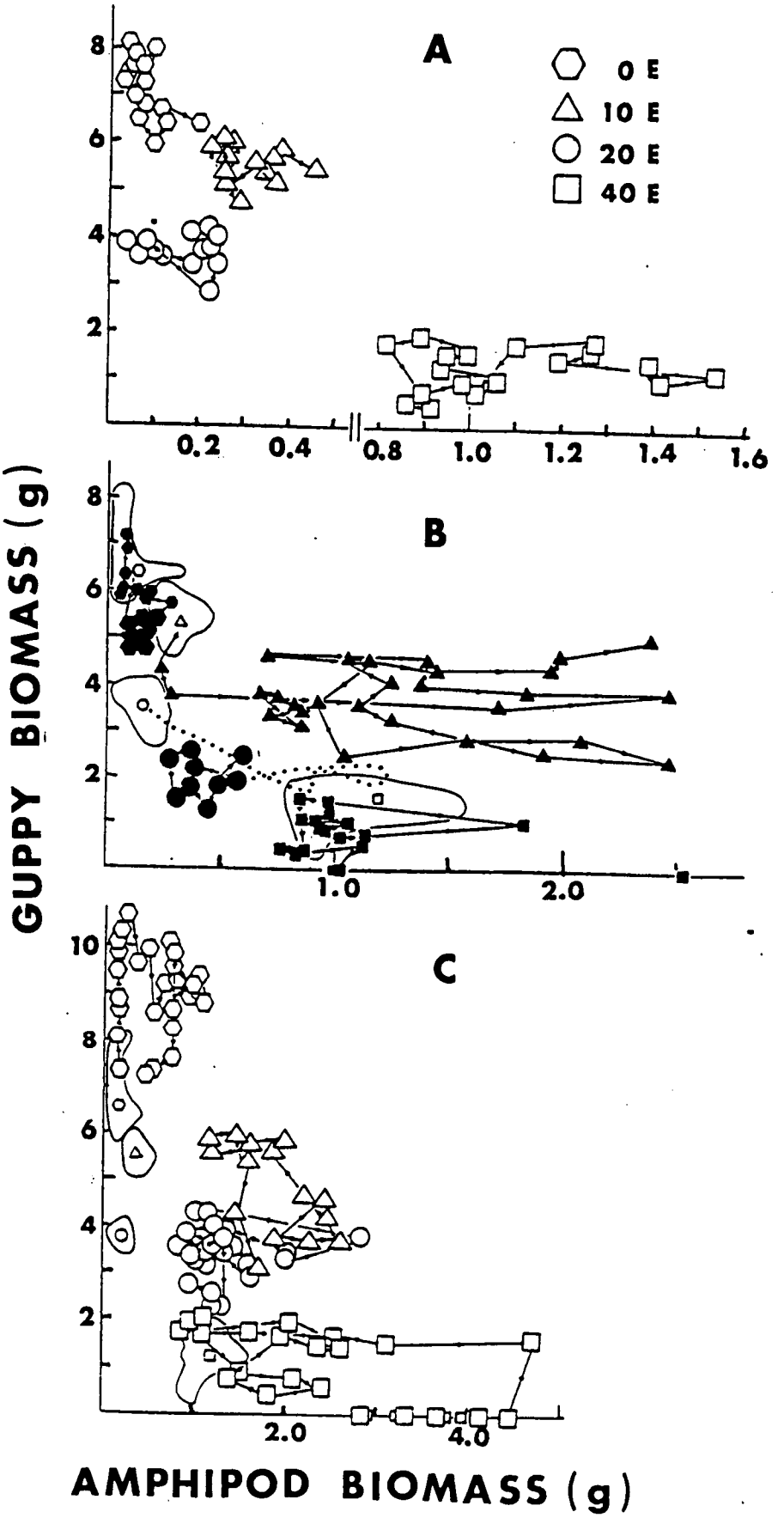

A
0 E
10 E
20 E
40 E
8
6
4
2
0.2
0.4
0.8
1.0
1.2
1.4
1.6
B
8
6
4
2
1.0
2.0
C
10
8
6
4
2
2.0
4.0
GUPPY BIOMASS (g)
AMPHIPOD BIOMASS (g)

Figure 7. Guppy-snail phase planes at LOW I. A. Near steady-state behavior during toxicant introduction. B. Behavior of the systems during recovery from toxicant introduction. Fish were restocked twice at 40E during recovery. (After Woltering et al., in prep.)

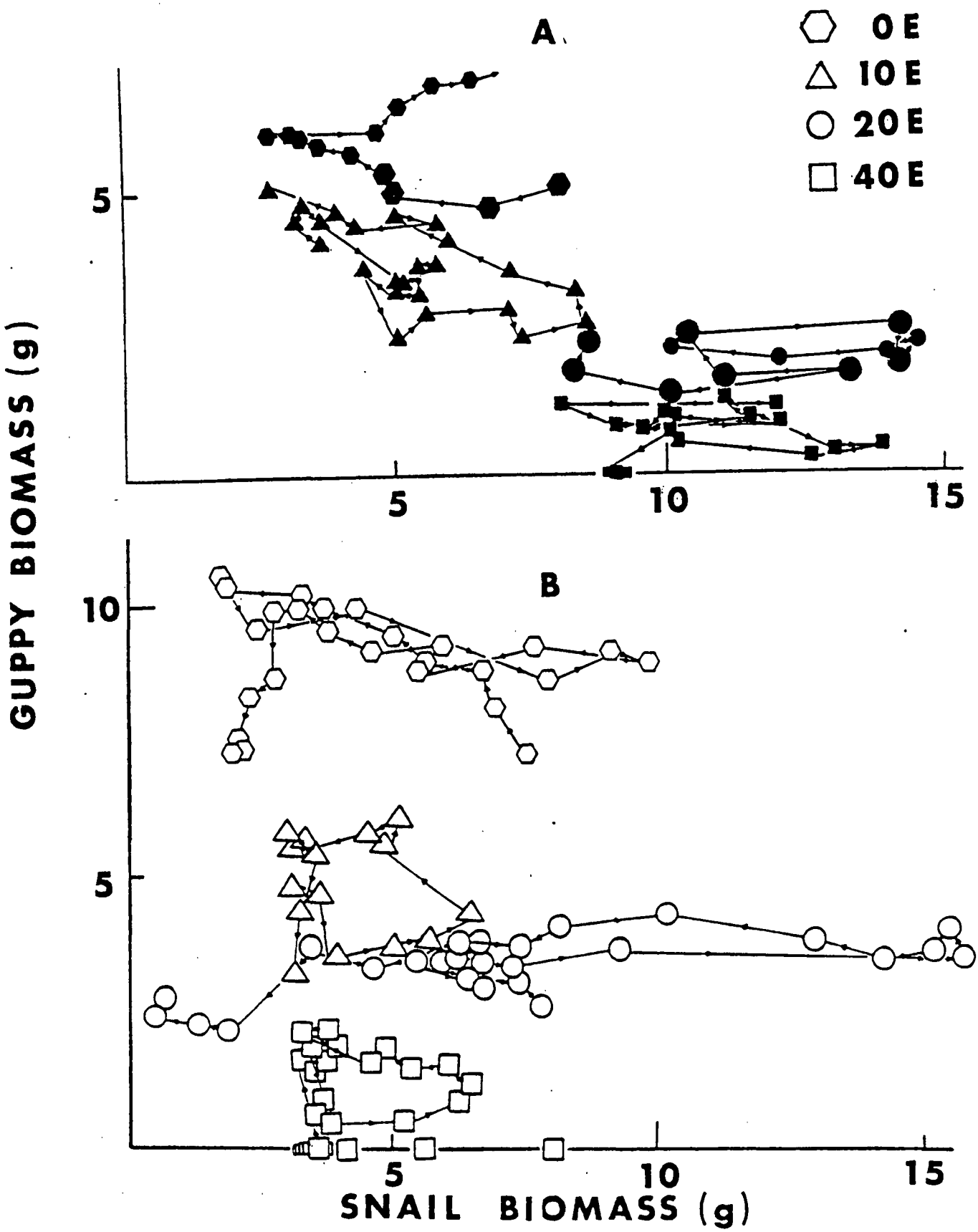

A
0E
10E
20E
40E
5
5
10
15
B
10
5
5
10
15
GUPPY BIOMASS (g)
SNAIL BIOMASS (g)

Figure 8. Guppy-amphipod phase plane at HIGH I. Open symbols indicate near steady-state behavior at HIGH I prior to toxicant introduction. Closed symbols indicate behavior at HIGH I during toxicant introduction. The trajectories show actual system behavior prior to establishing near steady-states. The hatched section represents the domain of behavior of the systems at LOW I. (After Woltering et al., in prep.)

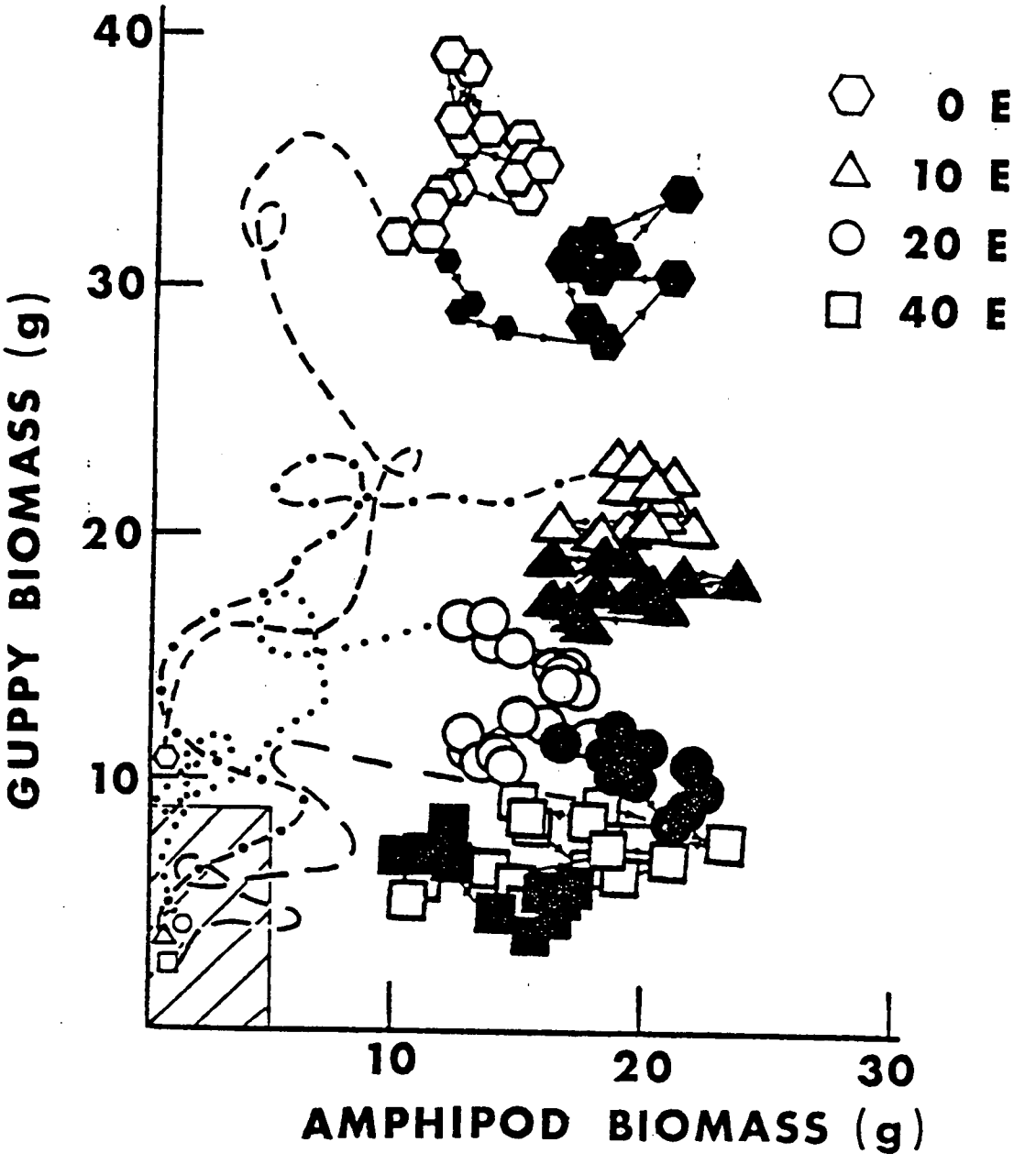

40
30
20
10
GUPPY BIOMASS (g)
0 E
10 E
20 E
40 E
10
20
30
AMPHIPOD BIOMASS (g)

Figure 9. Guppy-snail phase plane at HIGH I. Outlined symbols indicate near steady-state behavior at HIGH I for guppy-snail-planaria systems. Open symbols indicate near steady state behavior at HIGH I for guppy-snail-amphipod systems prior to toxicant introduction. Closed symbols indicate behavior at HIGH I for guppy-snail-amphipod systems during toxicant introduction. The trajectories show actual system behavior prior to establishing near steady-states. The hatched section represents the domain of behavior of the systems at LOW I. (After Woltering et al., in prep.)

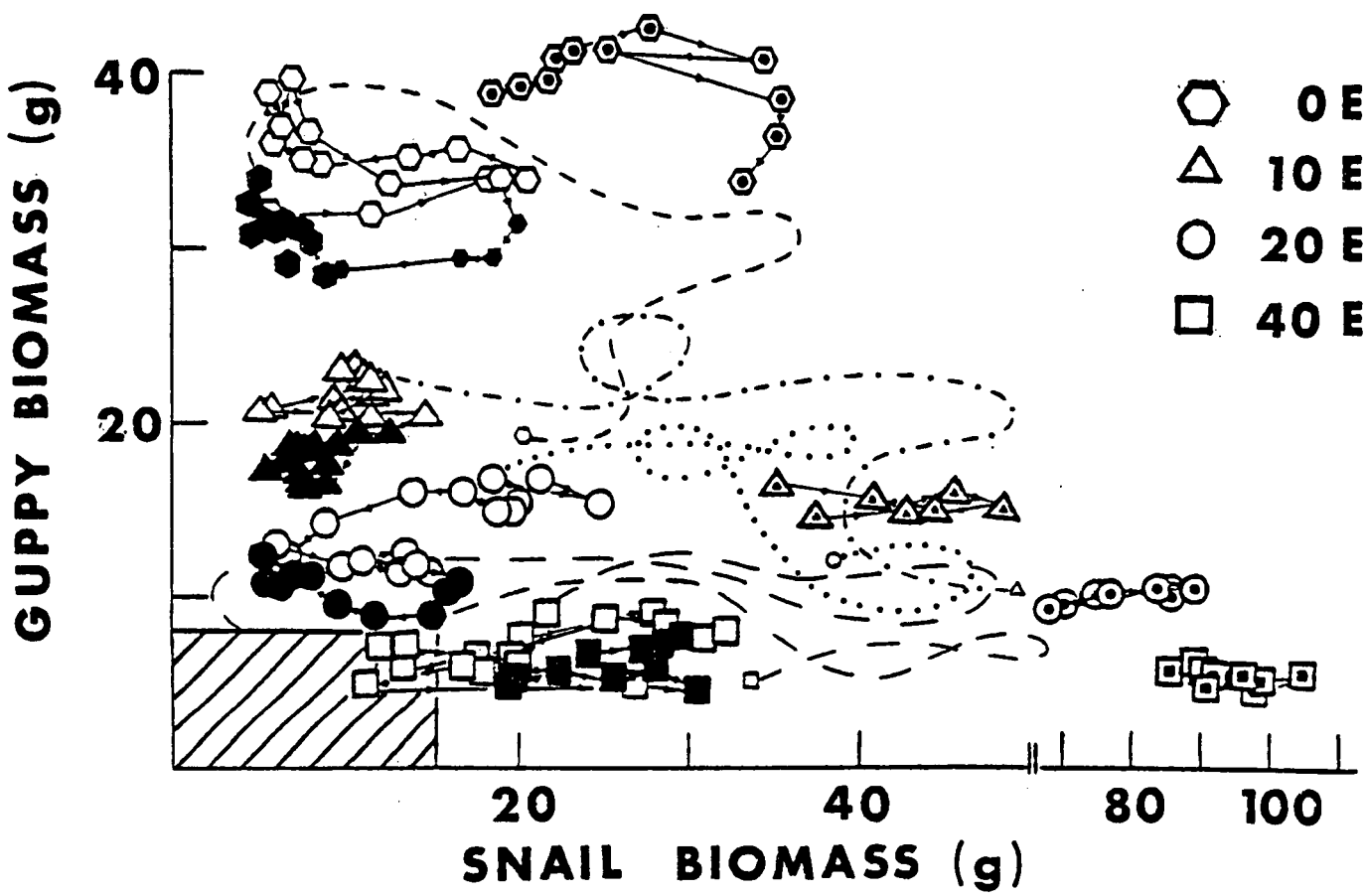

GUPPY BIOMASS (g)
40
20
0 E
10 E
20 E
40 E
20
40
80
100
SNAIL BIOMASS (g)

Table 2. Guppy, amphipod, snail, planaria, and leech near steady-state behavior mean biomasses ($\overline{B}$), number of sample periods (n), and biomass range during n in laboratory ecosystems.

SYSTEM		GUPPIES			AMPHIPODS			SNAILS			PLANARIA			LEECHES
		n	$\overline{B}$(g)	Range(g)	n	$\overline{B}$(g)	Range(g)	n	$\overline{B}$(g)	Range(g)	n	$\overline{B}$(g)	Range(g)	Density
LOW I	0E	16	7.08	5.87- 8.03	16	0.09	0.01- 0.33		N.S.			F		N
Prior to	10E	13	5.55	4.68- 6.10	13	0.30	0.22- 0.45		N.S.			F		N
Toxicant	20E	13	3.72	2.78- 4.11	13	0.16	0.03- 0.24		N.S.			M		N
	40E	18	1.29	0.71- 1.96	18	1.08	0.81- 1.54		N.S.			M		N
LOW I	0E	8	5.05	4.71- 5.39	8	0.13	0.09- 0.20	4	6.2	4.8- 8.0	8	<	0.00- <	N
Toxicant	10E	29	3.74	2.35- 5.00	29	1.31	0.23- 2.45	24	5.2	2.7- 8.5	29	<	0.00-0.01	F
Intro.	20E	9	1.99	1.31- 2.55	9	0.41	0.25- 0.59	8	11.2	8.2-14.2	8	0.02	0.01-0.05	N
	40E*	3	0.00	-----	3	1.52	1.03- 2.53	3	9.0	8.8- 9.2	3	0.05	0.03-0.08	N
LOW I	0E	26	9.06	7.25-10.73	26	0.48	0.04- 1.02	26	4.7	1.8- 9.8	26	<	0.00-0.01	N
Recovery	10E	15	4.80	3.17- 5.91	15	1.81	1.13- 2.60	15	4.1	3.1- 6.4	15	0.01	0.00-0.04	F
	20E	26	3.41	2.19- 4.27	26	1.30	0.84- 2.73	26	7.4	0.1-15.8	26	<	0.00- <	F
	40E	26	0.94	0.00- 2.09	26	2.55	0.86- 4.67	26	4.4	3.3- 8.0	25	0.05	0.01-0.13	N
HIGH I	0E	11	39.40	33.81-42.69	11	0.00	0.00- 0.00	11	27.06	18.60-35.56	11	0.48	0.24-1.02	M-N
Planaria	10E	7	15.39	14.47-16.37	7	1.08	0.09- 2.80	7	42.0	35.1 -48.3	7	1.31	0.02-2.88	N
	20E	8	10.04	9.53-10.41	8	0.74	0.28- 1.37	8	79.6	68.4 -89.7	6	0.49	0.07-1.72	N
	40E	9	5.38	4.96- 5.94	9	0.00	0.00- 0.00	9	94.14	90.54-104.56	9	1.59	0.82-2.50	M-N
HIGH I	0E	15	35.30	32.06-39.79	15	13.28	9.56-15.42	15	11.22	5.12-20.66	15	<	0.00-0.01	M
Prior to	10E	13	21.55	20.30-23.14	13	19.38	16.02-21.59	13	10.14	5.22-14.64	13	<	0.00- <	M
Toxicant	20E	17	13.79	11.27-17.02	17	14.78	12.24-17.75	17	14.98	5.36-25.03	14	0.24	0.03-0.59	F
	40E	17	7.31	5.04- 9.28	17	16.32	10.33-23.11	17	21.14	11.83-32.16	17	0.01	0.00-0.06	H
HIGH I	0E	10	31.18	28.38-34.19	10	17.54	12.76-20.85	10	6.40	4.46- 9.16	10	0.00	0.00-0.00	N
Toxicant	10E	14	18.04	16.63-19.71	13	18.48	15.79-23.35	14	8.34	5.24-12.45	14	0.00	0.00-0.00	N
Intro.	20E	10	10.72	8.88-12.49	10	19.86	16.30-22.29	10	10.01	5.26-16.02	10	0.17	0.10-0.29	N
	40E	10	6.27	4.84- 8.44	10	14.15	10.12-17.13	10	25.62	19.47-30.82	10	0.00	0.00-0.00	N

N.S. = not sampled. 0.00 = no individuals found. < = less than 0.01 g. N = none, F = few, M = moderate, H = high.

* This represents system structure after extinction.

one, with reductions in NSS guppy biomass owing to increased E being accompanied by increases in NSS biomass of the snail competitor. Amphipods were abundant in these systems (Table 2). Interestingly, leeches maintained a relatively high density in the system at 40E but did not severely reduce snail biomass. Snails may have been able to sustain relatively higher predation intensities by leeches at HIGH I, 40E because the low density of the guppy competitor and the high rate of energy and material input may have made more food available for snails, leading to higher rates of reproduction and production.

At HIGH I in systems where planaria were not controlled (outlined symbols, Fig. 9), amphipod populations were maintained at very low levels or driven to extinction by planaria predation (Table 2). That planaria were capable of preying effectively on amphipods was verified by placing planaria and amphipods together in small dishes and observing predation take place. The form of the relationship between guppies and snails in the systems in which planaria were not controlled was an inverse one, similar to that observed in the HIGH I systems in which planaria were controlled. The relationship, however, was shifted to the right on the phase plane. At each E, snail populations maintained higher NSS biomasses when planaria were abundant and amphipod densities severely reduced, than when planaria were controlled and amphipods were abundant (Table 2). Reduction in intensity of competition with amphipods owing to reduced amphipod densities may have allowed snails to maintain these higher densities. NSS guppy densities did not appear to be greatly affected by amphipod elimination.

When the amphipod competitor was absent, changes in NSS guppy biomass had a much greater effect on NSS snail biomass. In these systems there was

over a three-fold difference in snail biomass between 0E and 40E. In the systems in which amphipods were present the difference in snail biomass between 0E and 40E was less than two-fold.

NSS amphipod biomasses in systems where planaria were controlled appeared to be unaffected by changes in guppy and snail biomasses resulting from guppy exploitation (Fig. 8). Because of the large amount of rock substrate available as an amphipod refugium at HIGH I and a greater availability of their preferred food, the alfalfa ration, guppies may not have preyed as effectively on amphipods and thus had little direct predatory effect on their biomasses. The nature of the competitive interactions of amphipods with guppies and snails is less clear. Competitive interactions between amphipods and snails appear to be relatively intense, as evidenced in Figure 9 by the large decreases in snail biomasses that occurred when planaria were controlled and amphipods were abundant. And yet, in systems where planaria were controlled, changes in snail biomass brought about by changes in the biomass of guppies had little apparent effect on amphipods (Fig. 8). The situation is further confused by the presence of Hyallela (densities unknown) in the systems at 0E and 20E, with the systems at 0E being composed mostly of Hyallela.

Structure and Organization of the Laboratory Communities After Introduction of Dieldrin

In general, the responses of the laboratory communities to continuous exposure to one ppb of dieldrin broadly conformed to the responses outlined in the Introduction (Fig. 2). Responses entailed alteration in system structure and organization, characterized by shifts in location or position of the system NSS points in phase space. All systems, with the exception of the system at LOW I, 10E, established NSS's during exposure to dieldrin

(Figs. 6B, 7A, 8, 9). Although dieldrin altered system structure and organization, in the sense of shifting the location of NSS points, about the same forms of relationships between populations were maintained. Thus, at LOW I, after dieldrin introduction, an inverse relationship was maintained between NSS guppy and amphipod biomasses (with the exception of 10E) and between NSS guppy and snail biomasses (Figs. 6B, 7A). At each E, during dieldrin introduction, the guppy population maintained lower biomasses and the amphipod population higher biomasses than the biomasses these populations maintained prior to dieldrin introduction (Table 2). Since censusing of snail populations at LOW I did not begin until about six months after dieldrin introduction, effects on snail biomass in the four systems exposed to dieldrin cannot be determined. At HIGH I, after dieldrin introduction, the forms of the NSS relations between populations were similar to the forms of these relations prior to dieldrin exposure (Figs. 8, 9).

Experiments were conducted at our laboratory on the effects of dieldrin on individual organisms of the species present in the laboratory systems to enable us to better explain the effects observed in the systems. The 96-hour LC50 of newborn guppies was about 5 ppb and that of adult females about 20 ppb. Dieldrin concentrations of 1 ppb and 2 ppb affected age-specific growth, survival, and reproduction of guppies (Kulbicki 1980). The 96-hour LC50 for amphipods was about 50 ppb. Sublethal effects on amphipods could not be reliably determined, because of difficulties in maintaining individuals and populations in aquarium studies outside the laboratory communities. Thus, a dieldrin concentration of one ppb in the laboratory systems probably directly affected guppy survival, growth, and reproduction (Woltering 1981, Liss et al. 1980) and only indirectly affected other populations through its effects on guppies.

At LOW I, OE, after introduction of dieldrin, there was an immediate decrease in guppy biomass (Fig. 6B). Amphipod populations increased slightly as a result of the decrease in biomass of their guppy predator and competitor. Numerous male and adult female guppies died in the first few months after exposure. Such mortality was not apparent in the other three systems receiving dieldrin. At OE prior to dieldrin introduction, the guppy population maintained a relatively high NSS density and apparently there was less food available per individual and slower individual growth than at higher exploitation rates (Liss et al. 1980). Thus, the fish were in relatively poorer condition and apparently were highly susceptible to dieldrin intoxication.

After the introduction of dieldrin, the system appeared to establish a new NSS at a guppy biomass of about five grams and an amphipod biomass of about 0.4 grams. The system maintained this structure for about eight months. Although dieldrin was still being introduced, the system began to recover from toxicant perturbation, with guppy biomass gradually increasing and amphipod biomass decreasing. The structure of the recovering system eventually overlapped the NSS structure that existed prior to dieldrin introduction.

At LOW I, 10E, amphipod biomass became highly variable after dieldrin introduction, exhibiting as much as a four-fold difference in density (Fig. 6B). The reasons for this are not known, however, it was not due to colonization of this system by other species. These large fluctuations in amphipod density and to a lesser extent guppy density (about a two-fold fluctuation) preclude identification of a well-defined NSS region on the guppy-amphipod phase plane. However, a NSS region is much better defined on the guppy-snail phase plane (Fig. 7B). The relatively large fluctuations in amphipod

biomass did not appear to greatly influence guppy and snail dynamics.

At LOW I, 20E, the system established a new NSS structure in the presence of dieldrin with NSS biomass of guppies lower and amphipod biomass higher than their NSS biomasses prior to dieldrin introduction (Fig. 6B).

At LOW I, 40E, guppy populations went extinct after 15 months of continuous exposure to dieldrin (Figs. 6B, 7A, also see Fig. 2). For the first eight months after introduction of dieldrin, there were no obvious changes in the structure of the system. Guppy populations exploited at 40E maintained very low densities and often had size distributions with over 70 percent of the biomass in one large female. This sometimes resulted in significantly more or less than the prescribed 40 percent of the biomass being exploited in any given month. Over many months, however, mean exploitation rate was near 40 percent.

This system had been exploited by 77 and 82 percent in two of the 18 months prior to dieldrin introduction. The population recovered from these incidences of "overexploitation". After ten months of continuous exposure to dieldrin, the system was again overexploited at 75 percent (a one gram female). The population did not recover in the following five months and went extinct with the removal of a 0.2 and 0.5 gram female. The two fish carried a total of 42 eggs and embryos. For seven months prior to extinction, the number of newborn fish was at least 70 percent lower than the number of newborns present prior to dieldrin introduction. There had been no newborn fish present in the tank for three months prior to extinction.

Severe reduction in density, simplification of age structure, and possible reduction in genetic variation and adaptive potential sometimes associated with low population densities (Franklin, 1980, Soule 1980,

Frankel and Soule 1981) must surely make populations more susceptible to chance extinction. Thus, we can never be sure that extinction was causally related to dieldrin exposure, but the available evidence makes this a plausible explanation.

Severe reduction and elimination of offspring recruitment occurred for several months prior to extinction. These low levels of recruitment were not apparent prior to dieldrin introduction at similar adult densities. Furthermore, the few females that were present prior to extinction carried sufficient eggs, if they would have survived and grown, to replenish the adult stock. This suggests that reduction in offspring survival and recruitment to mature size classes may have been the proximate cause of extinction. Offspring survival may have been reduced due to accumulation of dieldrin in eggs.

In the laboratory community at LOW I, 40E into which dieldrin was not introduced, the guppy population persisted for 65 months, until the termination of the experiment, occasionally being subjected to the same kind of "overharvest" as the population exposed to dieldrin. This further supports the conclusion that guppy population extinction was related to exposure to dieldrin.

Finally, nine months after extinction, when dieldrin introduction had been terminated, the system was restocked with guppies. Nine months afterward this population essentially went extinct, the only remaining fish being an adult male. The system was again restocked. Possibly the fish were able to accumulate in their eggs enough dieldrin from that remaining in the organic sediments and their food organisms to again bring about reductions in offspring survival.

After extinction of guppies, amphipod biomass increased, reaching levels that the population had not attained since guppies were introduced. In addition, behavioral changes occurred, the amphipods moving more freely throughout the tank rather than restricting their movement primarily to the rock nests.

During introduction of dieldrin, NSS guppy biomass was inversely related to NSS snail biomass. Increased E resulted in a reduction in NSS guppy biomass and an increase in NSS biomass of the snail competitor. This is the same form of relationship observed at HIGH I (Fig. 9).

At LOW I, system response to dieldrin varied with exploitation rate, responses ranging from perturbation and recovery at OE to guppy extinction at 40E. The response of the laboratory communities to dieldrin appeared to be dependent upon the level of I as well as E. At HIGH I, all systems established new NSS's after introduction of dieldrin (Fig. 8, 9). The alteration of system structure and organization at each exploitation rate was much less than at LOW I. At HIGH I, during dieldrin introduction, the guppy population at each E maintained somewhat lower NSS biomasses than the biomasses it maintained prior to dieldrin introduction. However, at HIGH I the changes in mean NSS biomasses of guppies as well as amphipods induced by exposure to dieldrin were not nearly as great as the changes that occurred at LOW I (Table 3).

At HIGH I mean NSS biomasses of snails at OE, 10E, and 20E appear to have been reduced somewhat by exposure to dieldrin (Table 2). However, the domain of NSS behavior of snail biomass prior to dieldrin introduction is rather large (Fig. 9, Table 2). Although mean NSS snail biomasses prior to and after dieldrin introduction are different, the domain of behavior of snail biomass after dieldrin introduction is within the domain of behavior prior

Table 3. Percent change in mean NSS biomasses following toxicant introduction.

SYSTEM	GUPPIES		AMPHIPODS		SNAILS	
	LOW I	HIGH I	LOW I	HIGH I	LOW I*	HIGH I
0E	-28.7	-11.7	+44.4	+32.1	-	-43.0
10E	-32.6	-16.3	+366.7	-4.6	-	-17.8
20E	-46.5	-22.3	+156.3	+34.4	-	-33.2
40E	-100.0	-14.2	+41.0	-13.3	-	+21.1

* No snail data were taken in systems prior to toxicant introduction.

to dieldrin introduction. Thus, for snails, the mean values may not be indicative of the actual magnitude of effect on snails.

At LOW I, the guppy population exploited at 40E was driven to extinction apparently by exposure to dieldrin. At HIGH I, the guppy population at 40E persisted for nine months after dieldrin introduction, until the experiment was terminated. This population was not exposed to dieldrin for as long a period of time as the population at LOW I. However, the population maintained a relatively high density and there was no indication from observations of offspring survival and recruitment that the population was in danger of extinction. Prior to introduction of dieldrin into the system at HIGH I, 40E, the mean NSS number of newborn fish (fish less than 10 mm) was 60. For the four successive months prior to termination of the experiment, the number of newborns observed in the system was 64, 99, 93, and 63. At LOW I, 40E, for many months prior to extinction the number of newborns was considerably lower than the number maintained prior to dieldrin introduction. Population persistence may be determined by the levels of I as well as E, as is shown in Figures 2 and 3.

Recovery of Systems at LOW I From Dieldrin Perturbation

Changes in community structure and organization after termination of dieldrin introduction were examined in the four systems at LOW I to determine if the systems would recover to structures they maintained prior to dieldrin introduction. Over the time period in which recovery was evaluated the systems maintained structures that were different from the structures they maintained during dieldrin introduction (Figs. 6B, 6C, 7A, 7B), however they did not return to the structures they maintained prior to toxicant introduction (Fig. 6A). Recovery of these systems was evaluated for nearly

two years. Thus ample time was available for the systems to return to their original structures.

Differences in system structures prior to recovery and structures during recovery were related to changes in system organization. During the period of recovery inadvertent colonization of the systems by the amphipod Hyallela azteca and leeches occurred. This colonization was unrelated to dieldrin exposure. Furthermore, unavoidable long-term changes in the system such as accumulation of organic sediments also may have occurred. These kinds of changes in system organization brought about changes in system capacity. A system whose capacity has changed cannot recover or return to its original structure(s) even if the environment can be restored to its original state(s). Changes in system capacity brought about by colonization make it difficult to ascertain whether capacity had been altered by exposure to dieldrin.

In the system at OE, amphipod and guppy biomasses were higher than the biomasses these populations maintained prior to dieldrin introduction or during dieldrin introduction (Fig. 6C, Table 2). Guppy biomass had begun to increase even before termination of dieldrin introduction at this exploitation rate. Snails maintained about the same biomass during recovery as they maintained during dieldrin introduction (Fig. 7A, B). Hyallela became the dominant amphipod species in this system, nearly excluding Gammarus, which persisted only at very low densities when Hyallela was not present (e.g. Fig. 6A).

At 10E, during recovery, the guppy population returned to about the same density it maintained prior to dieldrin introduction, although guppy biomass was somewhat more variable during recovery (Fig. 6C). Amphipod biomass was

considerably higher during recovery than prior to or during dieldrin introduction. The reasons for this are not known. Interestingly, few Hyallela were present in this system. Snail biomass during recovery was about the same as the biomass the snails maintained during dieldrin introduction (Figs. 5A, B). Both amphipod and snail biomasses were less variable during recovery than during dieldrin introduction.

At 20E, during recovery, guppies maintained about the same biomass they maintained prior to dieldrin introduction (Fig. 6C). Amphipod biomass was considerably higher during the recovery phase than prior to recovery. Hyallela colonized this system and was fairly abundant. Snail biomass was lower and far more variable during recovery than during dieldrin introduction (Fig. 5A, B). Leeches colonized the system and these together with an increase in the abundance of the guppy competitor may have accounted for the reduction in snail biomass.

The guppy population at 40E had suffered extinction during dieldrin introduction, after which amphipod biomass increased considerably (Fig. 6B, C). Nine months after extinction occurred and three months after dieldrin introduction had been terminated, guppies were restocked at a density and size structure similar to that which existed prior to dieldrin introduction. After restocking, amphipods were reduced to the biomass they maintained prior to dieldrin introduction (Fig. 6C). Nine months after restocking the guppy population effectively went extinct, being composed at that time of only one male. Guppies were again restocked. Some Hyallela were present in this system. Snails maintained lower biomasses during recovery than during dieldrin introduction (Fig. 7A, B). The reasons for this are not clear.

At 0E, the guppy population maintained a higher biomass during recovery than it maintained prior to and during dieldrin introduction. It is possible

that the capacity of this population was altered evolutonarily as a consequence of exposure to dieldrin. This will be considered in the discussion. At 10E and 20E, the guppy populations maintained about the same biomasses during recovery as they maintained prior to dieldrin introduction.

Amphipod population biomasses at all E were higher during recovery than at any time prior to the recovery phase. At 0E, 20E, and possibly 40E, this may have been related to colonization of the systems by Hyallela. Hyallela may make more efficient use of the resources than Gammarus and/or be less susceptible to biomass reduction due to predation and possibly competition from guppies and snails.

At 20E and 40E, snail populations maintained lower biomasses during recovery than during exposure to dieldrin. This may be related to the presence of leeches in the systems and increases in densities of the guppy competitor.

At 20E, 40E, and, at least in part, at 0E changes in community organization brought about through colonization of the systems by Hyallela and leeches can account for differences in structure of the communities during the recovery phase and prior to recovery. Colonization, by bringing about changes in community organization and consequent changes in system capacity, shifted the location in phase space of the system NSS points at each level of I and E.

Guppy Life History Patterns and Guppy Population Production and Yield Prior to and During Dieldrin Introduction

The life histories of individual organisms include the patterns of growth and reproduction they manifest when exposed to different sets of environmental

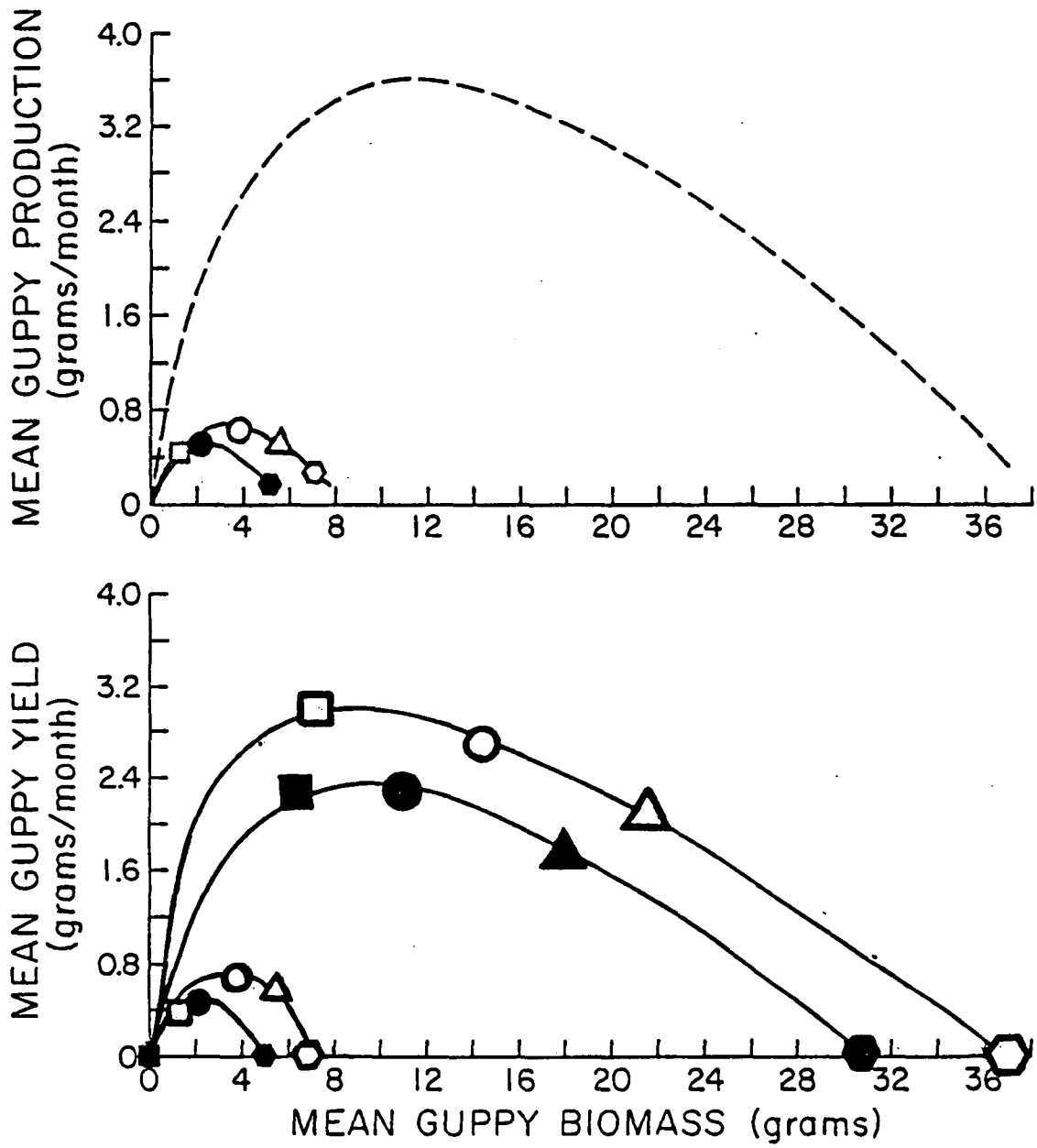
conditions. Guppy size-specific relative growth and reproduction rates near steady-state were affected by exploitation rate, exposure to dieldrin, and level of habitat availability and energy and material input. These effects were reported elsewhere (Liss et al. 1980) and will only be summarized here.

Size-specific guppy growth was able to be determined only at LOW I. Size-specific relative growth rates were density-dependent, increasing with decreases in population biomass brought about by increased E. At LOW I, the highest growth rates occurred at 40E where population biomass was lowest, and the lowest growth rates occurred at OE where population biomass was greatest. In general, at both HIGH I and LOW I, size-specific fecundity also appeared to be density-dependent. At each E, size-specific fecundity and probably growth were greater in fish at HIGH I than in fish at LOW I, this apparently reflecting the greater availability of food.

At LOW I, dieldrin appeared to reduce the relative growth rates of juvenile fish and small mature females up to 24 mm in length and possibly of larger fish. Dieldrin also reduced size-specific fecundity of mature female guppies. At LOW I, 40E, reduced growth and fecundity but especially poor survival of newborn fish may have been responsible for bringing about population extinction.

NSS curves of guppy production, or total tissue elaboration, and yield are shown in Figure 10. At each I, increased E resulted in reduction in NSS guppy biomass, essentially shifting production and yield values from right to left along each dome-shaped curve. Increased I increased guppy food resources, this resulting in increased guppy biomass, production, and yield at each E. Thus the magnitude of the production and yield curves increased as a result of an increase in I. Dieldrin altered guppy life history patterns by reducing size-specific growth and reproduction, as well

Figure 10. Mean NSS guppy production and yield as a function of mean NSS population biomass for LOW I (smaller symbols) and HIGH I (larger symbols). Open symbols indicate NSS production and yield prior to toxicant introduction and closed symbols indicate production and yield during toxicant introduction. Production at HIGH I was not able to be determined, but the relative position that such a curve would occupy is shown by the dashed line. (After Woltering et al., in prep.)


MEAN GUPPY PRODUCTION (grams/month)
4.0
3.2
2.4
1.6
0.8
0
0
4
8
12
16
20
24
28
32
36
MEAN GUPPY YIELD (grams/month)
4.0
3.2
2.4
1.6
0.8
0
0
4
8
12
16
20
24
28
32
36
MEAN GUPPY BIOMASS (grams)

as survival, this accounting for decreased guppy biomass and reduction in the magnitude of production and yield curves at each I. These kinds of changes in the magnitude of yield curves conform to those derived in Figure 4.

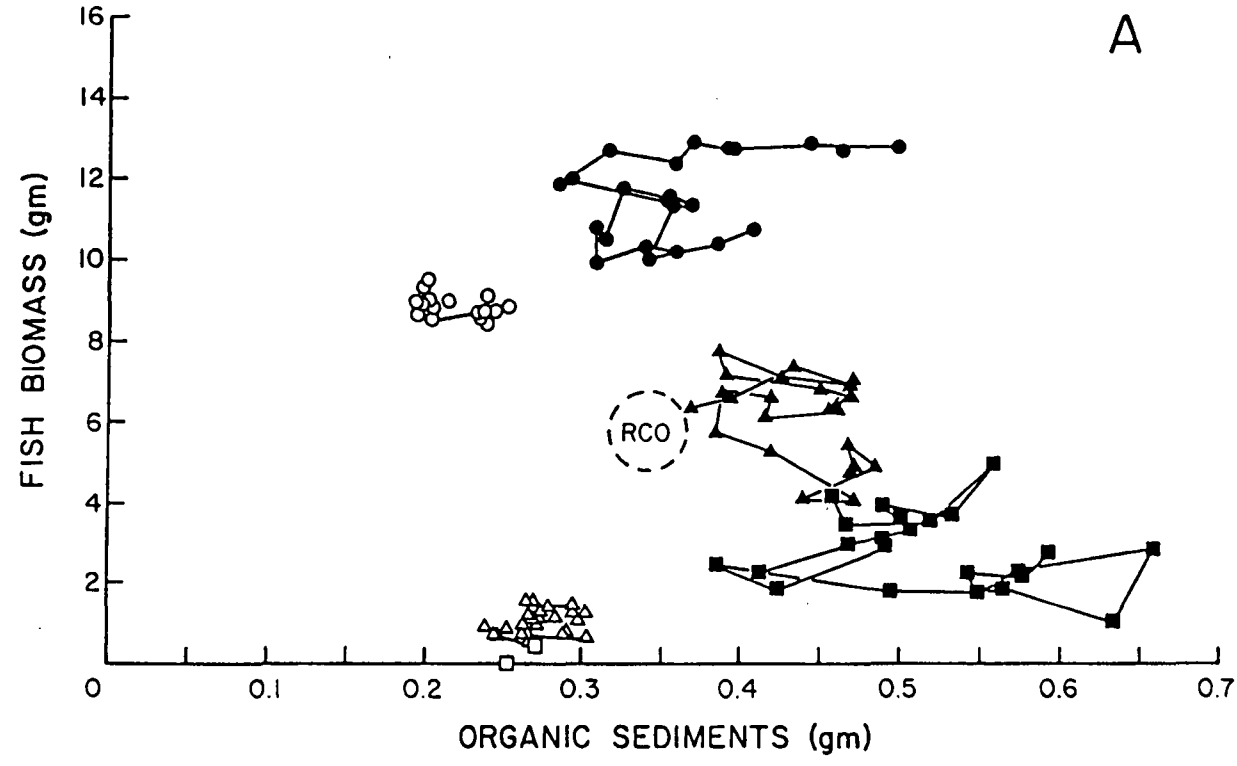
Structure and Organization of Simple Laboratory Communities in Ancillary Experiments

The laboratory communities in the ancillary experiments were intended to be persistent systems having simpler organization and being of shorter duration than the more complex laboratory communities. NSS structure and organization of the systems is shown in Figures 11 and 12 (Lee 1983). NSS domains of behavior are reasonably well-defined for most systems.

The alfalfa ration, food resource of both guppies and snails, is introduced daily and becomes part of the organic sediment. Thus organic sediment biomass may be an index of food biomass and this should be related to the biomass of guppies and snails. At both LOW I and HIGH I, when the snail competitor is not present in the system, guppy biomass is inversely related to sediment biomass (Fig. 11), with increased E resulting in a reduction in guppy biomass and an increase in sediment biomass. The relationship between guppy and sediment biomass was shifted to the right on the phase plane when I was increased from LOW I to HIGH I (Figure 11B). At HIGH I, the biomasses of both guppies and sediments are greater than the biomasses they maintained at corresponding E at LOW I. These responses are similar to those derived in Figures 1 and 3.

At both HIGH I and LOW I, the presence of a snail competitor shifted the relationship between guppies and organic sediments to the left on the phase planes (Fig. 11). When snails were present, the biomasses of both guppies and sediments were less than the biomasses they maintained when snails were

Figure 11. Phase plane representing NSS guppy and sediment biomasses at LOW I (A) and HIGH I (B) when the snail competitor is absent (G-A systems, solid symbols) and when snails are present (G-S-A systems, open symbols). NSS behavior of systems at 0E (circles), 25 E (triangles), and 40E (squares) is shown. Actual trajectories of G-A systems at HIGH I, 0E (a) and HIGH I, 40E (b), and G-S-A systems at HIGH I, 0E (c) and HIGH I, 40E (d) are shown. RCO is the region of common origin of all trajectories, that is, the biomasses at which populations were first introduced into the systems. After Lee (1983).


A
FISH BIOMASS (gm)
ORGANIC SEDIMENTS (gm)
RCO
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
2
4
6
8
10
12
14
16

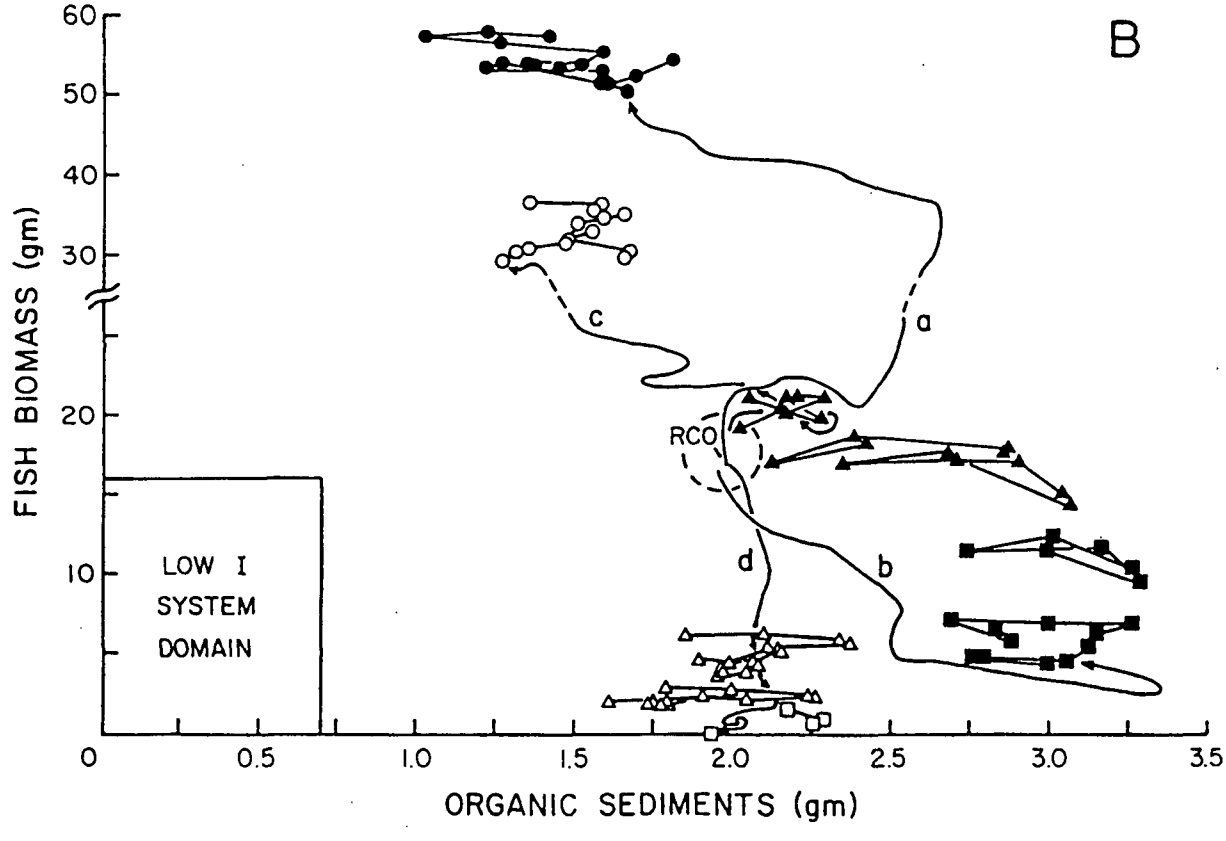
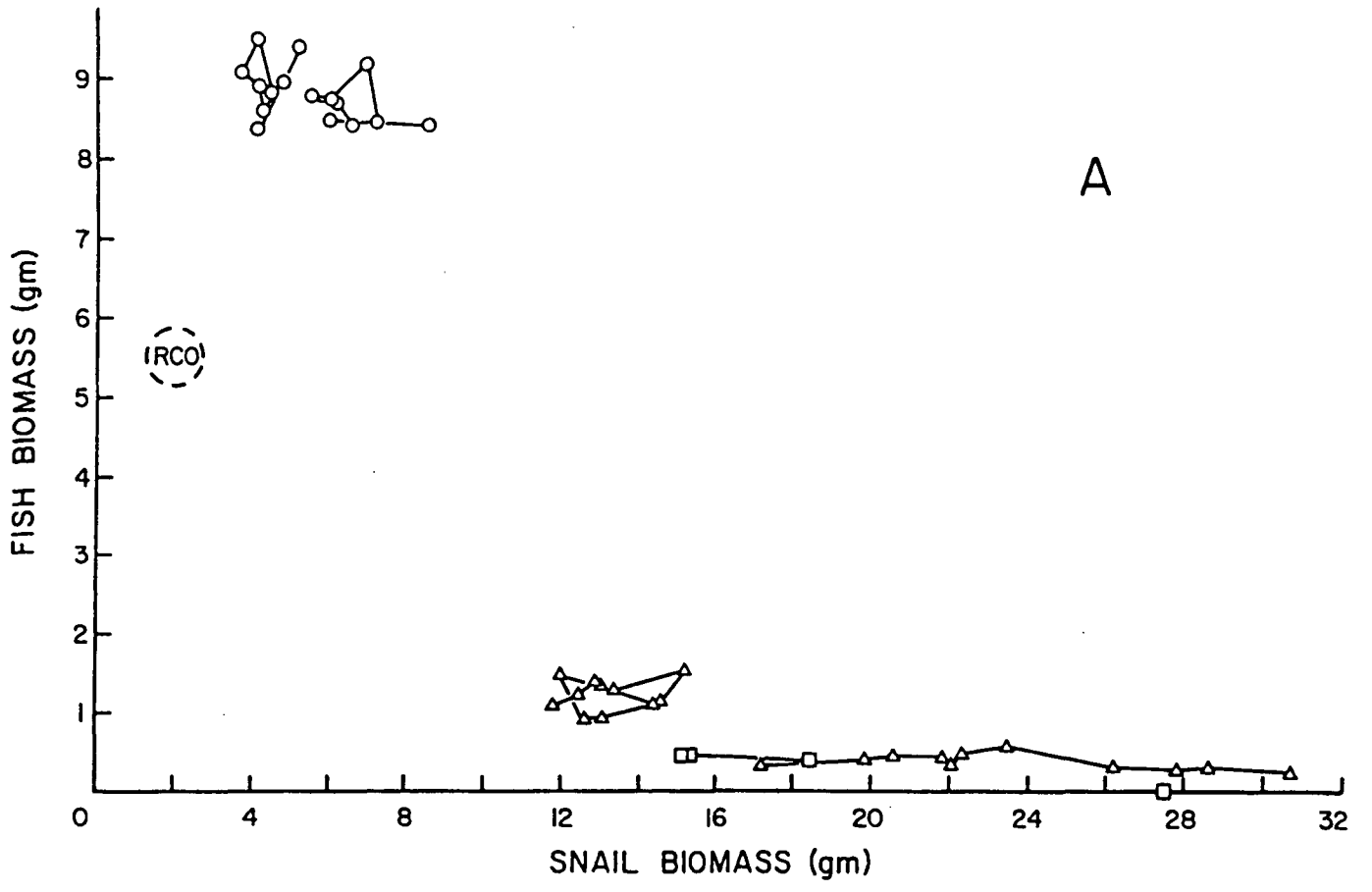
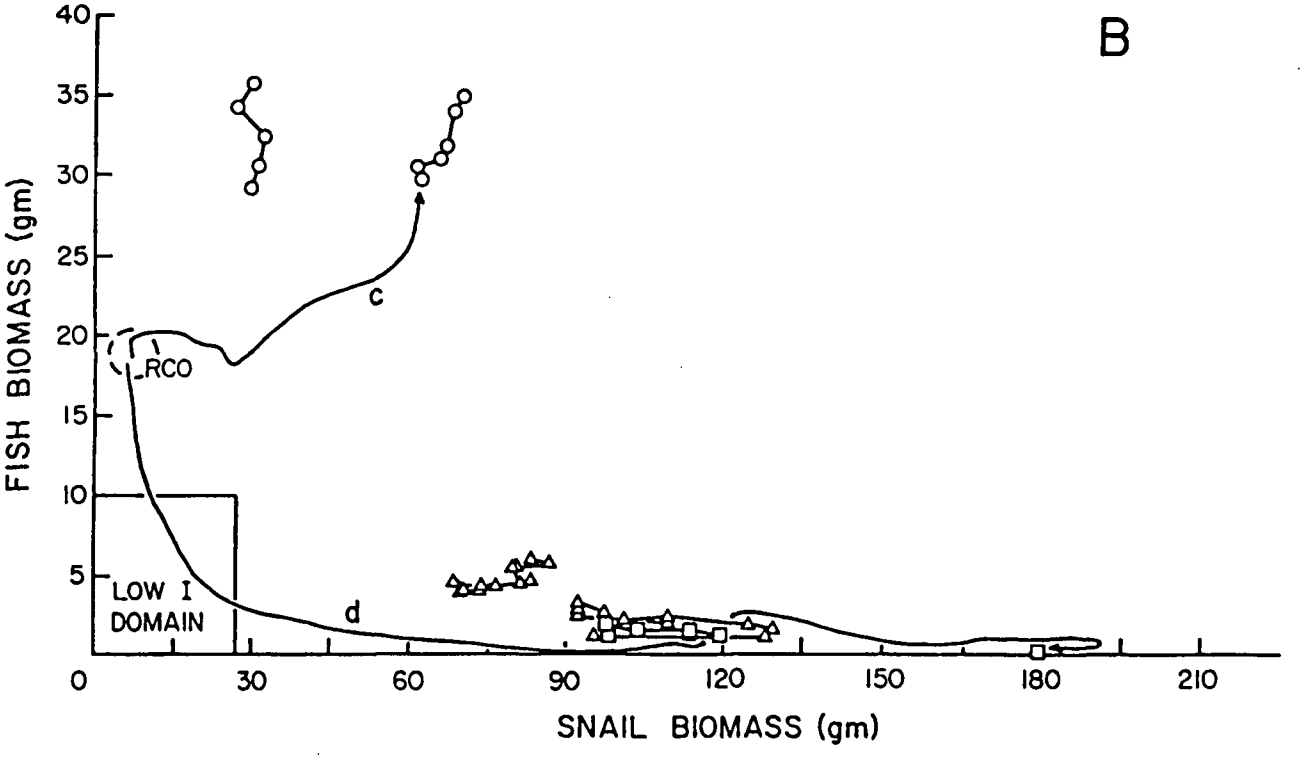

B
FISH BIOMASS (gm)
ORGANIC SEDIMENTS (gm)
LOW I
SYSTEM
DOMAIN
RCO
a
b
c
d
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
10
20
30
40
50
60

Figure 12. Phase plane representing NSS guppy and snail biomasses at LOW I (A), and HIGH I (B). NSS behavior for systems at OE (circles), 25 E (triangles), and 40E (squares) is shown. Actual trajectories of G-S-A systems at HIGH I, OE (c) and HIGH I, 40E (d) are shown. RCO is the region of common origin of all trajectories that is, the biomasses at which populations were first introduced into the systems. After Lee (1983).


A
FISH BIOMASS (gm)
SNAIL BIOMASS (gm)
RCO
0
4
8
12
16
20
24
28
32
1
2
3
4
5
6
7
8
9


B
FISH BIOMASS (gm)
SNAIL BIOMASS (gm)
RCO
LOW I
DOMAIN
c
d
0
30
60
90
120
150
180
210
5
10
15
20
25
30
35
40

absent. Presumably the presence of the snail competitor made less food available for guppies, which was reflected in reduction in sediment biomass. Consequently guppies were not able to maintain the NSS densities they maintained when snails were not present. Furthermore, at both LOW I and HIGH I, guppy populations at 40E were driven to extinction or were about to be driven to extinction in the systems in which the snail competitor was present.

At each I, in systems where snails were present, the phase plane relationship between guppy and snail biomasses was an inverse one, with a decrease in guppy biomass brought about by increased E being accompanied by an increase in the biomass of the snail competitor (Fig. 12). Increased I shifted the inverse relationship between these populations to the right on the phase plane, increasing the biomasses of both guppies and snails at each E. Thus the relationships between NSS guppy and snail biomasses observed in the ancillary, simpler laboratory communities were similar to the relationships between these populations observed in the more complex laboratory systems (compare Figs. 7, 9, and Fig. 12).

DISCUSSION

In the Introduction to this report, we advanced some premises or generalizations that partially define a perspective for understanding natural systems, their dynamics, and their response to toxicants. The perspective primarily provides a way of thinking about natural systems and was used to design, conduct, and interpret the research reported here.

It may be helpful to repeat the premises or generalizations here. Our view entails the following:

1. Under different states of the environment of a natural system, the system will come to have different steady-state structures and organizations and thus can be understood to be a multisteady-state system.

2. Dynamics or changes in structure of an n-dimensional system can be understood as an n-dimensional trajectory in continuous pursuit of an n-dimensional steady-state point whose location in phase space is continually changing as a result of changes in the state of the environment of the system.

We can add an additional generalization:

3. Any performance of a system, including its response to a toxicant, is jointly determined by its organization (capacity) and conditions in its environment.

Energy and material resource input and habitat availability, I, and exploitation, E, were defined as part of the environment of both the more complex and the simple laboratory systems. Different environmental states were generated by fixing I and E at different levels. At each environmental state, the systems established NSS's, or localized domains of behavior in phase space (Figs. 6, 7, 8, 9, 11, 12). Under different sets of environmental conditions, or different environmental states, the systems established different NSS structures. Thus, the laboratory systems can be understood as being multisteady-state systems in the sense that we have used that concept here.

Even in systems that are as simple and intensively studied as these laboratory communities, the roles of the dominant species in organizing the communities are difficult to ascertain. NSS relationships between populations in the communities were similar to those derived in Figures 1, 2, and 3. At both LOW I and HIGH I, increased E reduced NSS biomass of guppies, leading to an increase in NSS biomass of the snail competitor (Figs. 7, 9, 12). At HIGH I, the NSS relationship between guppies and snails was shifted to the right on the phase plane, with both guppies and snails maintaining higher biomasses than they maintained at LOW I (Fig. 9, 12B). The role in organizing the communities of guppy-snail competition for food was made more clear through experiments with the simpler laboratory systems. In these systems, an inverse relationship existed between NSS guppy biomass and the NSS biomass of organic sediments, an index of food level (Fig. 11). At HIGH I, both guppies and organic sediments maintained higher biomasses at each E than they maintained at LOW I (Fig. 11B). These relationships are similar to the ones derived in Figure 1. The addition of the snail competitor shifted to the left the relationship between guppy and sediment biomass at each I (Fig. 11). At both HIGH I and LOW I, the biomasses of both guppies and organic sediments were lower when the snail competitor was present than when it was absent. This is similar to the results theoretically derived in Figure 3 when an unharvested competitor was added to the system.

In the systems in which the snail competitor was absent, guppy populations were able to persist at 40E at both LOW I and HIGH I (Fig. 11, solid squares; Fig. 3, open triangle). However, at 40E at both level of I, guppy populations were driven to extinction in the systems in which the snail competitor was present (Fig. 11, open squares; Fig. 3, vertically-barred

triangle). Guppy and snail populations were able to coexist at both levels of I when guppies were less heavily exploited (Fig. 11, open circles and triangles; Fig. 3, vertically-barred square). Further, as suggested in Figure 3, the populations may have been able to coexist if the rate of input of the alfalfa-OTD ration, I, were increased to a level greater than 4.0 grams per day and/or if the snails were harvested.

The role of amphipods in organizing the communities is less well understood than the roles of guppies and snails. In the systems at HIGH I in which planaria were controlled, amphipods were very abundant, maintaining densities that were equal to or a little greater than the densities of snails. In these systems snails maintained NSS biomasses at each E that were lower than the biomasses they maintained in the systems in which amphipods were absent, the NSS relationship between guppies and snails being shifted to the left on the phase plane (Fig. 9). This is evidence that amphipods affected snail populations, perhaps through competition for food. However, at HIGH I, changes in E which brought about changes in guppy and snail biomass had no affect on the biomass of amphipods (Fig. 8). It seems as though the competitive relationship between amphipods and snails, at least at HIGH I, was unidirectional; amphipods, through changes in their density, can alter snail density, but changes in snail density have no apparent affect on amphipods.

If this is so, guppies have the capacity to affect snail populations through competition with them for food and by altering amphipod densities through predation. At HIGH I, apparently, amphipods may not have been preyed upon very heavily by guppies perhaps because they were protected from predation by the greater availability of rock substrate and/or because guppies preferred

to feed upon the alfalfa - OTD ration, which was much more attainable than amphipods and was much more abundant at HIGH I than at LOW I.

At LOW I, NSS guppy biomass was inversely related to NSS amphipod biomass (Fig. 6). Increased E resulted in reduction in the biomass of guppies and brought about an increase in amphipod biomass. Prior to stocking of guppies in these systems, amphipods maintained biomasses of up to 7.5 grams. After guppies were stocked, the highest mean NSS biomass amphipods attained was 1.08 grams at 40E. Further, amphipod biomass at this E increased rapidly to about 4.0 grams after guppy extinction (Fig. 6C).

These changes in amphipod biomass were probably brought about chiefly through predation by guppies on amphipods, although competition for the alfalfa-OTD ration may also have been involved. At LOW I, rock substrate which served as a refugium from predation was much less abundant than at HIGH I. At LOW I rocks covered only 20 percent of the bottom of each tank. Predation on amphipods by guppies was probably much greater at LOW I than at HIGH I.

Amphipods were maintained at such low densities at LOW I that they could not have been the major food source for guppies and were probably ineffective competitors of both guppies and snails. Amphipod biomasses were kept at low levels through predation by guppies, whose densities were maintained by feeding on the more accessible alfalfa-OTD ration. Thus, the dynamics of amphipod as well as guppy populations would have been quite different had an alternative food for guppies not been available. At LOW I, guppy and snail populations were inversely related and probably competed for food. At the same time, however, an indirect facilitative interaction between guppies and snails may have existed, for the guppy kept amphipods, a potentially effective

competitor of snails, at low densities. The structure and dynamics of communities are an outcome of very complex direct and indirect interactions between species. This makes it difficult to anticipate or predict a priori what the effect will be on community structure of the addition or loss of a species or a change in density of an existing species.

Colonization of a community by new species changes its organization and thus its capacity. Communities with different capacities will exhibit different performances, including structure, yield, and response to toxicants, even under the same set of environmental conditions. In terms of isocline models, changes in system structure due to changes in system capacity are reflected in alteration in the location in phase space of the isocline systems and thus of the steady-state points under each set of environmental conditions (Thompson 1981). Thus, steady-state points may be shifted in phase space not only due to changes in system environment (e.g. I and E) but also due to changes in system organization and thus capacity. Change in organization through colonization by new species and extinction of old is the process of community development.

Systems at HIGH I in which amphipods were present and those in which they were absent had different organizations and capacities and so had different structures even at the same levels of I and E (Fig. 9). At each level of I and E, the location in phase space of the NSS domains of these systems was different. Similarly, in the simpler systems, communities in which snails were present and those in which they were absent had different organizations and exhibited different performances at given levels of I and E (Fig. 11). And, after introduction of dieldrin had been terminated at LOW I, the communities were colonized by Hyallela and leeches altering their organization. Consequently they did not return to the structures they

maintained prior to dieldrin introduction (Fig. 6C). Colonization by new species and disappearance of old is not the only way in which system capacity may be altered. It may also be changed through evolution of the populations composing the system. This will be discussed below.

Toxic substances may alter the structure and organization of ecological systems, such a change bringing about a shift in location in phase space of the n-dimensional system steady-state point existing at each set of environmental conditions (Fig. 2). In the laboratory communities, exposure to dieldrin brought about these kinds of shifts in NSS community structure (Figs. 6B, 8, 9).

The response of a system to a toxicant is determined jointly by system organization and system environment (generalization 3). The response of the laboratory communities to dieldrin was related to the levels of environmental factors I and E. At LOW I, response was dependent upon E, ranging from perturbation and recovery at 0E to population extinction at 40E (Fig. 6B). At each E, the structure of the system at HIGH I was not altered as much by exposure to dieldrin as system structure at LOW I (Figs. 8, 9).

Using a theoretical example, we can further explicate the interplay of system environment and system organization in determining system response to a toxicant. Let us consider as an example predator extinction, such as occurred for the guppy population in the more complex laboratory communities, for population extinction is one of the more serious effects a toxicant may have on a system. Referring back to Figure 4, assume the presence of a competitor of the predator shifts the prey isocline at each I to the left. At LOW I, 40E when a competitor is present but toxicant has not been introduced, the predator population is able to persist (Fig. 4, solid square). This is analogous to the situation in the laboratory community at LOW I, 40E prior

to dieldrin introduction (Fig. 6A). Introduction of a toxicant at a sufficiently high concentration may so lower the predator isocline parameterized by 40E that it no longer intersects the prey isocline parameterized by LOW I and the predator population is driven to extinction (Fig. 4, vertically-barred square). At LOW I, the guppy population exploited at 40E was driven to extinction apparently as a result of exposure to dieldrin (Fig. 6B). Heavily exploited predators in systems of low productivity may be particularly vulnerable to extinction as a result of exposure to a toxicant. The life history and evolutionary reasons that may underlie this will be discussed below.

Any change in system environment that leads to a positive intersection of the predator and prey isocline will facilitate the persistence of a predator exposed to toxicant. This includes changes that shift the prey isocline to the right (e.g. increased I, horizontally-barred square; more favorable physico-chemical conditions for the prey; etc.) and/or shift the predator isocline upward (e.g. decreased E, vertically-barred circle; more favorable physico-chemical conditions for the predator; etc.). Thus, in the laboratory communities, the guppy population exploited at 40E was able to persist when exposed to dieldrin when I was increased to HIGH I (Figs. 8, 9). Further, the less heavily harvested populations--those exploited at 0E, 10E, and 20E--were able to persist at LOW I when exposed to the pesticide (Fig. 6B). However, it is quite likely that at HIGH I had E been increased to some level greater than 40E the guppy population would have been driven extinct by exposure to dieldrin. And, at levels of E less than 40E, guppy populations would not be able to persist in the presence of dieldrin if I were reduced to a level lower than LOW I.

Changes in system organization may also have profound effects on predator persistence. Competitors of the predator or competition on lower trophic

levels may shift the prey isocline to the left. Thus, in the absence of competitors, the prey isocline at a given I would lie further to the right on the phase plane (see Fig. 3), possibly bringing about a positive intersection of the predator isocline parameterized by 40E, TOX and the prey isocline parameterized by LOW I (Fig. 4, stippled square) and enabling a predator exposed to toxicant to persist. This suggests that, in the laboratory communities, had competitors of the guppy not been present, the population at LOW I, 40E may have had a better chance of persisting when exposed to dieldrin. Ancillary experiments confirm that guppy populations can maintain much higher densities, especially at high E, when their snail competitors are absent from the system (Fig. 11). Thus the presence of species that are competitors of a predator but are not affected by the toxicant as much as the predator population may render the predator more sensitive to toxicant perturbation and more vulnerable to extinction. Since competition may be a ubiquitous process in natural systems, it may be important in determining population and community response to a toxicant. In general, any change in system organization or system environment that shifts prey isoclines to the left and/or lowers predator isoclines renders a (predator) population more vulnerable to extinction by a toxicant by lowering its steady-state density or creating conditions in which isoclines do not intersect in positive phase space.

Changes in environmental conditions not only bring about changes in community structure and organization, but also concomitant changes in individual organism life histories. Individual organisms have life history capacities to alter their life history patterns in response to changes in their environments in ways favoring their survival and reproduction and the

persistence of their populations (Warren and Liss, 1980). It is through such developmental alteration in life history patterns, as well as evolutionary alterations in the kinds of individual organism life history capacities composing populations, that populations maintain concordance with and so are adapted to their environmental systems.

The community provides the environmental context in which individuals develop and populations must be adapted to persist. Different community structures--different kinds and densities of prey, predators, and competitors, etc.--constitute different developmental environments for individuals and different evolutionary environments for populations. Changes in community structure bring about developmental changes in individual organism life history patterns as well as evolutionary changes in the kinds of individual organism life history capacities composing populations. Thus, different life history patterns and capacities can be associated with different community structures.

In the laboratory communities, changes in conditions in the environment of the community such as I, E and exposure to dieldrin altered NSS community structure. Entailed in this is alteration of life history patterns and life history capacities. Referring again to the model shown in Figure 1, at each I, increases in E result in reduction in steady-state predator biomass and increases in steady-state prey biomass. Steady-state predator life history patterns that may exist at lower and higher exploitation rates are summarized in Table 4.

As exploitation rate and, thus, mortality due to fishing increases, we expect reduction in length of life and number of reproductions per lifetime. But due to reduction in predator biomass and increase in the biomass of the food resource, we might also expect faster juvenile and adult predator growth,

Table 4. Some possible predator life history patterns at low and high exploitation rates (After Kulbicki, 1980).

Life History Traits	Low Exploitation Rate	High Exploitation Rate
Longevity	long lifespan low adult mortality	shorter lifespan due to very high mortality resulting from exploitation
Number of clutches in a lifetime	many due to long lifespan	fewer due to the high mortality and shorter lifespan
Growth Rate	low due to low food availability and high population density	high due to high food availability and low population density
Age at first reproduction	later due to low food availability and low adult mortality	earlier due to high food availability and/or higher mortality
Size at first reproduction	smaller due to slower growth	larger size at first reproduction
Clutch size	low food availability will result in small clutches	larger clutches because of high food availability and better growth

increased size at first reproduction (or perhaps decreased age at first reproduction), and increased fecundity. These kinds of changes in guppy life histories were observed in the laboratory communities (Woltering, 1980, Liss et al. 1980) as well as in other exploited guppy populations (Liss, 1974), in clupeids (Burd and Cushing, 1962; Beverton, 1963), in trout and perch (Alm, 1959), and in whitefish (Miller, 1956). Thus, when some populations are exploited at high rates, they may develop life history patterns normally associated with higher values of the intrinsic rate of increase (r) - more rapid growth, earlier maturity or larger size at maturity, and higher fecundity at first and at subsequent reproductions. Development of such life history characteristics can be understood as adaptations to environments that bring about increased mortality, shortening of lifespan and reduction in number of reproductions per lifetime. This is simply to say that density-dependent changes in life histories are adaptive and enable populations to persist where mortality rate is high. Populations whose organisms cannot manifest these kinds of characteristics may not be able to persist at high levels of exploitation (or mortality).

Toxic substances may so alter life history patterns and the adaptive capacities of populations that populations are no longer able to persist in their environments or may persist at reduced densities under given sets of environmental conditions. In the laboratory communities, dieldrin apparently altered guppy life history patterns by reducing growth and fecundity and, at LOW I, 40E, by increasing mortality of offspring (Woltering 1980, Liss et al. 1980). At LOW I, 40E, dieldrin may have caused extinction of the population by effectively preventing the individuals from exhibiting the life history patterns--more rapid growth, higher fecundity, increased offspring

survival--that adapted the population to persist at this very high exploitation rate.

Thus heavily exploited populations, where rapid growth, high fecundity, and good juvenile survival are essential for persistence, may be more "sensitive" to reductions in growth, fecundity, and survival caused by toxic substances. At lower exploitation rates, alterations in life history pattern caused by dieldrin resulted in reductions in guppy population density, but the populations were able to persist. But surely higher concentrations of toxicant, which would bring about more severe alterations in life history patterns--greater reductions in growth, fecundity, and survival--would cause extinction of populations exploited at even these lower rates.

Now, at higher I, because of the greater availability of food, a population may be able to persist when exposed to a toxicant and exploited at 40E, as shown in Figure 4. The range of exploitation rates over which populations can persist when exposed to a given level of toxicant may be greater at HIGH I than at LOW I. But, as we discussed before, there will surely be some exploitation rate higher than 40E at which a population even at HIGH I will not be able to persist.

At any time, the capacity of a population to adapt evolutionarily to changes in its environment, including exploitation and toxic substances, is determined by its genetic organization. But evolutionary changes entail changes in genetic organization and thus alteration in the capacity of a population to adapt to future changes in its environment. Evolution can be understood as a continual change in a population's adaptive capacity (Warren and Liss 1980). Changes in genetic organization are accompanied by changes in the kinds of individual organism life history capacities composing the population. Thus changes in community capacity may be brought about

through evolutionary changes in the capacities of populations composing the community as well as by changes in organization resulting from species colonization and extinction.

Evolutionary changes in populations can be brought about by exploitation (Schaeffer and Elson 1975, Silliman 1975, Moav et al. 1978, Ricker 1981) and exposure to toxic substances (Culley and Ferguson 1969). At LOW I, the guppy population exploited at OE was able to adapt developmentally and perhaps evolutionarily to the presence of dieldrin and so recover from dieldrin perturbation. Natural selection could have favored those individuals that had the life history capacity to survive, grow, and reproduce most efficiently in the presence of dieldrin--the so-called "resistant" individuals. These individuals exhibit life history patterns that are well adapted to the presence of dieldrin, thus enabling the population to increase in biomass while still being exposed to the pesticide.

The population had begun to recover from toxicant perturbation long before toxicant introduction into that system was terminated. Mean NSS biomass of the population after termination of dieldrin introduction was about 30 percent greater than the mean NSS biomass the population maintained prior to dieldrin introduction (Table 2). This provides some evidence that the capacity of the population had been altered. The difference between mean NSS biomass after termination of dieldrin and mean biomass prior to dieldrin introduction is not nearly this great for any of the other populations. Although Hyallela had colonized this system during recovery, amphipod biomass was still far too low to have been a significant food resource for the guppies. Thus the changes in amphipod species composition and biomass during recovery cannot account for the increase in guppy density.

However, in adapting to the toxicant the population at 0E may have lost some of its capacity to adapt to other environmental conditions. Thus the population may not adapt and perform as well under different or continually changing environmental conditions as it would have adapted and performed if it had not been exposed to toxicant.

In the laboratory communities at LOW I, populations exploited at 10E and 20E did not recover from toxicant perturbation throughout the time that dieldrin was being introduced. The unexploited population maintained a greater density than the populations exploited at 10E and 20E. Perhaps greater population density increased the probability that "resistant" genes or sets of genes were present in the population and so speeded evolutionary adaptation and recovery from perturbation. And, of course, the population exploited at 40E, which maintained a very low density was apparently particularly sensitive to dieldrin and was driven to extinction.

Several workers have argued that, for genetic reasons alone, reduction in density renders natural populations more vulnerable to extinction (Franklin 1980, Soule 1980, Frankel and Soule 1981, Kapuscinski 1983). They argue that reduction in population size may be accompanied by inbreeding, leading to reduction in genetic variation (reduction in heterozygosity) and fixation of deleterious alleles. The life history traits most severely affected by inbreeding are the so-called "fitness traits"--those associated with survival and reproduction. The problem is thought to be especially severe in isolated populations that are not subjected to infusion of new genes by gene flow. Inbreeding and its negative effects on life history traits--growth, reproduction, and survival--would act in opposition to any adaptive density-dependent increases in these performances that would tend to be brought about as a result of reduction in the density of a population

and increase in the density of its food resources. Toxicants that themselves reduce growth, survival, and reproduction would, in effect, reinforce the negative effects of inbreeding at low population densities. Moreover, inbred individuals may be far more susceptible to toxicants; their growth, survival, and reproduction may be affected more by a toxicant than non-inbred individuals.

Loss of genetic variation would amount to reduction in the capacity of a population to adapt evolutionarily to changes in environmental conditions, including toxicant introduction. Thus intensive exploitation may reduce the adaptive capacities of population by reducing their density and consequently genetic variation (Kapuscinski 1983). Populations subjected to high mortality rates and maintained at low densities may be especially sensitive to toxic substances for life history reasons--the individuals need to maintain high growth and reproduction rates for the population to persist but both toxicants and inbreeding effects reduce these--and for evolutionary reasons--the populations have a severely reduced capacity to adapt evolutionarily to the toxicant.

To relate this to guppy population extinction brought about by dieldrin is purely speculative, but certainly many of the conditions conducive to intensive inbreeding and reduction in genetic variation were present in the population at LOW I, 40E. Prior to dieldrin introduction, the population had maintained very low densities for many generations, being composed at most of only a few mature fish at any one time. Further, the population was completely isolated from gene flow.

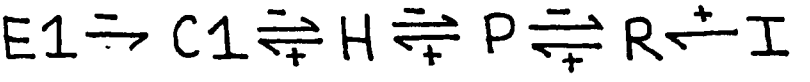
At HIGH I, 40E, individual guppies were able to survive, grow, and reproduce better than fish at LOW I due to greater food availability. The density of the population at HIGH I, 40E was much greater than the density at LOW I and, thus, perhaps genetic diversity was also greater. All of these

factors may have enabled the population at HIGH I, 40E to better withstand toxicant exposure.

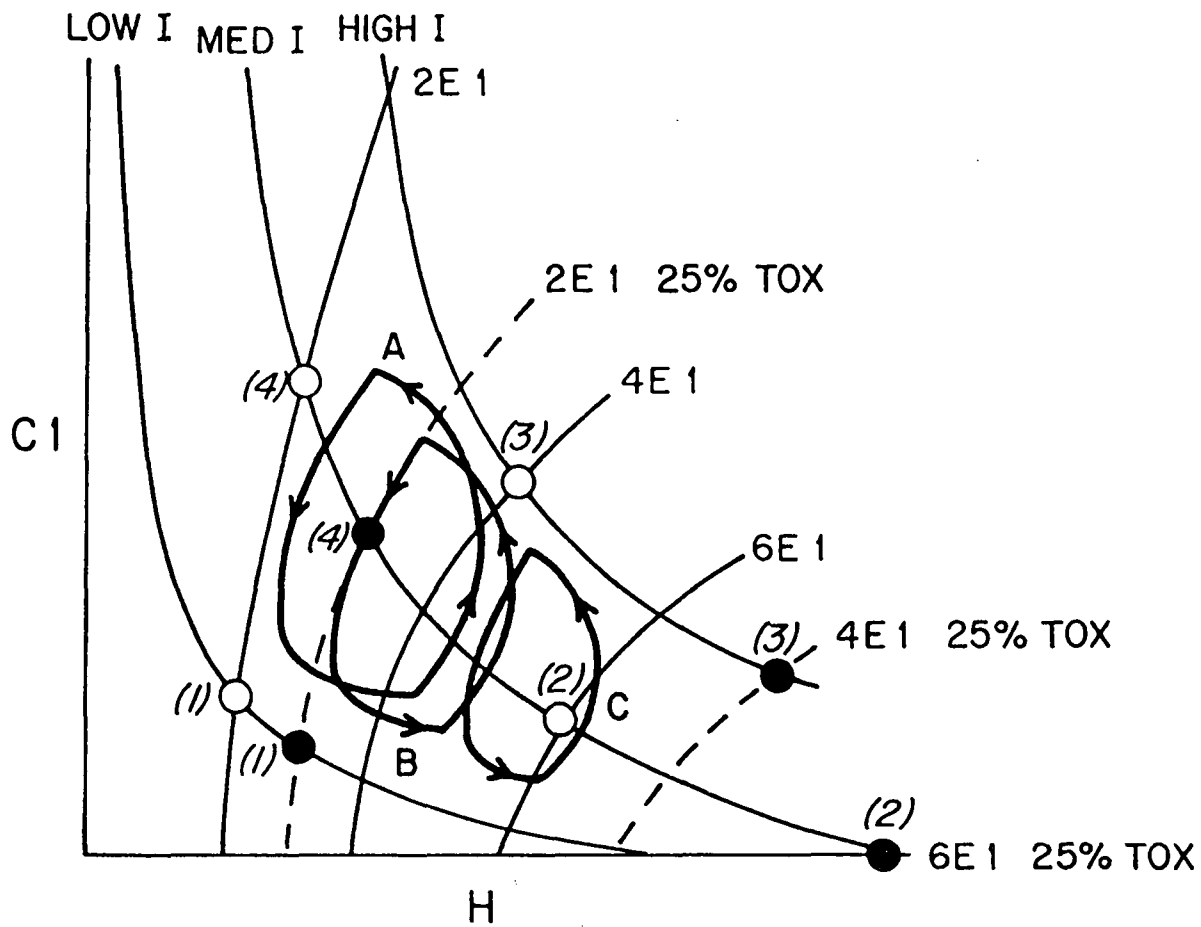
For the most part, to this point, we have been concerned with systems at steady-state for two related reasons. First, we wished to illustrate theoretically and empirically some of the system generalizations posed in the Introduction, including the multisteady-state nature of systems and the relation between system steady-state structure and system environment. Second, system steady-states have explanatory utilty, for they are the "targets" of system trajectories; their location in phase space, and thus where trajectories want to go, changes with changes in environmental conditions. Both the complex and the simple laboratory communities established (near)steady-states. Their structure and organization was given meaning with multisteady-state models. We evaluated effects of a toxicant under different sets of environmental conditions in terms of the extent to which the NSS location of the system in phase space (NSS system structure) was altered by exposure to the toxicant.

In natural systems and in many kinds of laboratory systems environmental conditions may be continually changing and systems may never establish steady-states or even NSS's. The second generalization of the set posed in the Introduction states that system dynamics, or changes in system structure and organization, can be understood as an n-dimensional system trajectory in continuous pursuit of an n-dimensional system steady-state point whose location in phase space is continually changing with changes in the state of the system's environment. What, then, are some implications of changing environmental conditions in understanding the effects of toxic substances on ecological systems and how can these effects be evaluated?

Figure 13. Phase plane representation of the relationship between C1 and H1 in a



system. E1, units of harvesting effort on C1, and I constitute the environment of the system. Stable trajectories are generated when I and E repeatedly cycle in the sequence (1) LOW I, 2E1, (2) MED I, 6E1, (3) HIGH I, 4E1, and (4) MED I, 2E1. Trajectory A represents changes in C1 and H when toxicant is not present. The steady-state points the trajectory tracks toward under the different sets of environmental conditions are indicated by open circles. Under the same environmental cycle, trajectories B and C represent changes in C1 and H when toxicant causes reductions in C1 growth, reproduction, and survival of 10 percent and 25 percent respectively. Predator isoclines and steady-state points (solid circles) at each E and I for the 25 percent reduction are shown. Only the trajectory is shown for the 10 percent reduction. The particular sequence of environmental conditions used here has no special significance. It is intended as an example of how interacting populations respond numerically to changes in environmental conditions. The isoclines and trajectories on this phase plane were generated through computer iteration using the command control language SIMCON. (We appreciate the assistance of Grant Thompson, Oak Creek Laboratory of Biology in performing these simulations.)


LOW I
MED I
HIGH I
2E 1
2E 1 25% TOX
A
(4)
4E 1
C 1
(3)
(4)
6E 1
(3)
4E 1 25% TOX
(2)
(1)
C
(1)
B
(2)
6E 1 25% TOX
H

Shown in Figure 13 is a stable "control" trajectory (A) generated when environmental conditions change in a regularly repeated sequence (1) LOW I, 2E1,; (2) MEDI, 6E1; (3) HIGH I, 4E1; (4) MED I, 2E1. The steady-state points that the trajectory tracks toward under the different sets of conditions are indicated by the open circles. Before the trajectory converges on a particular steady-state, environmental conditions change, altering the location of the steady-state point in phase space and consequently diverting the trajectory toward a new steady-state. A "stable" trajectory pattern is eventually established, repeated with every cycle of change in environmental conditions.

A toxic substance alters the location of the steady-state point in phase space at each I and E, the extent of these changes being dependent upon system organization and the particular levels of I and E. This alters the form and location in phase space of the stable trajectory generated by a particular sequence of change in I and E. Shown in Figure 13 are the stable trajectories generated by the same sequence of I and E used to generate the "control" trajectory, but with toxicant-induced reduction in growth, reproduction, and survival of C1 of 10 percent (B) and 25 percent(C). The trajectories of systems exposed to the toxicant occupy different regions of phase space than the control trajectory. There is considerable overlap of the trajectory generated by a 10 percent reduction with the control trajectory. Such a difference in system behavior may be difficult to detect under field conditions. The trajectory generated by a 25 percent reduction occupies a different region of phase space than the control trajectory. It is interesting that at MED I, 6E1, 25% TOX the intersection of the predator and prey isoclines is along the H1 axis. This means that had conditions remained fixed at MED I, 6E1, 25% TOX, C1 would have been driven to extinction. But before the trajectory could converge on this point, conditions changed; E1 was reduced

from 6E1 to 4E1 and I increased from MED I to HIGH I, effectively shifting the predator isocline upward and the prey isocline to the right and generating a positive intersection in phase space. Thus, the extent of translocation of the stable toxicant trajectory in phase space is no indication of the potential severity of toxicant effects. Had environmental conditions not become more favorable a 25 percent reduction in growth, reproduction, and survival would have led to the extinction of C1.

Fundamentally, when viewed within our perspective, the form of a system trajectory is determined by the location of the system in phase space relative to the steady-state point it is going toward and how that point is shifted in phase space as environmental conditions change (Liss et al., in prep.). This is so, we believe, for any performance of any system whatsoever, including community structure and organization, population density, production, and yield, and toxic substance uptake and concentration. If the environment of a system had no regular cycle of change, a trajectory would wander throughout phase space, pursuing an ever-shifting steady-state point and having no particular unique form. It may be that under these conditions toxic substances may be more difficult to detect under field conditions, unless they are severe, because there is bound to be considerable overlap in domains of behavior of systems that have been exposed to a toxicant and systems that have not.

But more than this, if we insist on confining ourselves to short-term experiments on natural or laboratory systems and not worrying about environmental conditions, we must begin to wonder about the meaning of our observations and their relevance to possible effects a toxicant may have on natural systems. Any single measurement or series of measurements defines only a single point on a trajectory or a segment of a trajectory. This may have little significance if environmental conditions are continually changing

and the trajectory is moving throughout phase space; it may tell us little about toxicant effects and thus may be misleading in attempting to manage toxic substances.

Frequently, in laboratory microcosm research, experiments are conducted under a single set of environmental conditions. Unless the system establishes a steady-state, the measurements represent only points on a trajectory going toward a steady-state point, but the location of the point in phase space is unknown. And, even if the system were to establish a steady-state, this would represent only one in an infinite family of possible steady-states. Toxicant effects measured under this particular set of conditions may have little significance, for system response may vary with conditions in the environment of the system. If the laboratory community experiment reported here was conducted under only one set of environmental conditions, one may get quite different impressions of the effect of dieldrin depending upon whether conditions were fixed at, say, LOW I, OE, LOW I, 40E, or HIGH I, 40E. Conducting experiments on any ecological system over ranges of important environmental conditions provides better definition of the domain of toxicant effects on the system (Warren and Liss 1977). This simply amounts to better understanding of toxicant effects and this understanding must be the basis of toxic substance control.

With laboratory systems we are attempting to model developing, adapting, persistent natural systems of great organizational complexity. It is not clear that any laboratory system can model natural systems very well. An important consideration in developing laboratory models is the kind or class of system to be modeled, for different kinds or classes of systems have different capacities (Warren et al. 1983). The model should reflect something of the organization, capacity, and performances of that kind or class

of natural system if there is to be any hope of extrapolating laboratory results to natural systems.

In many kinds of microcosms, resources are inadequate and environmental conditions insufficient to maintain persistence of the systems for any length of time. In these systems what is it that we are measuring when we investigate toxic substance behavior and effects? Essentially the origin (0,0) is the steady-state point on a phase plane upon which such a system will converge. The toxicant effect we measure, at best, is simply how much faster an already dying system will meet its demise. We believe these sorts of systems should not be favorably viewed as toxicant testing tools simply for reasons of expedience, that is, simply because they can produce data over a relatively short time period. These systems may fulfill the criteria of being short-term, replicable systems but they may fall far short of other important criteria--they possess few of the properties of developing, adapting, persistent ecosystems. Microcosms of this kind should not be passed off as methods for evaluating toxicant behavior and effects in ecosystems. The information on transport, accumulation, and metabolism of toxicants generally garnered from these microcosms may be better obtained with individual organism feeding experiments through incorporation in the experiment of different food consumption rates and other kinds of differences in environmental conditions (Warren and Liss, 1977).

But by suggesting that well-conducted individual organism experiments can provide the same kind of information gained from short-term, nonpersistent microcosms, we do not wish to imply that the individual organism test will suffice for determining impacts on higher levels of organization. We do not believe this is so. Individual organism experiments when conducted under

different sets of environmental conditions and with a life history perspective (Sterns 1976, Warren and Liss, 1980, Kulbicki 1980), can be useful in understanding the impacts of a toxicant on life history patterns and capacities and probably provide a lot of the same kind of information on uptake rates and metabolism as is obtained in many kinds of microcosm studies. But, based solely upon information of toxic effects on individual organism growth, survival, and reproduction in the laboratory, we have almost no way of knowing how a toxicant may affect the densities, yields, genetic structure, adaptation, persistence, etc. of populations or the structure, organization, development, and persistence of communities. There is no theoretical basis for supposing that effects on population and community capacities and performances can be simply predicted from effects on individual organisms. The kinds of results obtained in our laboratory community experiments could not have been predicted from the results of any individual organism experiments with dieldrin (Liss et al. 1980). And, the organization of natural communities is far more complex than the organization of our laboratory communities.

Laboratory models of ecosystems are probably needed to illustrate or demonstrate theoretical generalizations pertaining to toxic substance behavior and effects and provide "tests" of the effects toxicants may have on natural systems. Their utility depends upon the frameworks, theories, and models available for their design, conduct, and interpretation. We are concerned, however, that proper evaluation of community or ecosystem level effects may be fundamentally incompatible with the criteria that toxicity tests be essentially short-term and replicable.

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