AN ABSTRACT OF THE THESIS OF

Daniel Mark Woltering for the degree of Doctor of Philosophy

in Fisheries presented on October 3, 1980

Title: ORGANIZATION AND THE ADAPTATION OF AQUATIC

LABORATORY ECOSYSTEMS TO RESOURCE AVAILABILITY,

EXPLOITATION, AND A TOXICANT

Abstract approved: Signature redacted for privacy.

Charles E. Warren

Organization and the adaptation of aquatic laboratory ecosystems to resource availability, exploitation, and a toxicant were examined in a 34-month study. Sixteen 560-liter microcosms including prey, predator, and competitor populations were employed over a wide range of energy and habitat resource availability and exploitation of the top predator. Chronic exposure to the pesticide dieldrin was used to perturb systems near steady states. Empirical generalizations from ecological theory, productivity theory, and fishery exploitation theory were incorporated to explain in part such performances as development, structure, and persistence of the laboratory ecosystems, their communities, populations, and individual organisms.

Dynamic (developmental) and near steady-state community structure and organization were detailed for guppy, amphipod, snail, planaria, and algae populations and for a benthic detritus and

microorganism component. Near steady-state population performances including density, production, yield, and size-specific growth and reproduction were determined for the guppy population in order to demonstrate the concordance of life history, population, and community level performances with changes in environmental conditions. A system of isoclines on a series of interrelated resource - utilizer and competition phase planes was employed to gain a better understanding of the structure and apparent organization of the laboratory systems.

The 16 systems were established with a 0.6 gram/day alfalfa ration, 20 percent of each tank bottom covered with gravel for invertebrate habitat, and 0, 10, 20, or 40 percent guppy exploitation per month. Exploitation directly affected the size of the guppy populations near steady state (through observed changes in production, yield, growth, and reproduction) and indirectly affected the size of snail and amphipod populations which responded to competition and/or predation from guppies. Following many months of near steady-state system behavior (i.e. restricted fluctuations of population biomasses), eight systems were shifted to a 4.0 grams/day alfalfa ration and 95 percent gravel cover. These high energy and habitat level systems were characterized by relatively complex trophic and habitat resource partitioning. These systems developed different population interactions and community structure and had much higher population densities.

At the same time, four low energy and habitat level systems (one

at each guppy exploitation rate) with well established near steady states began continuous exposure to 1. 0 ppb dieldrin in the water. The response of the laboratory systems to the toxicant was determined by the levels of prevailing environmental conditions as well as by the system's organization and the capacity of the populations to adapt and to persist. There were both density-dependent (via exploitation) and time-dependent components to the response to toxicant perturbation. In general, dieldrin reduced the growth and reproduction of the guppies, this resulting in smaller population biomasses. Amphipod biomasses increased in response to reduced predation and competition. The ecosystem with 0 percent exploitation (i. e. the largest guppy biomass) responded immediately with apparent dieldrin induced mortalities of mature fish. However, eventually the population recovered its lost biomass. There was no apparent initial response at 40 percent exploitation (i. e. smallest guppy biomass), but after 15 months of exposure the guppy population went extinct apparently from the combined stress of exploitation and toxicant.

Community organization and its expression in community development, structure, and persistence involved the adaptation of species populations to each other, to available energy and materials, to habitat, to climatic conditions including water quality and temperature, to exploitation, and to the introduction of the toxicant. Manipulating energy and habitat availability, exploitation levels, and toxicant

presence altered near steady-state community, population, and individual organism performances. In these responses to environmental conditions, there was a certain concordance of community, population, and life history patterns that constitutes adaptation of the community and its subsystems.

Organization and the Adaptation of Aquatic Laboratory
Ecosystems to Resource Availability,
Exploitation, and a Toxicant

by

Daniel Mark Woltering

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed October 1980

Commencement June 1981

APPROVED:

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ACKNOWLEDGEMENTS

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ORGANIZATION AND THE ADAPTATION OF AQUATIC LABORATORY ECOSYSTEMS TO RESOURCE AVAILABILITY, EXPLOITATION, AND A TOXICANT

I. INTRODUCTION

Any performance of an organismic system can be understood as the consequence of the system's capacity and of its environment at a particular time. Developmental and evolutionary adaptation alter the capacities of organismic systems and thus lead to different performances, such as structure, development, replication, and persistence. Changes in environmental conditions, even without change in the capacity of a system lead to different performances. Adaptation entails a certain concordance of the capacities as well as the performances of systems, subsystems, and their environments, a harmonious and apparently rule-governed behavior among them (Warren et al. 1979; Warren and Liss, in press).

The adaptive capacities and performances of organismic systems depend upon their organization. Organization entails the incorporation and concordance of the capacities as well as the performances of organismic subsystems and their level specific environments. Competition, predation, and human exploitation and management of organismic systems entails the alteration of their organization and thus of their adaptive capacities and performances. Not only the performances, but also the organization and capacities of organismic systems are thus in continuous change. An organismic system can be understood

to have a unique realized capacity at each developmental-evolutionary state, this realized capacity being a partial expression of the potential capacity of the system in interaction with its coextensive environment.

The states of population systems are in continuous developmental and evolutionary change. Systems of populations can be understood ideally as being multisteady-state systems, whether or not they achieve steady states, so long as sequences of system states tend toward particular steady states or track changes in potential steady states as environmental conditions change. Steady states are defined as the intersections of isoclines parameterized by known environmental variables (Booty 1975; Rosenzweig 1977). In such a system, properties or capacities of the organismic system together with environmental parameters and their changes become an explanation of system behavior.

An isocline theory of population systems articulated by Booty (1975), Liss (1977), and Warren and Liss (1977) employs a formal, graphical procedure that explicitly couples the dynamics of interacting populations to one another and to prevailing environmental conditions. Covariant changes in the densities of populations represented on predatory-prey or competition phase planes are interpreted as tending toward some steady state parameterized by values of environmental variables. Changes in these values lead to new steady states and thus a multisteady-state view of population systems. As will become

apparent, such a graphical representation allows us to bring together important aspects of environmental conditions and resources, life history patterns, population system outcomes of predation and competition, and production and yield of exploited populations, aspects that have not generally been unified in ecological theory.

Community structure, population density, and life history patterns are concordant, time variant, level specific performances entailed in ecological systems. Particular patterns of population densities and thus of community structure are the result of the growth, reproduction, survival, and behavioral interactions of individuals in component populations. These patterns depend upon the prevailing set of external environmental conditions. Through developmental and evolutionary alterations of life history patterns, individual organisms and their populations tend to maintain concordance with their environmental systems. Since different community structures represent different environmental states for the incorporated organisms, individual organisms develop different life history patterns in concordance with different community structures (Kulbicki 1979; Warren and Liss, in press). This generalization will allow us more closely to couple life history patterns, populations, communities, and environmental conditions.

The levels and kinds of energy and material available to an ecological system, patterns of climatic conditions, colonization

opportunities, species interactions including predation, competition, and mutualism, and the spacio-temporal distribution of primary physical habitat types are joint determinants of community organization and thus of whatever performances including structure and persistence communities may exhibit. Too often in ecological theory and observation, these determinants have been treated separately in hypotheses intended to account for differences in the diversity of communities, as may be observed along latitudinal gradients (Pianka 1966). In recent years, some ecologists have attempted to use two or more of these hypotheses together to account for observations on community structure and diversity (Connell 1975; Glasser 1979; Hall et al. 1970; May 1976; Menge and Sutherland 1976; Wiens 1977; Wilber 1972; and Whittaker 1975). For clarity, these hypotheses may be stated separately, but it is as a system of generalizations that they should be employed in explanation and understanding of community organization and any of its manifestations. The productivity hypothesis states that total energy available to a community is the primary determinant of the diversity and abundance of organisms (Connell and Orias 1964). The time-stability hypothesis asserts that climatic constancy and length of time for species colonization are the primary determinants of community diversity (Sanders 1969). The spacial heterogeneity hypothesis states that the structural complexity of habitat is the primary determinant of species diversity (MacArthur 1964; Cody 1968).

The competition hypothesis maintains that competition among species populations for trophic and habitat resources arrayed in space and time primarily determines community composition (MacArthur 1972; Diamond 1975). And the predation hypothesis asserts that "key" predators allow for coexistence of some competitors and thus maintain community diversity (Paine 1966; Connell 1975).

The organization of an ecological system and the levels and kinds of energy and material available to that system determine the system's capacity to produce each of its populations. This productive capacity an ecological system has for each of its populations will be referred to as its productivity for a given population. Productivity, as a capacity term, was distinguished by Ivlev (1945) from production or the particular density-dependent rate of tissue elaboration for a product of interest. Production can be calculated as the product of mean relative growth rate and mean population biomass. So long as food is limiting, relative growth rate of individuals declines with increasing population biomass. A curve of production plotted against biomass is thus low at low biomass, high at intermediate biomass, and low at high biomass, this forming a hump-shaped curve (Warren 1971; Warren and Davis 1971). Such a curve defines a level of productivity, including all production values associated with different biomasses along it. Higher levels of productivity are defined by higher and wider curves of production. Alteration in primary energy and

material resources or diversion of energy and material anywhere along the trophic pathways leading to a product of interest can alter the productivity of a system for that product. Decrease in energy and material input and direct and indirect interspecific competition can thus decrease the productivity of a system; changes in production owing · simply to biomass reduction through predation or exploitation do not constitute changes in productivity. But exploitation may alter the adaptive capacities of populations and communities and thereby alter productivity.

Human exploitation and management of an ecological resource entails the exploitation of the life history and evolutionary adaptive capacity of a particular population, whereby developmental adaptation of life history patterns and evolutionary adaptation of the population tend to favor its persistence in the face of exploitation and increased mortality. Classical fishery exploitation theory (and simple productivity theory) account for the increased loss to mortality in terms of increased recruitment and growth and decreased natural mortality tending to maintain a steady-state biomass (Schaefer 1968). In such a view, the effects of overfishing can be corrected by decreasing fishing pressure so as to allow the population to return to some steady-state biomass at which maximum yields are possible. This may sometimes happen. But it is at least as probable that changes in the capacity of the exploited population or its biological community will make return

to some desired steady state impossible.

Not only changes in energy and material resources and levels of exploitation but the presence of toxic substances can lead to life history and evolutionary adaptation of populations (Schaffer and Elson 1975; Kulbicki 1979). But just as adaptation to changing resources or exploitation may come at some loss of other adaptive capacity, so adaptation to toxic substances may not indefinitely be beneficial. And often now, populations must adapt to both exploitation and toxic substances and continue to adapt to factors of their historical environment. Thus explanation and understanding of the adaptive capacities of individual organisms, populations, and communities becomes not only of much ecological interest but of much practical importance as well.

The above set of statements, being about ecological systems and how we might understand them, constitutes a view of ecology from conceptual framework through theory to the empirically observable. As such, it is a set of hypotheses to be examined as to their utility and conformity with observational experience. Many, if not most, of the statements are implicit in extant ecological theory although perhaps they have not been stated and organized in just this way.

The goal of this thesis is to advance understanding about the adaptive relations among organismic systems, their capacities,

organization, environments, and performances. Explanatory objec-
tives include:

(1) to demonstrate, explicitly couple, and explain the dynamic
interactions in a system of populations together with its external
environment;

(2) to demonstrate and explain the concordance of community,
population, and individual organism capacities and perform-
ances;

(3) to develop a simple, visual, and yet comprehensive explana-
tion for observed patterns of structure in systems of populations
and relate this to organismic capacities;

(4) and, finally, to extend the utility of this view of ecological
systems to the problem of toxic substances in the aquatic envi-
ronment, in particular, to demonstrate the effect of the pre-
vailing level of environmental conditions on the response of
ecosystems to toxicant perturbation.

In order to approach this goal and these explanatory objectives,
studies of aquatic laboratory ecosystems were undertaken. These
studies employed sixteen 560-liter laboratory microcosms including
prey, predator, and competitor populations over a wide range of two
ecologically interesting environmental factors, resource availability
(energy and habitat) and exploitation of the top predator. Chronic
exposure to the pesticide dieldrin was used to perturb systems near

steady states. Dynamic and near steady-state community structure and organization were detailed for guppy, amphipod, snail, planaria, and algal populations and for a benthic detritus and microorganism component. Near steady-state population performances including density, production, and yield, and size specific growth and reproduction were determined for the guppy population in order to demonstrate the concordance of life history, population, and community level performances with changes in environmental conditions.

II. MATERIALS AND METHODS

Biological and Physical System

Sixteen aquatic ecosystems were established at the Oak Creek Laboratory of Biology. Each was a multispecies system composed of persistent populations of guppies (Poecilia reticulata), amphipods (Gammarus fasciatus), snails (family Planorbidae), planaria (Dugesia sp.), and benthic microinvertebrates including flagellates, rotifers, nematodes, gastrotriches, and protozoans. Green and blue-green algae and diatoms were present. In addition, each laboratory system had fifty grams of the aquatic plant Ceratophyllum demersum maintained as cover for the newborns of the cannibalistic adult guppies. Habitat and escape cover for invertebrates was provided by a substrate of 1.5 cm quartzite gravel four centimeters deep. A gelatinous mixture of 60 percent alfalfa and 40 percent Oregon Test Diet (Sinnhuber et al. 1977) served as the primary energy input in the laboratory ecosystems. Daily rations of consistent quality were taken from freezer storage and cut into small pieces before being dispersed over the gravel.

Each laboratory system was maintained in a fiberglass tank measuring 1.2 m x 1.1 m x 0.4 m 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 con-
stant levels. Fluorescent lights above each tank provided an average
intensity of about 20 footcandles (ft-c) at the water surface. Photo-
period was controlled by a timer set for 14 hours light and 10 hours
darkness. .

Experimental Design (Phase I)

Initially all 16 laboratory ecosystems had a similar experimental
design (identified as low energy input and low habitat availability) in
which there were three circular nests of gravel covering 20 percent of
the bottom area of each tank, and a 0.6 gram per tank daily alfalfa
ration was provided. In April 1975, 200 amphipods having approxi-
mately the same size distribution were stocked in each system. The
systems remained undisturbed during the next year except for periodic
sampling to monitor the development of the invertebrate populations.
Population growth indicated that environmental conditions including
food availability were adequate to support amphipod populations of up
to 5000 individuals. Sediment accumulation and the formation of a
benthic microflora and microfauna ensued. Snails and planaria were
introduced inadvertently with the aquatic plants and persisted at low
densities.

In April 1976, guppies were introduced into three systems and a
monthly sampling program was initiated to determine (1) the

approximate biomass and number of guppies the systems could support, and (2) the levels of monthly exploitation the guppy populations could sustain and still persist. In November 1976, each of the remaining 13 systems was stocked with 37 guppies having similar size distributions, sex ratios, and a total biomass of 4.5 grams. Monthly exploitation rates for the guppies were set at 0, 10, 20, or 40 percent of the population biomass, four systems being exploited at each level (Fig. 1).

Experimental Design (Phase II)

In March 1978, following many months of relatively little change in the population biomasses (identified as near steady state), eight of the laboratory ecosystems (two at each guppy exploitation level) were modified to establish a higher level of energy input and habitat availability. The gravel habitat and escape cover was increased to cover 95 percent of each tank bottom. Energy input was increased to 4.0 grams of alfalfa ration daily. The monthly sampling procedure was continued unchanged.

In April 1978, the organochlorine insecticide dieldrin was introduced so as to maintain a concentration of 1 part per billion (ppb) in four of the low energy and habitat systems (one at each guppy exploitation level). The four remaining systems at low energy input were left unaltered in design to the end of the study. Each of the 12

Figure 1.   Experimental design and chronological order of
             environmental manipulations. Sixteen laboratory
             ecosystems were established in April 1975 each with
             20 percent gravel cover, 0.6 gram/day alfalfa ration,
             and 200 amphipods. Guppies were introduced and a
             28-day sampling-exploitation schedule was begun in
             November 1976. Four systems began continuous expo-
             sure to 1 ppb dieldrin in April 1978, at the same time,
             eight systems were shifted to 95 percent gravel cover
             and 4.0 grams/day alfalfa. Data collection for this
             thesis ended in August 1979; however additional moni-
             toring and manipulations are scheduled for 3 years.

16 Laboratory Ecosystems

Guppy Exploitation Rates
(percent per month)   0%   10%   20%   40%

Laboratory System No.   3 7 13 11   14 12 10 8   4 5 16 2   1 6 15 9   Dates
                                                                                          11/76

Low Energy Input and Habitat
Availability Level
(0.6 g alfalfa/day, 20% gravel
            cover)

                                                                                          4/78
Toxicant Perturbation (T)   T O   T O   T O   T O
                                                                                          3/78

High Energy Input and Habitat
Availability Level
(4.0 g alfalfa/day, 95% gravel
            cover)

                                                                                          10/78
Planaria Removal (X)   X O   X O   X O   X O

                                                                                          8/79

altered systems had at least 18 months to establish near steady-state behavior (baseline response) for comparison with changes in system behavior brought about by the new environmental conditions.

Sampling Procedures

Organisms in each laboratory ecosystem were censused and its guppy population exploited every 28 days. Guppies were removed from the tanks by netting. 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).

All sizes of fish were exploited. During sampling the fish were ordered according to size, and assigned a number. Exploitation followed a continuous number scale with a pre-set exploitation schedule for each system (0, 10, 20, or 40 percent per month). For example, a 10 percent exploitation system called for the exploitation of fish numbers 8, 18, 28, 38 ... A total of 26 fish in the population for the first month would have two fish exploited (the eighth and eighteenth largest); the following month, the largest fish in the population would be assigned number 27, the second largest number 28 (which would be exploited), the third number 29, etc. In this way all fish had an equal chance of being exploited over their lifetime. Total population

and size class biomasses (i. e. the combined weight of all individuals) and yields (i. e. the weight of the catch at a given sampling date) were calculated for each guppy population. Total population and size class production (i. e. the amount of tissue elaborated by the population between sampling dates) was estimated using the difference between the initial and final biomasses of the population over the 28-day intervals (Chapman 1968). Final biomasses were adjusted for any known mortalities and for fish changing size classes over the interval. Production includes somatic and reproductive (plus newborn fish) tissue elaboration. Density and size composition of the population, growth and survival of individuals, and fecundity of exploited females were also determined and related to environmental factors and to exploitation.

The gravel substrate, which was held in place by wire screen, and the Ceratophyllum were removed from the tanks and rinsed to dislodge invertebrates. Amphipods, snails, planaria, and sediments plus associated microorganisms were then removed by a siphon and a net. Individuals in each macroinvertebrate population was sized, counted, and then weighed as a group. The Ceratophyllum was weighed and restocked as necessary to maintain 50 grams in each system. Three one-percent subsamples of the sediment from each system were obtained with a sample splitting device. Dry weight and organic matter content were determined. The samples were dried at 70 °C for 72 hours and then ashed for three hours at 500 °C. Organic nitrogen content was determined by standard microkjeldahl technique (Berg and Gardner 1978). Microorganisms were identified

and their densities estimated with the aid of a Sedgwich Rafter Cell
(APHA 1971). All amphipods, snails, remaining sediments with
microorganisms, and unexploited fish and planaria were returned
to the tanks.

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 were determined
weekly in laboratory ecosystem water samples and periodically in
tissue samples of guppies, snails, plants, and sediments. Following
standard extraction procedures, analysis was done using a Varian-
aerograph 2000 gas chromatograph equipped with an electron capture
detector.

III. RESULTS AND INTERPRETATION

Trophic Organization of the Laboratory Ecosystems

Trophic organization entails that aspect of community organiza-
tion based on interactions between species populations for food re-
sources. Other aspects of community organization include life history
and habitat organization. Figure 2 represents the inferred trophic
interrelations in the laboratory ecosystems. This synthesized view
of the laboratory systems describes an organismic system and its
environmental system which together form an ecological system in
space and time.

Organismic System

The organismic system included prey, predator, and competitor
populations. The organic sediment component, including microorgan-
isms, was the common prey for the three major populations: guppies,
amphipods, and snails. Copepods were inadvertently introduced with
the amphipods but died out early in the study. Alfalfa ration, feces,
decomposed plants and animals, and benthic microorganisms made up
the 60 to 80 percent of sediments that were organic. The mean organic
nitrogen content of the sediments was 3.0 ± 0.5 percent for the 16
systems over 34 months. Identification, density estimates, and pos-
sible trophic interactions for the eight species of the benthic

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Figure 2. Kinetic diagram representing inferred trophic inter-
relations in the laboratory ecosystems. Population
interactions are designated as predation (p) or competi-
tion (c). Exploitation, dieldrin, alfalfa ration, and light
energy are variable environmental factors.
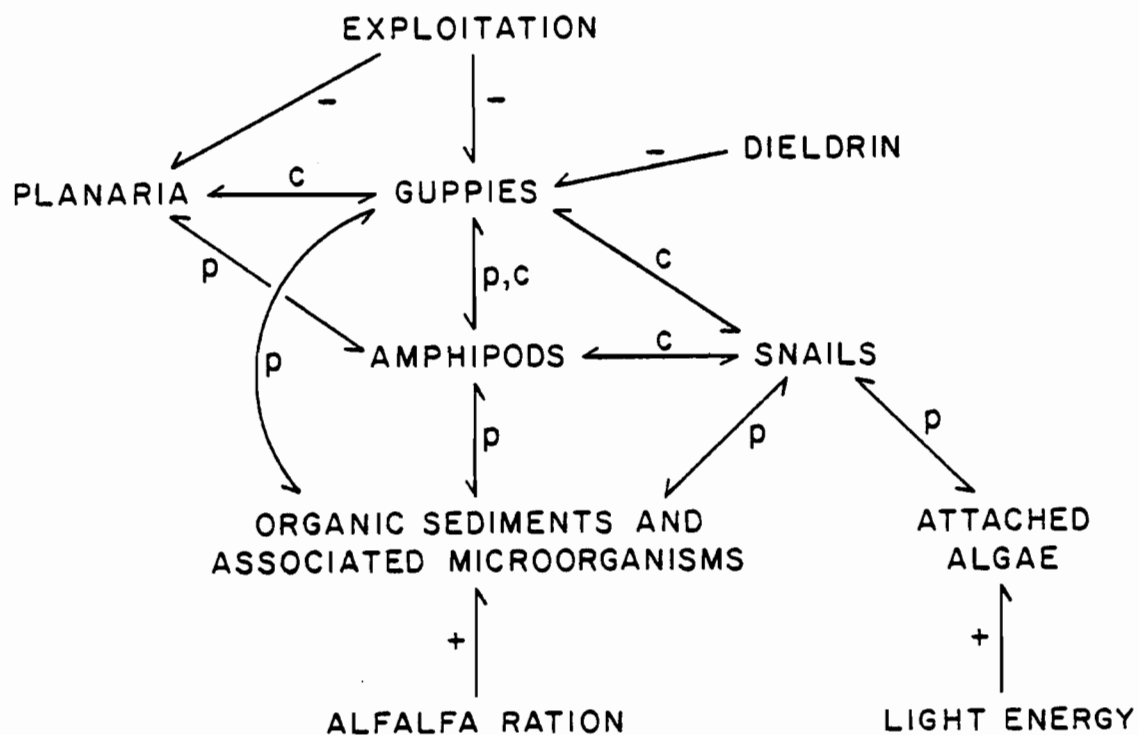
microfauna (including: nematodes, flagellates, rotifers, gastrotrichs
and protozoans) were reported by Finger (1980). An apparent link
between this benthic subsystem and the major predators was a
protozoan-nematode-guppy trophic chain. Inorganic sediment accu-
mulation was dependent in part on material in the incoming well water.
During periods of heavy rainfall (especially in the winter of 1977-1978)
the water in the laboratory ecosystems was turbid for several days,
this resulting in an increase in total sediment density. The initial
differences in sediment density between tanks and the subsequent in-
creases were directly correlated to the distance of a tank from the
diluter (see Appendix I). The shorter the piped water distance along
the common PVC pipelines, the greater the accumulation of inorganic
sediments. Alfalfa input, 0.6 or 4.0 grams per day, was the major
source of organic sediment differences between tanks at low and high
energy input levels.

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 ration, sediments,
and amphipods. Stomach samples showed the presence of all mater-
ials and microorganisms identified in the sediments, plus amphipod
parts. Newborn guppies were observed eating alfalfa and picking
through the sediments. Guppy biomass was primarily a function of
exploitation level and of food density, which was limited even at 40

percent exploitation.

The amphipods in these laboratory systems were detritivore crustaceans that ranged in size from 0.5 to 15.0 millimeters (4×10^{-5} to 4×10^{-3} grams). They were observed feeding in the sediments and on the alfalfa ration. Amphipods moved freely throughout the tank and were found among the gravel, on the plants, and on the sides of the tanks when guppies were absent or at low densities of guppies (including: the first year of the study; system No. 1 following extinction of the guppies; and systems with high guppy exploitation). Their movement was usually limited to among the gravel and the sediment when guppies were present. Amphipod biomass was primarily a function of the food and cover available and the density of the guppies. Later in the experiment, amphipod density became dependent upon the inadvertently introduced planaria populations. Planaria were more effective predators on amphipods than were guppies, the amphipods being unable to escape from planaria in the substrate habitat. Planaria were observed in all systems at low densities (i.e. 1 to 30 individuals) as early as October 1977. Following the increase in alfalfa input and substrate cover in eight systems, amphipod populations increased up to 15 times in biomass. Planaria populations increased following the increase in amphipods (see Appendix II and III). Complete elimination of planaria by exploitation allowed the amphipods to again increase in four systems. Planaria were not exploited in the remaining four

systems at high energy input and they eventually eliminated all the amphipods.

Snails were introduced as eggs attached to the aquatic plant Ceratophyllum. They were considered of minor importance in the systems with low energy input; the populations were small with individuals up to 15 mm in diameter and 1.0 gram. Snails were observed eating attached algae on the sides and bottom of the tanks as well as feeding in the sediments. High alfalfa input brought about dramatic increases in snail biomasses, after which snails were observed feeding directly on alfalfa. Censusing of snail populations was initiated about this time. Snail biomass was primarily a function of competitor densities and the availability of organic sediment and attached algae. Losses of snails to parasitism, predation on eggs, and other mortality was unaccounted for in these systems.

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 other species in the laboratory systems. Algal density varied between tanks from essentially macroscopically non-visible levels to a solid green-brown mat (see Appendix II and III). Differences in algal density and sediment accumulation patterns had apparent effects on resulting structure and organization of the systems.

Environmental System

The manipulated environmental components of the laboratory

ecosystems included energy and material input and removal, and toxi-

cant perturbation. Alfalfa was the major energy source, as was made

apparent by the increase in population biomasses corresponding to

the change from 0.6 to 4.0 grams per day of alfalfa ration. Eight

systems received approximately 1000 grams throughout the study

(low alfalfa input); the remaining eight received approximately 3000

grams total. The organic nitrogen content of the alfalfa ration was

3.0 percent. Light levels were kept relatively low to prevent algal

blooms. Intensities ranged from 15 to 23 foot-candles at the surface

of the water and were directly correlated with location of the tanks

in the laboratory (see Appendix II and III).

Monthly exploitation of the guppy populations simulated the

impact of a fishing pressure over the maximum range (0 to 40 percent)

allowing persistence of guppies in these systems. 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 additional fluctuations in population bio-

mass; however, over many months, mean exploitation rates were

near the intended percentages (see Appendix II and III), and guppy

population biomass, cohort dynamics, and life history patterns varied according to fishing pressure and energy input levels.

The environmentally stable insecticide dieldrin was used to demonstrate the response of the laboratory ecosystems to toxicant perturbation over the range of energy input and exploitation levels. At 1.0 part per billion (ppb), dieldrin appeared to directly affect guppy growth, reproduction, and survival. Dieldrin apparently affected the other populations mainly indirectly through changes in predation and competition. Earlier studies at this laboratory demonstrated the 96-hour LC50 of newborn guppies to be about 5.0 ppb and that of adult females to be about 20 ppb dieldrin. The 96-hour LC50 for amphipods was determined to be about 50 ppb. The benthic microorganisms showed no apparent changes in density at 150 ppb of dieldrin in ancillary experiments. Snail populations were not depressed at 1.0 ppb in the laboratory systems. Means and standard deviations for weekly water samples were: system No. 1, 0.95 ± 0.09 ppb; system No. 3, 0.98 ± 0.08 ppb; and systems No. 4 and 14, 0.96 ± 0.08 ppb dieldrin. Through food and the water, the lipophilic dieldrin accumulated in tissues of the organisms and in the sediments (see Appendix IV).

In nature, populations persist through interactions and adaptations in complex and fluctuating environments. Figure 2 illustrates some of the major trophic and behavioral interactions including

predation, competition, and omnivery in the laboratory systems. These interactions along with prevailing environmental conditions resulted in continuous gains and losses in population biomasses, which will now be interpreted as changes in population and community structure. So in part, the pattern of organization inferred for the laboratory systems will be used to explain their observed dynamic and near steady-state structure.

Dynamic and Near Steady-State Structure of the Laboratory Ecosystems

Figure 3 presents the co-occurring biomasses of five populations in system 16 over the 34 months. The patterns of trajectories for guppies and amphipods in 1976 and 1977, for planaria and amphipods from September 1978 through August 1979, and for amphipods and snails beginning with the recovery of amphipods in April 1979 can be viewed as dynamic population interactions including predation and competition. Near steady-state structure for the laboratory systems under a single set of environmental conditions was assumed when populations fluctuated in a very restricted area of phase space relative to previous and succeeding fluctuations following perturbation. System 16 was near steady state in 1977 at low levels of energy input and habitat availability. In February 1978 this system was shifted to high levels of alfalfa input and habitat. Guppy population and organic sediment dynamics give

Figure 3. Co-occurring biomasses for five major populations over the 34-month study. System No. 16 (at 20 percent exploitation), being representative of the laboratory systems, is used to show population responses to one another and to changes in environmental conditions. Each population is on its own biomass scale to facilitate comparison. Dashed lines for planaria and snails are extrapolations for time period prior to population censusing. Sediments are plotted as organic sediments; however, the pattern was similar for total sediments and for sediment organic nitrogen.

POPULATION DENSITIES

x GUPPY
● AMPHIPOD
△ SNAIL
o PLANARIA
▪ SEDIMENTS

INTRODUCE GUPPIES TO SYSTEM NO. 16
ESTABLISHED FOR ONE YEAR

SHIFT FROM LOW TO
HIGH ENERGY INPUT

(65 grams)

(50 grams)

EXPLOIT
PLANARIA

(0.5 grams)

(0.5 grams)

(5.0 grams)

(10 grams)

(11 grams)

(500 planaria)

(5.0 grams)

(10 planaria)

N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A

1977   1978   1979

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some indication that the system was approaching a new steady state in
1979 under the new environmental conditions. Amphipods, which had
been depleted by planaria, responded positively to removal of the
planaria. And snails appeared to be responding to the increase in
sediments (Fig. 3).

Co-occurring biomasses of two interacting populations can be
plotted on coordinate axes forming a common phase plane. This
graphical procedure explicitly couples the dynamics of interacting
populations to one another. Dynamic structure, or the development
of the interaction, is represented by the trajectories connecting the
points. Under constant environmental conditions, the trajectory of
coordinate biomasses may track toward a steady-state point on the
phase plane; changing the environment alters the direction of the
trajectory toward another steady state. By expanding the axes the
relative position of system behaviors near steady state are seen for
different environmental conditions affecting species interactions.
Figure 4 illustrates the phase plane behavior for the guppies and
organic sediments (hereafter referred to as sediment) in system 16
projected from their simultaneous time plots. Each point on the phase
plane represents the co-occurring biomasses of guppy and sediments
for a particular month; open symbols are for months with low energy
input, solid symbols are for high energy input months.

The phase plane representation for four of the laboratory

Figure 4. Derivation of a resource-utilizer (predator-prey) phase
plane for guppies and organic sediment in System No. 16.
Simultaneous time plots from Figure 3 are projected on
a third, phase plane. Resultant co-occurring biomasses
of predator and prey for each month are connected by a
trajectory which traces the development of the interaction.
Open symbols correspond to months with low energy input;
solid symbols for high energy input months. (after Holling
1973).

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GUPPY BIOMASS (g)

ORGANIC SEDIMENTS (g)

TIME →
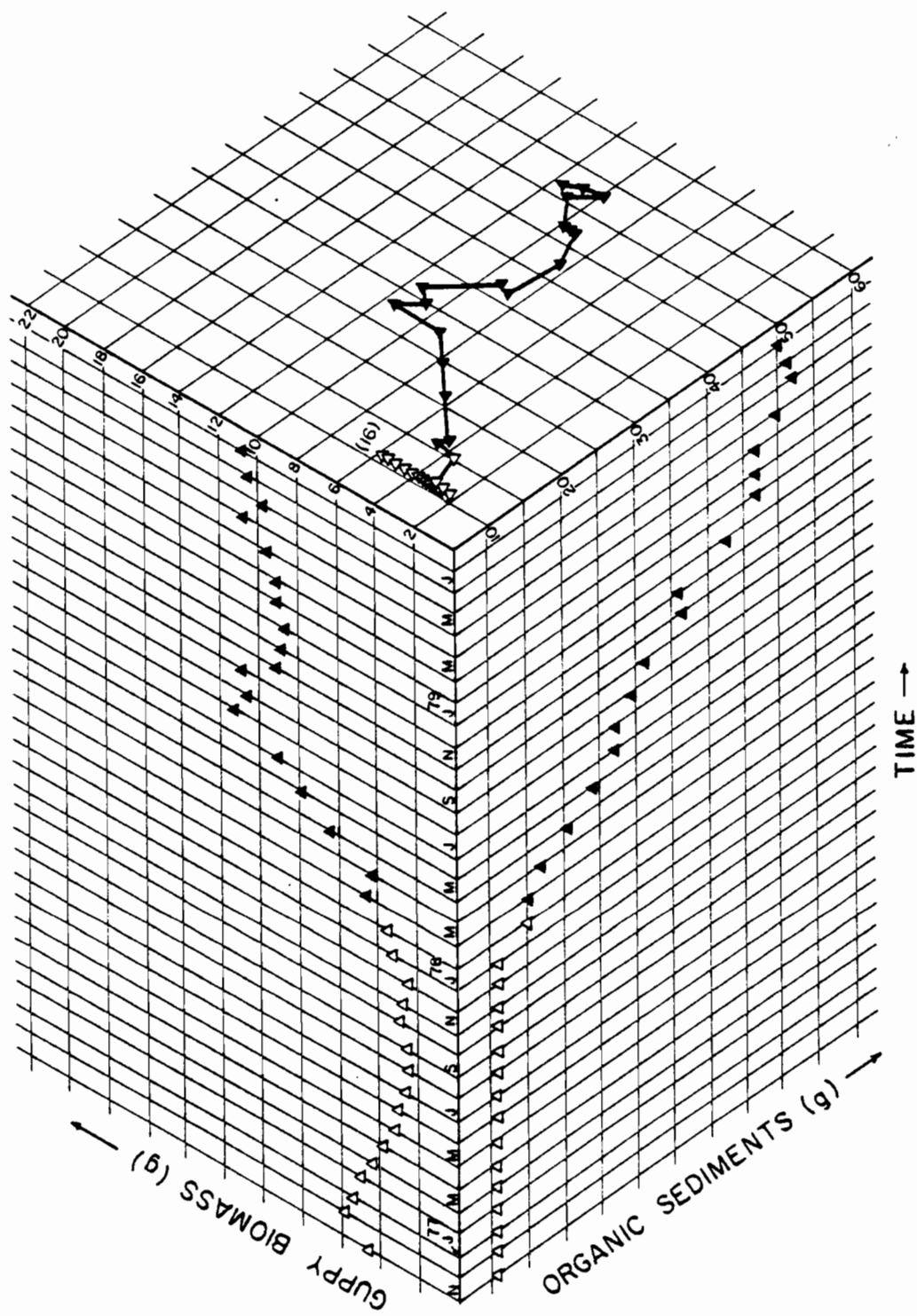
systems (one at each level of guppy exploitation) at low energy input and at high energy input with planaria removed is shown in Figure 5. The guppy and sediment populations are near steady states at low energy input, guppy biomasses being separated by the level of exploitation, and highest biomasses occurring at the zero level of exploitation. Both sediments and guppies increased with the shift to high alfalfa input and may be near new steady states toward the end of the trajectories. The trajectory for system 16 is the same as that shown in Figure 4.

Figure 6 shows for all 16 systems guppy, amphipod, and snail populations in relation to sediments as mean biomasses over periods when these populations were taken to be near steady states. Although steady states were probably approximated at low energy input, those represented at high energy input are much more problematical. Guppy population levels were directly determined by exploitation, according to which their near steady-state biomasses were sharply separated. Predation and competition can be inferred from the inverse sizes of guppy and amphipod, and guppy and snail populations corresponding to particular levels of exploitation at low energy input. In general, dieldrin changed the system structure by decreasing guppy biomass, which allowed amphipod biomass to increase. Near steady-state patterns were not as well defined for high energy input, but there were dramatic changes in structure relative to low energy input. Exploitation continued to have marked effects on guppy biomass, which

Figure 5.   Phase plane representation of four laboratory systems, one at each level of guppy exploitation ($\Diamond$ - 0, O - 10, $\triangle$ - 20, and $\square$ - 40 percent guppy exploitation). Guppy and sediment populations are near steady state (overlapping, co-occurring biomasses) at low energy input (open symbols). Shift to high energy input (solid symbols) results in increases in biomass of both populations, with systems approaching new near steady states at the end of the trajectories. The trajectory pattern for System No. 16 is the same as that in Figure 4. Populations are censused, and co-occurring population biomasses are plotted at one-month intervals. Time on the phase plane begins at the system-numbered point.
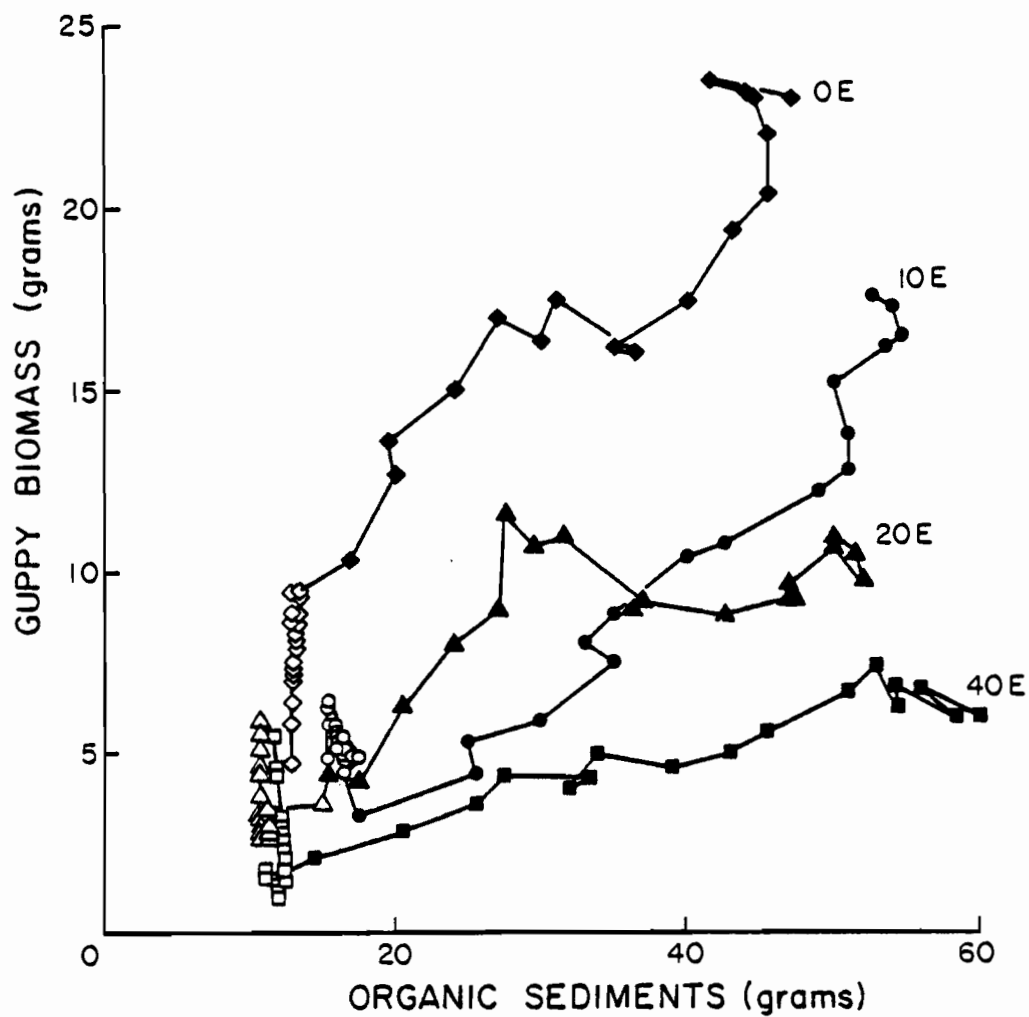
Figure 6.   Near steady-state structure for the 16 laboratory eco-
            systems. Guppy, amphipod, snail, and sediment mean
            population biomasses were calculated from near steady-
            state data (continuously overlapping biomasses) corres-
            ponding to low energy input (approximately 10-20 grams
            organic sediment), low energy input with dieldrin (indi-
            vidually circled system numbers), or high energy input
            (approximately 50-60 grams organic sediment). Popula-
            tion biomasses separate according to guppy exploitation
            level; competition and/or predation can be inferred from
            inverse sizes of populations in the same system.
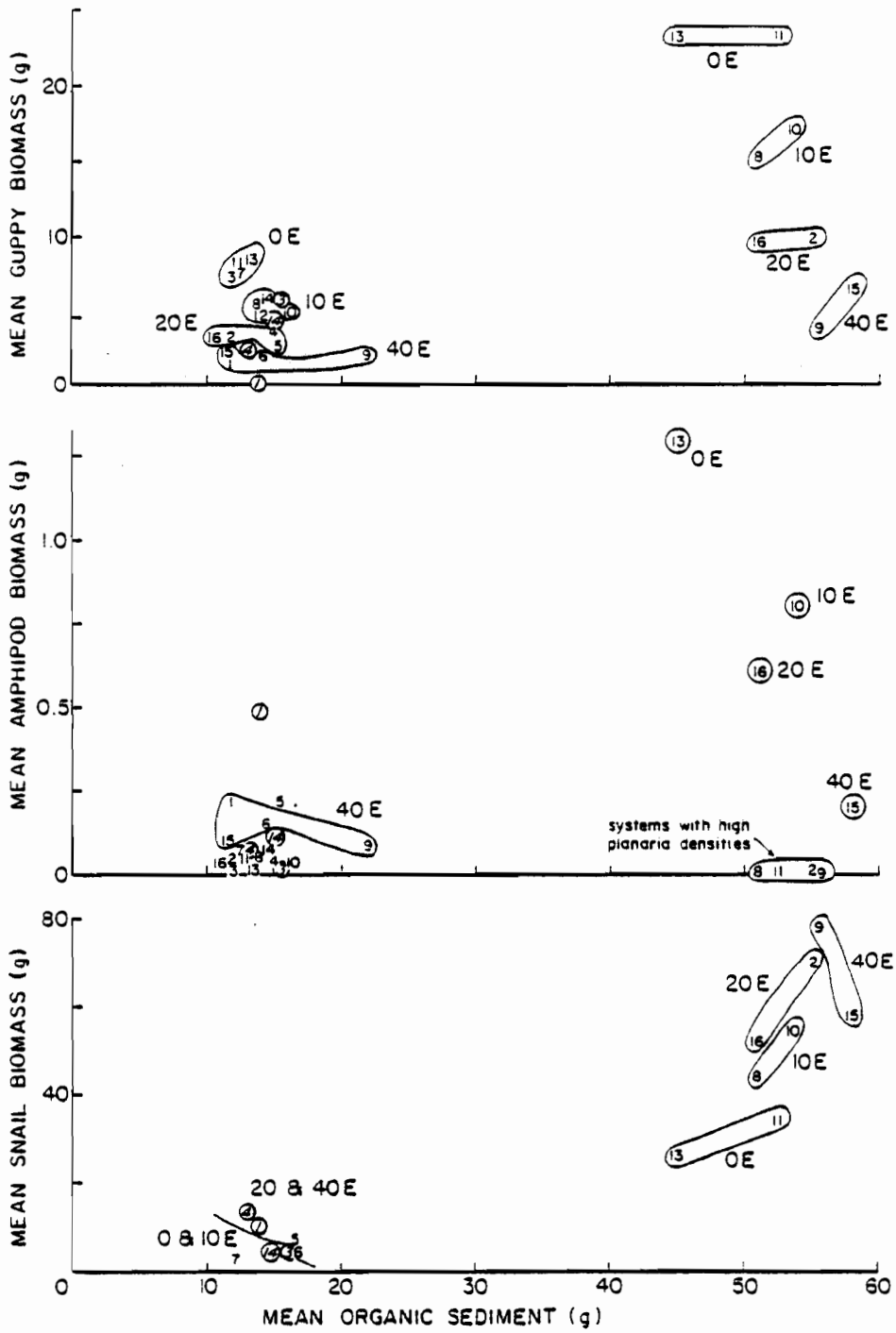
inversely affected the snail populations. Amphipods went nearly extinct

in the four systems with planaria. In the remaining four systems,

amphipods were negatively correlated with snails and positively with

guppies. This may suggest three-way competition in which guppies,

whose biomass was primarily a function of exploitation, in part deter-

mined the size of snail populations as did amphipods that benefited

from the guppy-snail interaction and were at the same time protected

from predation by the high level of habitat cover. Total biomass and

species abundance of benthic microorganisms dropped sharply in

those systems with high levels of energy and habitat cover, apparently

because of decreased dissolved oxygen in the gravel and sediment sub-

strate (Finger 1980). A pattern of relative invariance of organic

sediment density was evident over the range of exploitation for a given

energy input level. This result will require a detailed interpretation

of interspecies and species - environment interactions.

Predation and Competition at Different Levels of Habitat, Energy, Exploitation, and Toxicant

Phase Plane Dynamics

This section presents a series of phase planes coupling guppy,

amphipod, and snail populations. Patterns of the dynamic and the

near steady-state structures for a particular population are the same

on all phase planes on which that population appears. Figure 7

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illustrates the dynamic behavior of guppies and amphipods in replicate

systems (11 and 13) at zero percent exploitation. All 16 systems were

established with amphipods, low habitat, and low energy input for 12

to 18 months prior to introducing 4.5 grams of guppies per system in

November 1976. Amphipod biomass reached a maximum of 1.5 grams

without guppies present, the range at the time of guppy introduction

being 0.1 to 1.0 gram, because of population oscillations and inherent

differences between systems. Over approximately 18 months, the

fluctuations in guppy and amphipod biomasses decreased and near

steady states were established at low energy input (Fig. 7). Guppy

and amphipod biomasses increased rapidly when eight of the systems

were shifted to high energy input, as shown for systems 11 and 13 in

Figure 7. Not shown are the concurrent increases in planaria and

snail biomasses. These eight systems (excluding 13) had losses of

amphipods to predation by planaria. After planaria removal from

systems 10, 13, 15, and 16 the amphipods again increased. Amphi-

pods went nearly extinct in systems 2, 8, 9, and 11 without planaria

removal. During 18 months at high energy input, these systems

tended toward new steady states having much larger guppy, amphipod

(except in systems with planaria) and snail populations.

Figure 7. Phase plane representation of dynamic (developmental) and near steady state guppy and amphipod population biomasses in paired systems. Systems 11 and 13 are zero exploitation systems at low (open symbols) and high energy input (solid symbols). Approximately 4.5 grams of guppies were stocked in systems with established amphipod populations. System 11 lost its amphipod population to planaria predation; planaria were removed from system 13 prior to planaria population increase. Populations are censused, and co-occurring population biomasses are plotted at one-month intervals. Time on the phase plane begins at the lower set of system-numbered points.
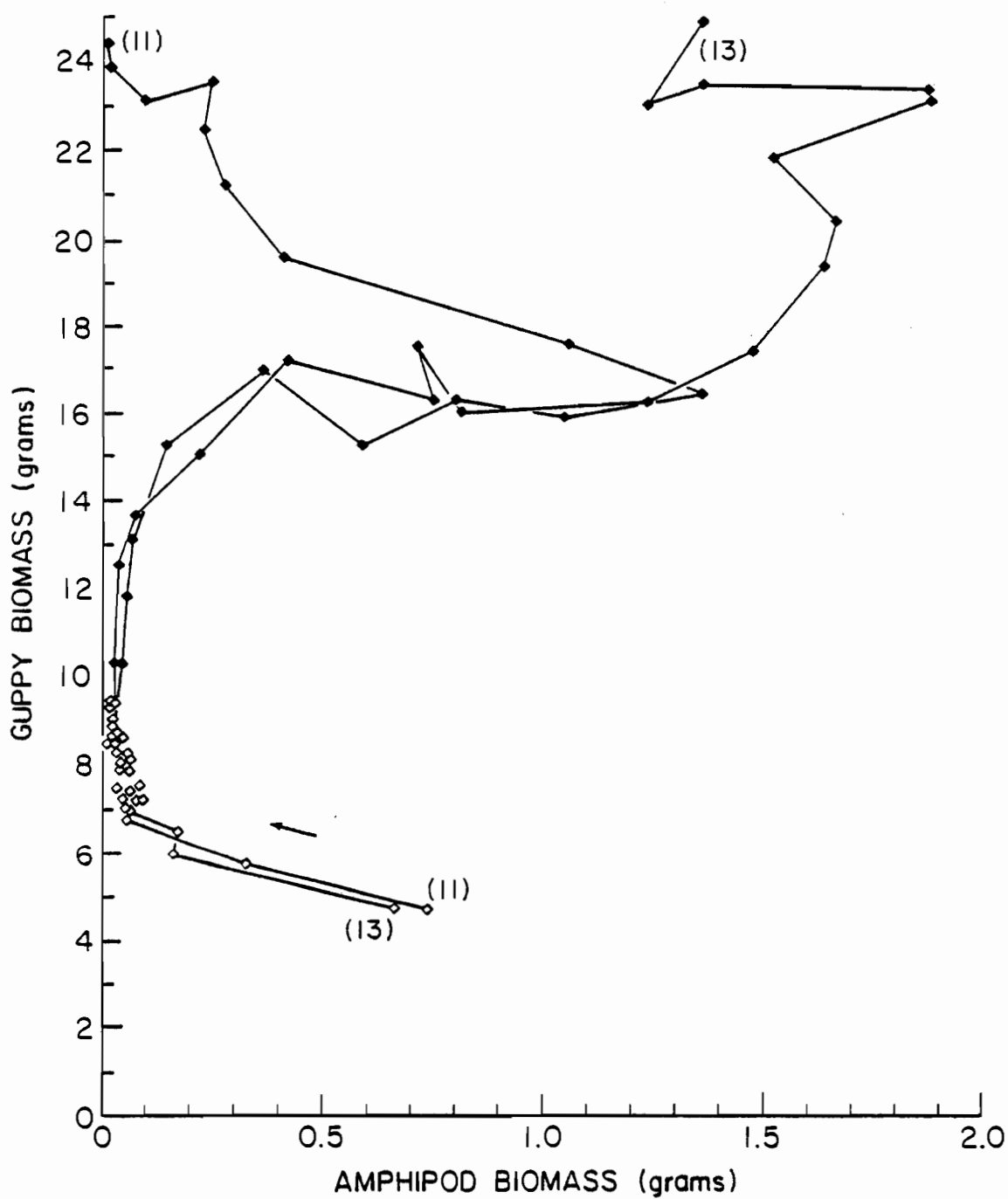
Low Habitat and Energy Input-High
Habitat and Energy Input

Figure 8 shows near steady-state structure for all 16 systems
at low energy input on a single guppy-amphipod phase plane. As exploi-
tation was increased from zero to forty percent, guppy biomass near
steady state decreased from approximately 9.0 to 1.0 grams. Near
steady-state biomasses of amphipods were inversely related to near
steady-state guppy biomasses, apparently because of predation and
competition. The eight systems that were shifted to high energy input
(Fig. 9) gave some indication of approaching near steady state condi-
tions after 18 months of response to sediment increases, planaria
predation and removal, and the apparent gain in importance of snails
as a competitor (Fig. 10). Guppies had increased threefold and amphi-
pods up to 15 times in systems where planaria were removed after
energy input was increased. Amphipods went nearly extinct in the
four systems having high densities of planaria. In these systems
guppy biomasses were not substantially different from those in sys-
tems with higher amphipod biomasses. The sediments that were usu-
ally consumed by the amphipods were among the substrate gravel
and mostly unavailable to the guppies. This additional sediment re-
source among the gravel was thus available to the snails, whose
biomass increased accordingly. A positive relationship between guppy
and amphipod biomasses was apparent in the high energy and habitat

Figure 8.   Phase plane representation of near steady-state guppy and
amphipod population biomasses at low energy input. The
16 systems are separated by exploitation level ($\diamondsuit$ - 0,
O - 10, $\triangle$ - 20, and $\square$ - 40 percent guppy exploitation).
Amphipods respond in a density-dependent manner to guppy
predation and competition. Differences in near steady-
state patterns for replicate systems in part reflects the
variability of other system components including: light
level, algae, snails, and sediments with associated micro-
organisms. Populations are censused, and co-occurring
population biomasses are plotted at one-month intervals.
Time on the phase plane begins at the system-numbered
point.
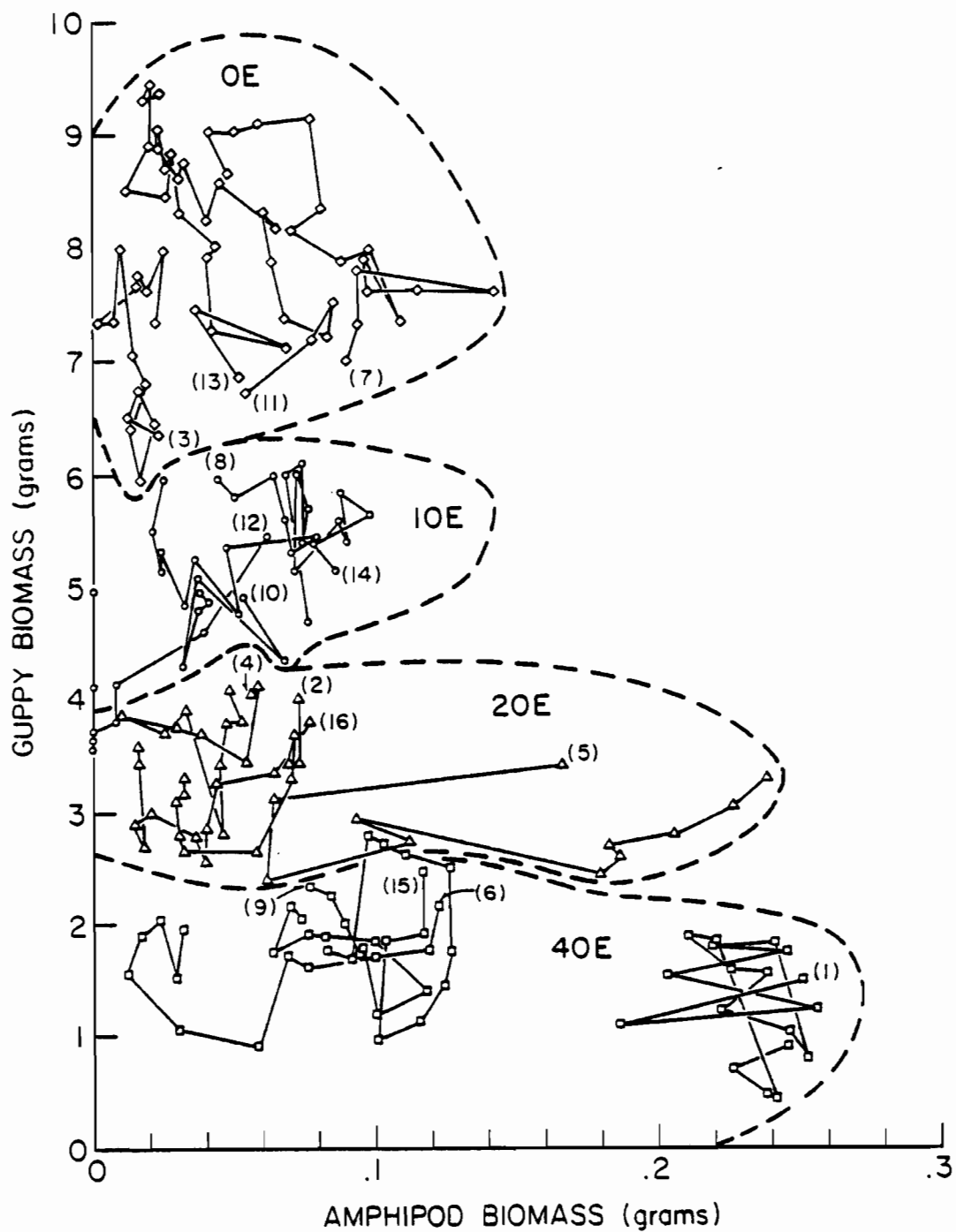
Figure 9.   Phase plane representation of near steady-state guppy
            and amphipod population biomasses at low energy input,
            just prior to shift to high energy input (see Fig. 10).
            The paired systems separate according to exploitation
            ($\diamond$ - 0, O - 10, $\triangle$ - 20, and $\square$ - 40 percent guppy ex-
            ploitation). Amphipod populations at 40 E are relatively
            large, likely in response to reduced predation/competition.
            Populations are censused, and co-occurring population
            biomasses are plotted at one-month intervals. Time on
            the phase plane begins at the system-numbered point.

Figure 10. Phase plane representation of guppy and amphipod popula-
tion biomasses approaching near steady states at high
energy input. Hatched area indicates relative position of
these eight systems at low energy input (see Fig. 9). The
trajectories between low and high energy input have been
removed to facilitate comparisons. Systems separate
according to exploitation ($\diamondsuit$ - 0, O - 10, $\triangle$ - 20, and
$\square$ - 40 percent guppy exploitation). Planaria predation
is responsible for nearly extinct amphipod populations in
systems 2, 8, 9, and 11. Snail populations and high gravel
habitat/cover for amphipods accounts for apparent positive
relationship between amphipods and guppies (see text).
Populations are censused, and co-occurring population
biomasses are plotted at one-month intervals. Time on
the phase plane begins at the system-numbered point.
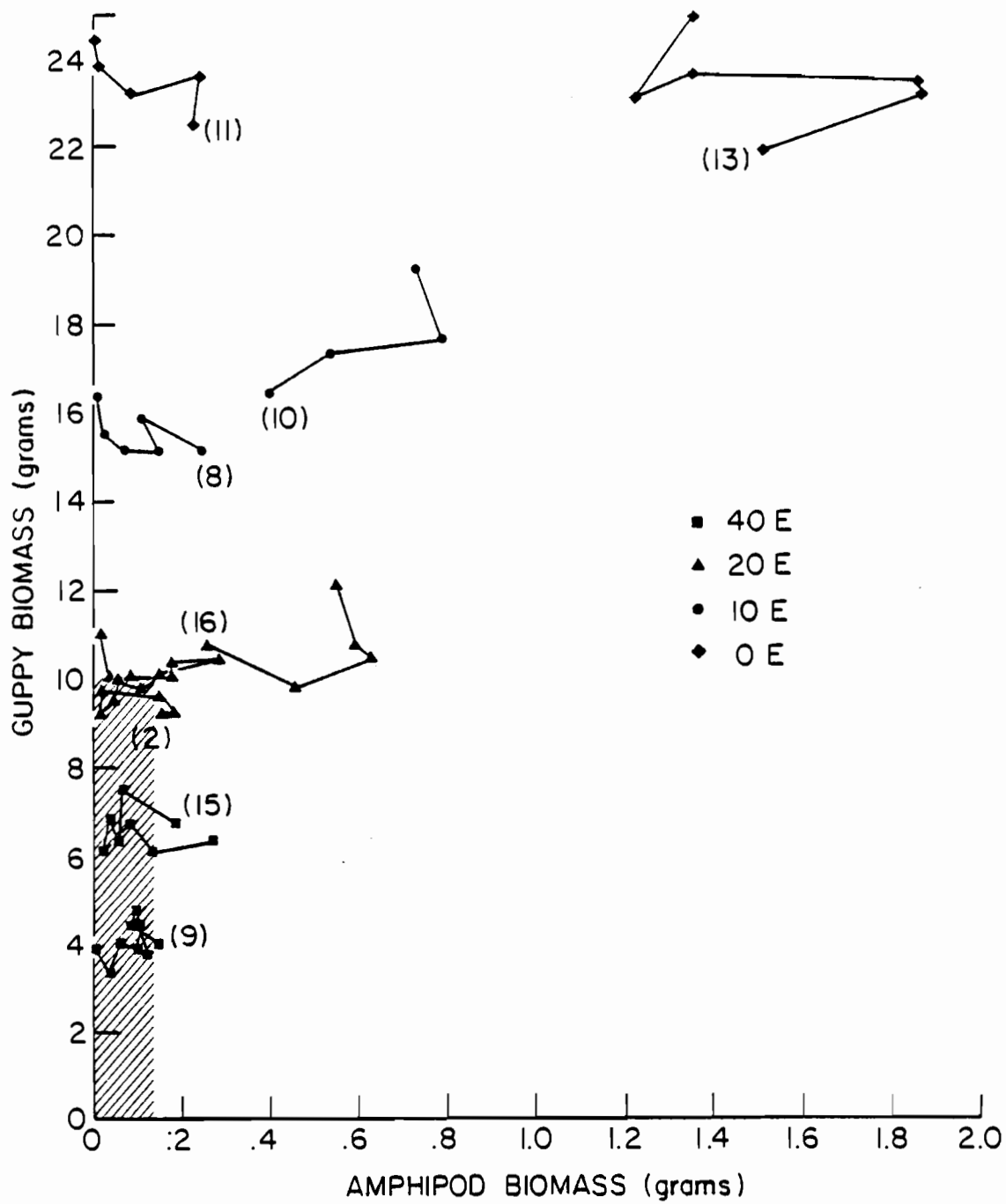
systems from which planaria were removed (10, 13, 15, and 16). This was in marked contrast to the negative or inverse predator-prey/competitor relationship observed between guppies and amphipods at low energy input. Guppies may not have been able to prey with much effect on amphipods because of the high level of substrate cover. At very high densities, amphipods may have saturated the cover, some becoming vulnerable to predation, and further increase inhibited, as perhaps in system 13 (Fig. 10). As exploitation decreased, guppies increased and put additional predation pressure on the sediments near the surface of the gravel substrate. This may have led to the decrease in snail biomass and ultimately more sediments for the amphipods deeper in the gravel. There appears, then, to have been a three-way competition for sediments, with gravel cover and guppy-amphipod predator-prey behavior playing major roles.

Constructing guppy-snail and snail-amphipod phase planes further detailed some of the proposed relationships involving snails. Snail populations were censused monthly beginning in October 1978. Provision of additional alfalfa and cover beginning in February and March 1978 resulted in large increases in snail populations relative to those systems remaining at low energy input (Figs. 11 and 12). There appears to have been a density-dependent relationship between guppies and snails in the dynamic and near steady-state structures. Differences in guppy biomass were directly related to exploitation;

Figure 11.   Phase plane representation of near steady-state guppy
and snail population biomasses at low energy input
(open symbols) and at low energy input with dieldrin
(solid symbols). Snail populations were censused
beginning in October 1978. Guppy populations respond
to exploitation ($\diamondsuit$ - 0, $\bigcirc$ - 10, $\triangle$ - 20, and $\square$ - 40
percent guppy exploitation). Snails respond in a density-
dependent manner to guppy competition for the sediment
resource. Populations are censused, and co-occurring
population biomasses are plotted at one-month intervals.
Time on the phase plane begins at the system-numbered
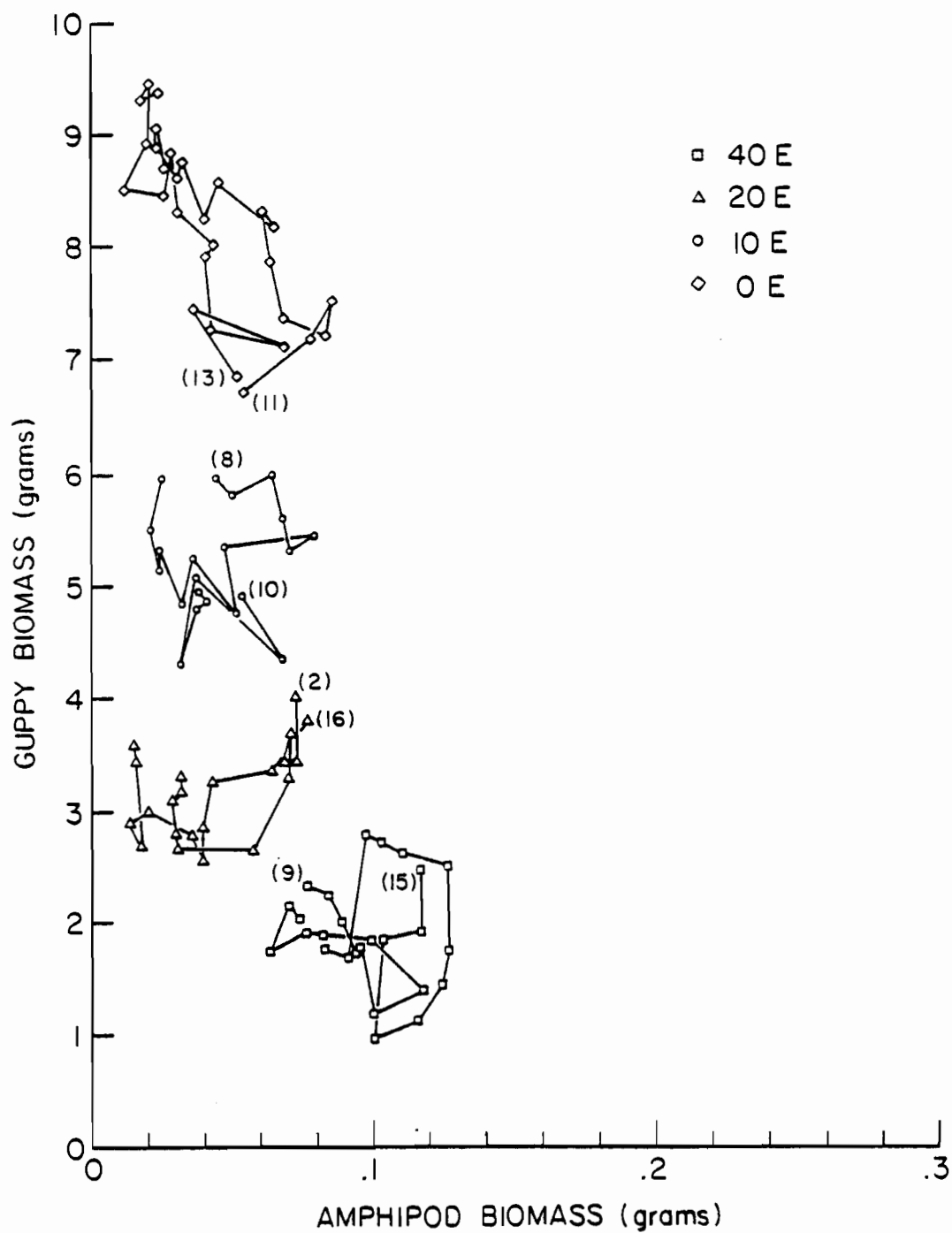point.
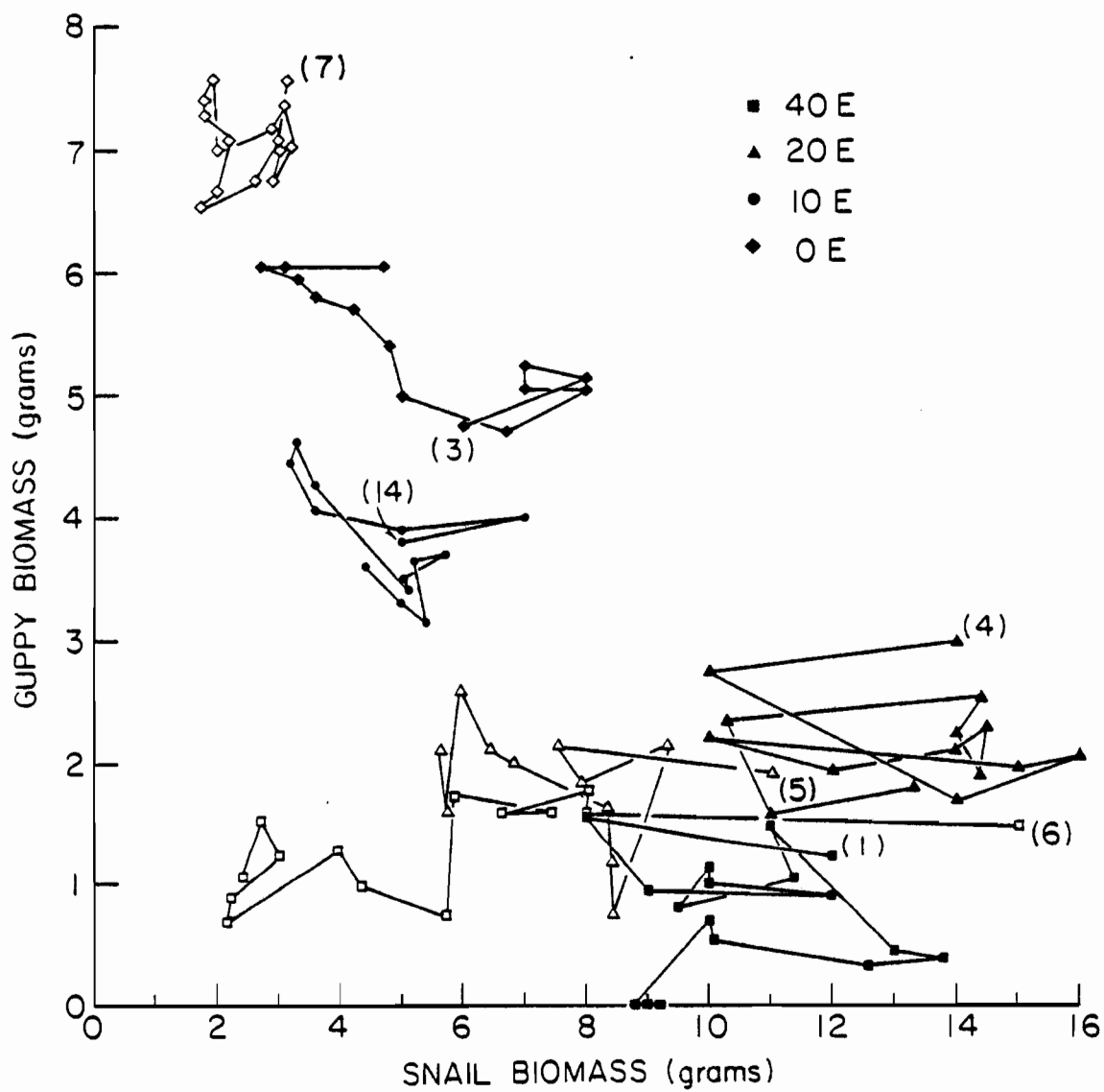
Figure 12. Phase plane representation of dynamic guppy and snail population biomasses and that approaching near steady states at high energy input. Hatched area indicates relative position of guppy and snail co-occurring biomasses at low energy input (see Fig. 11). Guppy populations respond to exploitation ($\diamondsuit$ - 0, $\bigcirc$ - 10, $\triangle$ - 20, and $\square$ - 40 percent guppy exploitation). Snails respond in a density-dependent manner to guppy competition for the sediment resource. Populations are censused, and co-occurring population biomasses are plotted at one-month intervals. Time on the phase plane begins at the system-numbered point.
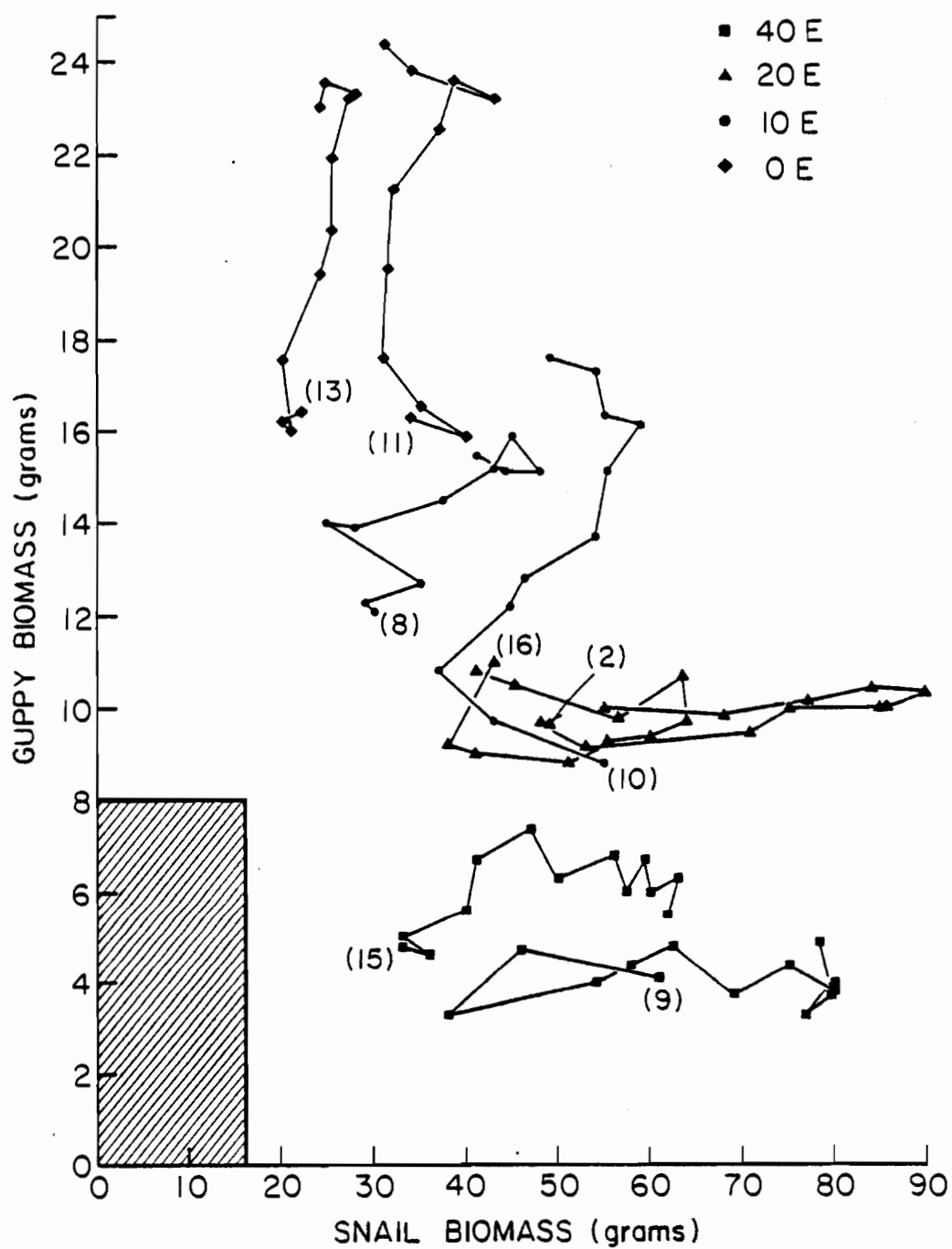
as exploitation decreased from forty to zero percent the rate of increase in guppy biomass was greater, and the time needed to approach near steady states was longer. Following a competition argument, large increases in snail biomass were associated with small increases in guppy biomass (e. g. systems 9 and 15 at 40E) and vice versa (e. g. systems 11 and 13 at 0E).

The dynamic structure exhibited on a snail-amphipod phase plane suggested a competitive relationship at the high level of energy input (Fig. 13). In response to predation by planaria, amphipod biomass decreased in seven of the eight systems (planaria in system 13 were removed before they had much effect). Snail biomasses concurrently increased, apparently because of increased availability of sediments among the rocks, no longer much utilized by amphipods and unavailable to the guppies. Planaria were then removed from systems 10, 13, 15, and 16 which allowed their amphipod populations to recover. Subsequently the snail populations in these systems stopped increasing and eventually decreased in biomass (Fig. 13). The amphipods through advantages including mobility and recruitment were able to regain their position in the food web. System 13, without planaria, had a large increase in amphipods and little change in snail biomass (Fig. 13). The four systems with amphipods near extinction (2, 8, 9, and 11) had higher mean snail biomasses than those systems with many amphipods present (Figs. 13 and 12). The difference between

Figure 13.   Phase plane representation of dynamic competitive
             interactions between snails, amphipods, and guppies
             at high energy input. Amphipod biomass decreases
             as predation by planaria ensues in seven of eight sys-
             tems (time begins at system-numbered point). Snail
             biomasses increase until planaria are removed (sys-
             tems 10, 13, 15, and 16) and amphipods recover, then
             snails decrease. Planaria were left in systems 2, 8,
             9, and 11, and were removed from system 13 before
             extensive predation on amphipods. The single points
             plotted for systems 2, 8, 9, and 11 (with amphipods
             nearly extinct) are snail mean values for Aug., Sept.,
             and Oct. 1979. Snail biomasses separate according
             to guppy biomass (i.e. ◇ - 0, O - 10, △ - 20, and
             □ - 40 percent guppy exploitation) because of competi-
             tion between them for sediments. Populations are
             censused and co-occurring population biomasses are
             plotted at one-month intervals.
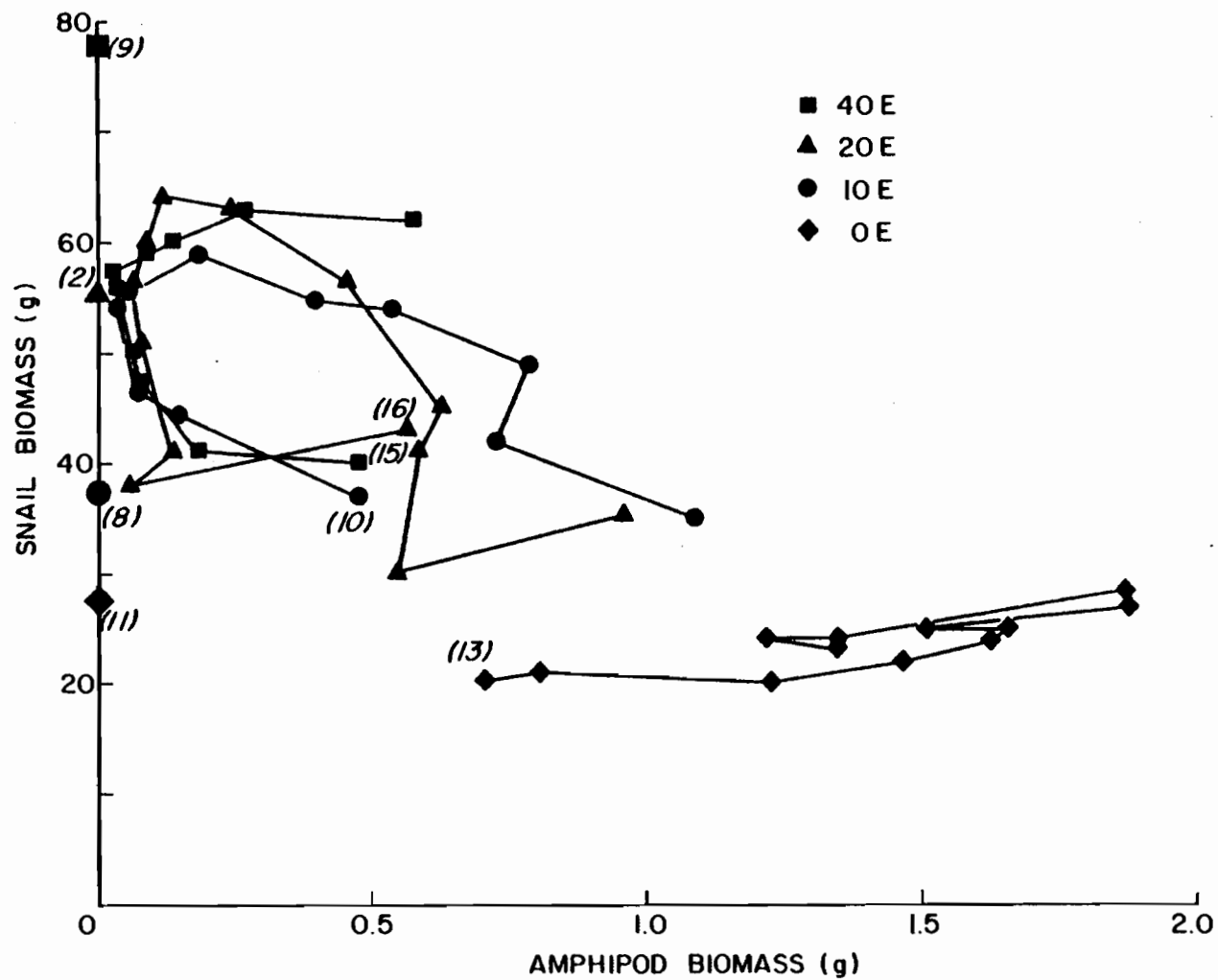
co-occurring biomasses of snails and amphipods as these approached

steady states with and without planaria were greater for systems with

higher levels of guppy exploitation. At low guppy exploitation, the

snails and amphipods had to compete with larger guppy populations.

This three-way competition for a finite food resource whose main

source (i.e. alfalfa ration) was independent of predator density prob-

ably accounts for the relative invariance of sediment density.

Low Energy Input-Toxicant Perturbation

The four systems with the tightest near steady-state patterns of

guppy and amphipod biomasses (1, 3, 4, 14, one at each exploitation

rate) were selected for toxicant perturbation. The four remaining sys-

tems (5, 6, 7, and 12) were kept unchanged at low energy input (Fig.

14). Over the 34 months, the guppies in these unaltered systems re-

sponded as expected to exploitation. However, the amphipods were

more varied in their dynamic structure; going extinct in system 12,

which was followed by an increase in guppy biomass. Snail biomass in

systems 5 and 6 decreased steadily during the final 18 months of the

study (Fig. 11), and may account for the corresponding increase in

amphipods (Fig. 14). Guppies and amphipods in systems 1, 3, 4, and

14 exhibited the anticipated inverse relationship of predator and prey or

competitor populations near steady states (Fig. 15). Systems 3 and 4

had lower amphipod biomasses near steady state than expected based on

their guppy biomasses and the near steady state of system 14. Snail

biomasses in these four systems (recorded after the introduction of

Figure 14. Phase plane representation of dynamic and near steady-
state guppy and amphipod population biomasses for the
four systems (5, 6, 7, and 12) that remained at low
energy input throughout the study. Trajectories begin-
ning at the system-numbered point, and going to the
asterisk-labeled point are the time period correspond-
ing to low energy input for all 16 systems. The systems
are separated by exploitation ($\diamondsuit$ - 0, $\bigcirc$ - 10, $\triangle$ - 20,
and $\square$ - 40 percent guppy exploitation). Amphipods went
extinct in system 12, and gradually increased in systems
5 and 6 where snails were gradually decreasing over the
same period (see Fig. 11). Populations are censused
and co-occurring population biomasses are plotted at
one-month intervals.

58
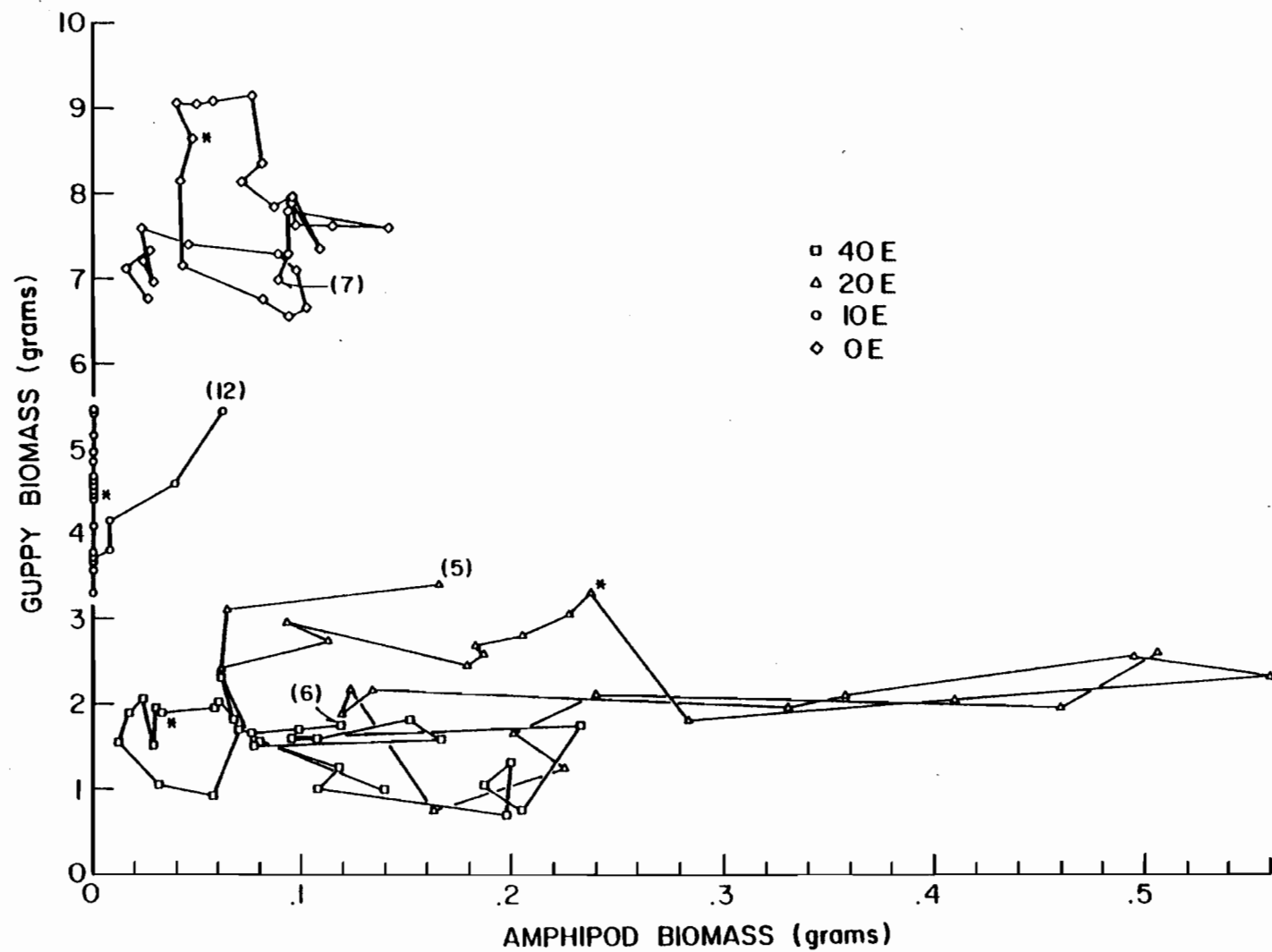
dieldrin) were inversely related to guppy biomass. Systems 3 and 4 had disproportionately high snail biomasses relative to the other low energy input systems (Fig. 11). Attached algal densities in systems 3 and 4 were much higher than in the other low energy input systems, this providing an additional food source for snails. With snails and amphipods competing for the sediments, relatively high biomasses of snails (because of an additional food resource) could explain the relatively low biomasses of amphipods in systems 3 and 4.

In general, the observed response to dieldrin was a decrease in guppy biomass accompanied by an increase in amphipod biomass (Fig. 15). The response of guppies and amphipods was dependent upon the level of guppy exploitation. At zero exploitation (system 3) there was an immediate and dramatic decrease in guppy biomass; amphipods responded with an increase in population size. Numerous male and adult female guppies died in the first few months. Direct mortality was not apparent in the other three systems receiving dieldrin. Thus there apparently was a density-dependent response to the toxicant. At zero exploitation guppies at high densities had less food per individual, this apparently resulting in relatively poor condition of the fish and increased susceptibility to the dieldrin. Selection must have occurred for the more tolerant fish, which were left to grow and reproduce. The guppy population gradually increased and eventually its biomass overlapped with that near steady state prior to dieldrin. Evolutionary and developmental adaptation apparently occurred in this system.

Guppy biomasses decreased in systems with 10 and 20 percent

exploitation (14 and 4) but without mortality directly induced by the

toxicant. Amphipod biomass increased in response, and new near

steady-state patterns developed with smaller guppy and larger amphi-

pod biomasses than occurred at the previous near steady states.

There were no obvious changes in guppy or amphipod biomass patterns

at 40 percent exploitation (system 1) for eight months. It appeared that

the amphipod biomass increase to 0.33 gram was enough to elicit an

intense predation response from the resident planaria population.

Amphipod biomass was reduced by two-thirds in the one month needed

to remove the planaria. This resulted in fewer amphipods as potential

prey for guppies, but also in more sediment available as food for

guppies. It is not likely that this lower amphipod biomass was influ-

ential in the subsequent decline of guppy biomasses. Because of low

density, systems at 40 percent exploitation often had a guppy popula-

tion size distribution with over seventy percent of the biomass in one

large female. This resulted in significantly more or less than the pre-

scribed 40 percent of the biomass being exploited in any given month.

System 1 had been exploited by 77 and 82 percent in the 18 months

prior to dieldrin introduction. In several months the system recovered

to its average biomass due to measureable increases in growth and re-

production of individual fish (see open symbols in Fig. 15 or 8). After

ten months of continuous exposure to dieldrin, system 1 was again

"overexploited" at 75 percent (a one gram female). The population did

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Figure 15.   Phase plane representation of dynamic and near steady-
state guppy and amphipod population biomasses at low
energy input (open symbols) and at low energy input with
continuous exposure to 1. 0 ppb dieldrin (solid symbols).
Guppy biomasses are separated by the level of exploita-
tion (◇- 0, O - 10, △ - 20, and □ - 40 percent guppy
exploitation). Amphipods respond in a density-dependent
manner to guppy predation and competition. Dieldrin
reduced guppy biomasses through time-dependent and
density-dependent effects on growth, reproduction, and
survival. Eventually, guppies in system 3 recovered
to pre-dieldrin levels, and went extinct in system 1.
Amphipod biomasses responded to reduced predation
and/or competition. Populations are censused and co-
occurring biomasses plotted at one-month intervals.
Time on the phase plane begins at the system-numbered
point.

GUPPY BIOMASS (grams)

AMPHIPOD BIOMASS (grams)

■ 40 E
▲ 20 E
● 10 E
◆ 0 E

(3)

(14)

(4)

(1)

8

7

6

5

4

3

2

1

0

0   .1   .2   .3   .56
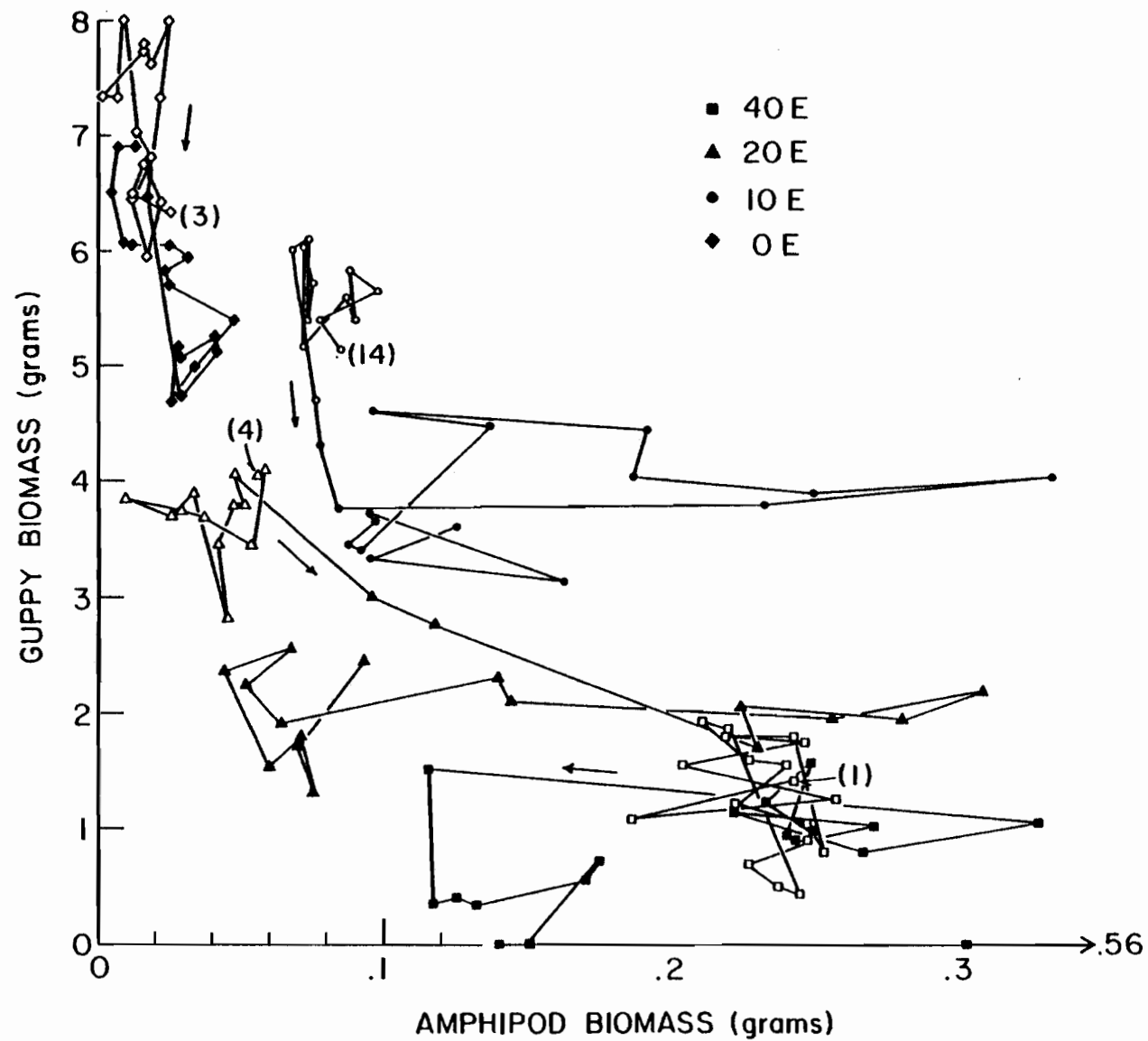
not recover in the following five months and went extinct with the re-
moval of a 0.2 and a 0.5 gram female. The two fish carried a total
of 42 immature oocytes; there had been no newborns for three months.
Amphipods were soon moving throughout the tank, and their biomass
reached a level of 0.56 gram not occurring since guppies were intro-
duced (Fig. 15). In the absence of guppies, snail biomass did not
increase but eventually decreased in this system with low algal den-
sity. This observation lends support to the argument that amphipods,
in the absence of guppies, had a competitive advantage (likely mobility
related) over snails for sediments.

Guppy Population Structure and Organization
Near Steady State

Population biomass is a result of the dynamic growth, reproduc-
tion, survival and behavioral interactions of individuals within the con-
text of prevailing community organization and environmental condi-
tions. Population biomass near steady state can be explored in terms
of biomass gains from production (growth and reproduction) and losses
to mortality including yield to exploitation. The concordance of selected
life history, cohort, and population dynamics of the guppy as related to
exploitation, dieldrin, and energy input levels is presented to provide
a greater understanding of organism-environment adaptive relation-
ships, and as a partial accounting for the near steady-state biomasses

64

of guppies in the laboratory systems.

Total Guppy Population Biomass, Production, and Yield Near Steady State

The multisteady-state pattern of guppy biomass for the 16 laboratory ecosystems can be explained in part by the different combinations of exploitation, energy input, and toxicant levels. Each point in Figure 16 represents the mean guppy biomass near steady state for a particular set of environmental conditions, and corresponds directly to a guppy trajectory pattern near steady state on a predation and competition phase plane. Mean guppy biomass decreased as the level of exploitation increased. Dieldrin led to a decrease in mean guppy biomass of approximately 24 percent at zero exploitation (followed by an eventual recovery of the biomass), 32 percent at ten percent exploitation, 46 percent at twenty percent exploitation, and 100 percent (eliminating the guppy population) at forty percent exploitation. The high level of energy input and habitat availability resulted in a threefold increase in mean guppy biomass within 18 months (Fig. 16).

The guppy populations must elaborate tissue at a rate equal to the exploitation rate (or higher if there was additional loss of biomass to mortality) to maintain a steady state biomass. Elaboration of guppy population biomass through growth and reproduction, combined in a single

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Figure 16.   Mean guppy population biomasses near steady state as
a function of the mean exploitation rate for the 16 labora-
tory ecosystems.   ◇- 0, O - 10, △ - 20, and □ - 40
percent are the intended exploitation rates. Guppy bio-
mass decreases with increasing exploitation at low
energy input (16 open symbols). Circled open symbols
are low energy input systems prior to dieldrin, which
decreased mean guppy biomass (4 solid symbols). High
energy input increased mean guppy biomass approxi-
mately threefold in 18 months (8 solid symbols). Curves
are fit by eye.
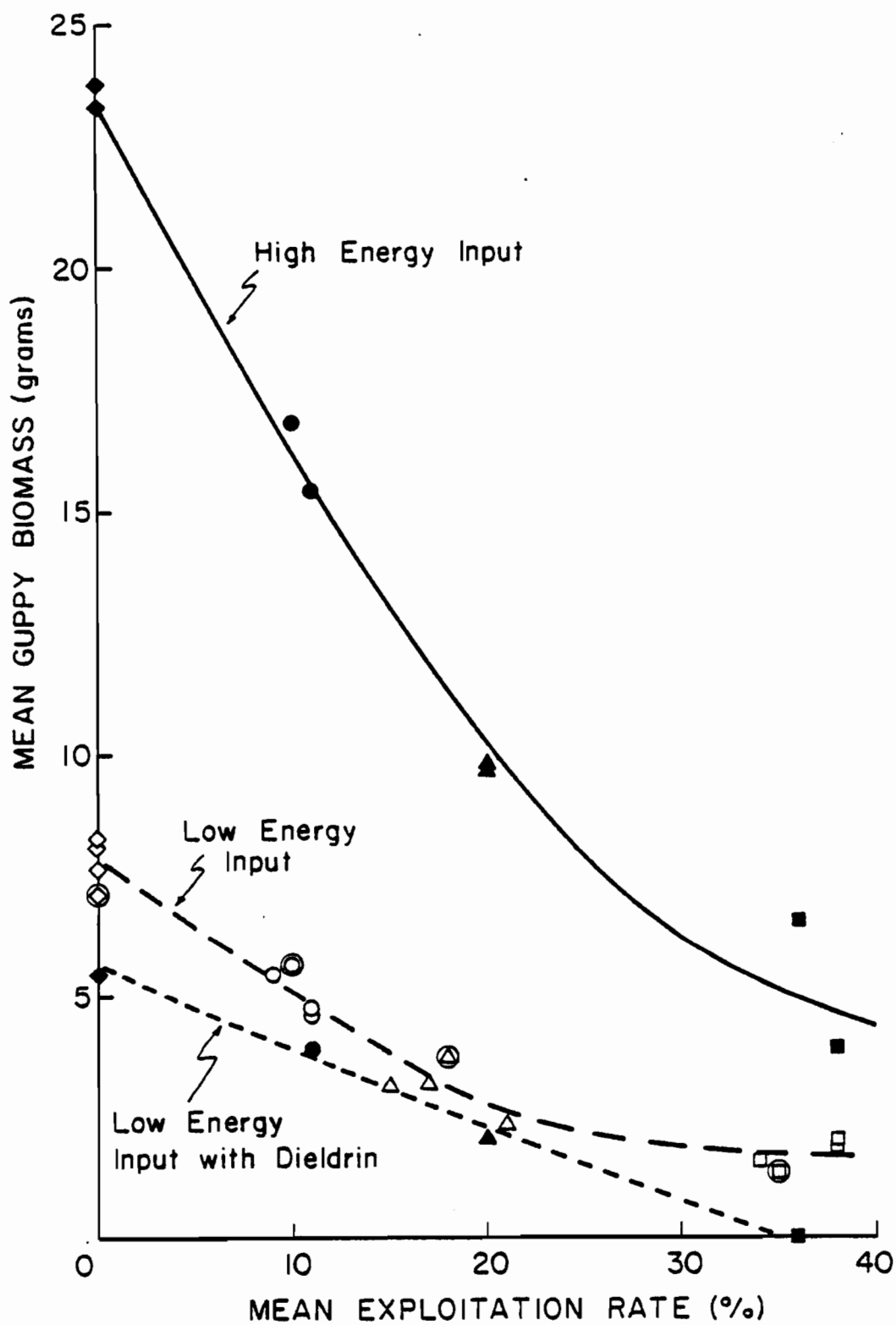
production term, was approximately equal to biomass losses from yield to exploitation (Fig. 17). These production and yield values are means calculated for the time period corresponding to near steady state for each population. Expressed as a function of mean guppy population biomass, families of production and yield curves were formed according to differences in environmental conditions, including energy input level and toxicant perturbation. Mean production and yield curves were highest for the systems receiving the high level of energy input, and lowest for the systems perturbed with dieldrin. For a given set of environmental conditions, increasing the exploitation rate decreased the mean guppy biomass and moved the production and yield values from right to left over the dome-shaped curves. Maximum production and yield occurred near 20 percent exploitation for all systems including those with low energy input, high energy input, and presence of dieldrin.

Dieldrin decreased mean production and yield in each of the four systems into which it was introduced (Fig. 17). The guppy population in the dieldrin treatment at 40 percent exploitation eventually went extinct. Growth of males, immature guppies, and mature females up to 19 millimeters in length was reduced to 50 percent of pre-dieldrin growth rates in the final five months before extinction. The number of newborn guppies was 70 percent below pre-dieldrin numbers during this five month period. One part per billion dieldrin

Figure 17. Mean guppy population production (upper axis) and yield (lower axis) near steady state as a function of mean population biomass near steady state. Mean guppy biomass is dependent upon the level of guppy exploitation ($\diamond$ - 0, $\bigcirc$ - 10, $\triangle$ - 20, and $\square$ - 40 percent per month). Open symbols are production and yield for low energy input systems; the four circled open symbols are low energy input systems prior to dieldrin introduction. Dieldrin reduced mean biomass, production, and yield (five solid symbols; the two solid squares are mean production, or yield, prior to guppy extinction, and then zero production, or yield, with guppies extinct). High energy input increased production and yield (8 solid symbols). Curves were fit by eye. Near steady state, yield plus unaccounted for natural mortality should approximate the production estimate.
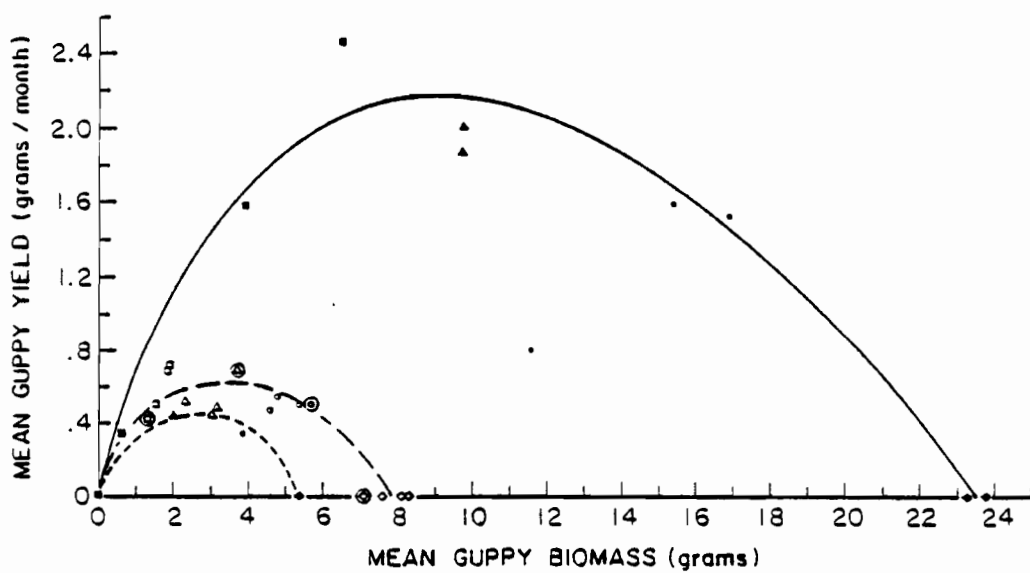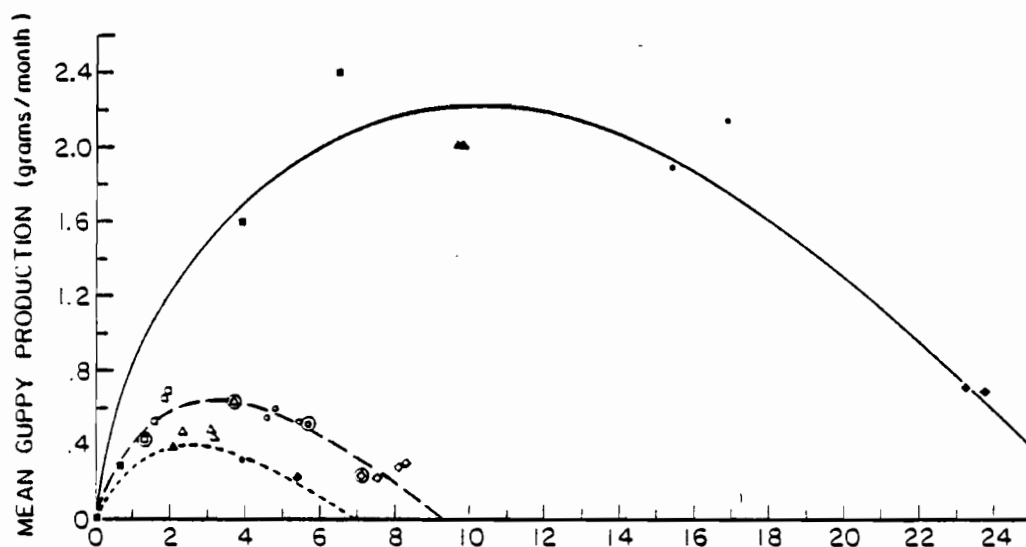
reduced mean guppy biomass from 7.1 to 5.4 grams at 0 percent ex-
ploitation; direct mortality of seven males and two large females in
the first two months of exposure accounted for a 1.5 gram decrease.
Mean production was approximately 0.23 gram per month both before
and after dieldrin introduction at 0 percent exploitation. The lower
mean biomass and equal production rates meant that growth and/or
reproduction of this population increased in response to dieldrin
perturbation. Developmental adaptation including increased growth
and reproduction, and decreased mortality of fish and progeny tolerant
to dieldrin would account for the eventual return of the population bio-
mass to 7.0 grams (Fig. 15).

Near steady-state production values in systems that were not
exploited (i.e. zero yield) were balanced by other mortalities. Non-
exploitation biomass losses for fish above the newborn size in the
four systems that received dieldrin were 0.17 and 0.31 gram per
month (before and after dieldrin introduction) for zero exploitation,
0.01 and 0.00 for 10 percent, 0.00 and 0.08 for 20 percent, and 0.00
and 0.00 for 40 percent exploitation. In systems with relatively low
densities of fish (i.e. low energy input and 40 percent exploitation at
high energy input) the newborn guppies were the only ones likely to
have unaccounted, or not observed, mortalities.

Guppy Population Size Distribution
Near Steady State

Total guppy population biomass and its gains (reproduction and growth) and losses (yield and other mortality) can be accounted for in terms of dynamics of the cohorts composing the populations. Guppy population size distributions near steady state provided insight into cohort dynamics and size specific life history patterns and into their adaptive relationships to changes in environmental conditions, population density, and community structure. Guppy populations in the four systems that were perturbed with dieldrin have been represented by eight size classes in Figure 18. These systems had relatively low guppy densities and unobserved mortality, and near steady-state biomasses were well established.

The sum of the mean biomasses for each size class equals the total mean biomass near steady state for that population. The pattern of change in size class biomass from newborn to the largest females can be taken to describe the biomass of a cohort as it moves through the population, so long as the population is at steady state. Mortality of newborns, including cannibalism, resulted in a relatively large decrease in the biomass of this size class in all four populations before and after dieldrin was introduced. Biomass was highest in the 30 to 34 millimeter size class, except at 0 percent exploitation where high density and corresponding low food availability resulted in few guppies

Figure 18.   Guppy size class mean biomasses near steady state for
              the four low energy input systems ($\diamond$ - 0, $\bigcirc$ - 10,
              $\triangle$ - 20, and $\square$ - 40 percent guppy exploitation) before
              (open symbols) and after (solid symbols) dieldrin intro-
              duction.   The pattern of change in size class mean
              biomass from newborns (NB, 0.01 gram) to the largest
              females (35-39 millimeter size class, 1.40 grams) can
              be taken to describe the biomass of a cohort as it moves
              through the population, so long as the population is at
              steady state.   At approximately 15 millimeters in
              length (0.10 g) guppies can be separated according to
              sex; the mean biomass of males (σ) and 15-19 mm
              females would be the mean size of the cohort at ma-
              turity.

MEAN NO. OF FISH

26	4.5	1.5	1.1	0.3	0.3	0.5	Control	0
20	2.8	1.2	0.5	0.3	0.3	0.3	Dieldrin	0

40 E

83	8.9	3.6	1.4	0.8	1.2	0.8	0.5
13	38	3.0	0.4	0.6	1.2	0.8	0

20 E

NB 15-19   25-29   30-34 mm
  10-14   20-24

NB 15-19   25-29   30-34   35-39 mm
  10-14   20-24

75	6.1	7.6	1.1	1.6	1.5	2.2	0.2
42	4.3	5.3	0.8	0.7	0.6	1.8	0.4

10 E

76	4.1	14.7	1.1	6.7	3.8	0.8	0
42	4.9	8.0	2.2	2.2	3.3	1.2	0.9

0 E

0.01 0.12 0.27   0.52   0.91   1.40 gm

0.01 0.12 0.27   0.52   0.91   1.40 gm

MEAN GUPPY SIZE CLASS BIOMASS (g)

MEAN SIZE OF A GUPPY IN DESIGNATED SIZE CLASS

reaching large sizes. Under heavy exploitation (i.e. 40 percent) a relatively even size distribution was maintained, except for an occasional large female, and fish did not reach the largest size class present in other systems. Dieldrin decreased total population biomass by decreasing the biomass of males, newborns and small females (Fig. 18). Female guppies no longer attained 35 millimeters in length at 20 percent exploitation but now began to reach that size at 0 percent exploitation, where growth rates and survival increased following the initial mortality owing to dieldrin.

Expressed as a percentage of total population biomass, the biomass of males decreased from 25 percent at zero exploitation to 12 percent at forty percent exploitation; the ratio of mean number of males to females decreased accordingly. As percentages of the populations, newborn biomass doubled, and 10 to 14, and 15 to 19 millimeter size class biomasses quadrupled with increases from zero to forty percent exploitation. The percent of newborns that reached the 10 to 14 millimeter size increased with higher exploitation. As the zero exploitation system with dieldrin recovered from toxicant-induced mortality, there was increased growth and survival of small fish and a more even size distribution from an increased contribution by small fish. Eighty-five percent of the population biomass at zero exploitation had been males and 20 to 29 millimeter females prior to dieldrin introduction.

Guppy Size Specific Growth and
Fecundity Near Steady State

As part of overall life history patterns, guppy relative growth rate and fecundity near steady state varied in response to exploitation, dieldrin, and energy input level, which altered population density and community structure. Growth rate was directly correlated with exploitation level (i.e. population density and food availability) the highest growth rates occurring at forty percent exploitation and the lowest occurring at zero exploitation, for a fish of a given size (Fig. 19). Relative growth rate decreased as the fish grew larger. Male guppies reached sexual maturity near 15 millimeters and their growth after that was often negligible; maximum size for males was approximately 20 millimeters.

Growth rate was expressed as a function of mean population biomass near steady state to examine the effect of dieldrin (Fig. 20). In general, dieldrin apparently reduced growth rates of males, newborns, immatures and small female guppies up to 24 millimeters in length. Growth was not separated into somatic and reproductive growth; the development of reproductive products is continuous in the viviparous guppy. There were reductions in reproduction with dieldrin; however, 10 to 14 millimeter fish, males, and newborns had reduced growth rates which would indicate reductions in somatic growth as well as reproductive growth in the presence of dieldrin.

Figure 19. Guppy size class mean relative growth rate near steady
state for the four low energy input systems before (open
symbols) and after (solid symbols) dieldrin introduction.
Growth rate is directly correlated with exploitation level
(i. e. population size) with highest growth rates occurring
at 40 percent and the lowest at 0 percent exploitation, for
a fish of a given size (◇ - 0, ○ - 10, △ - 20, and □ - 40
percent guppy exploitation). Relative growth rate de-
creases as fish grow larger; fish size expressed as
length (mm) and as mean weight (grams) for a given size
class (i. e. x-axes).

78
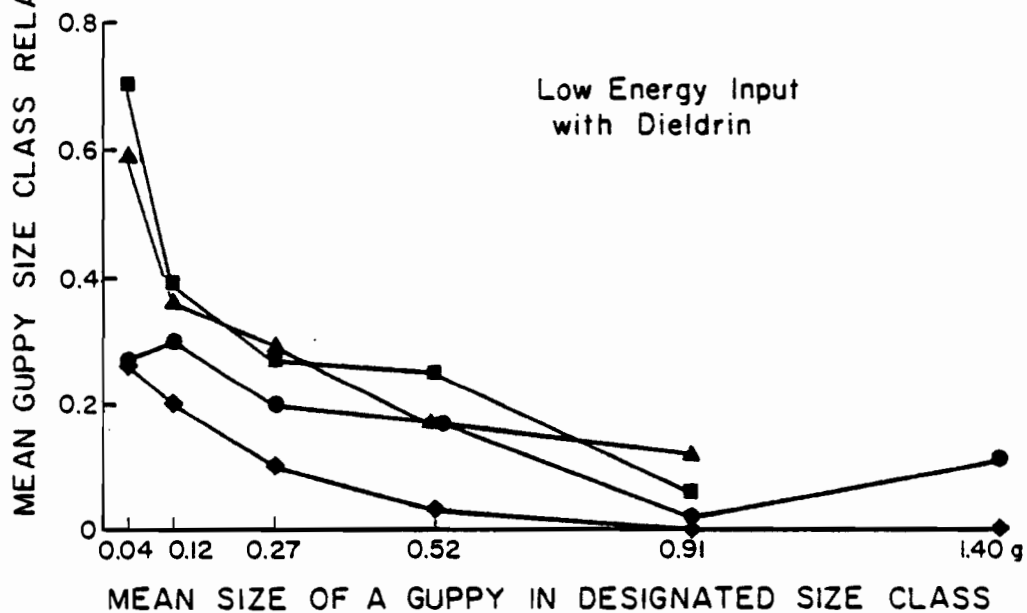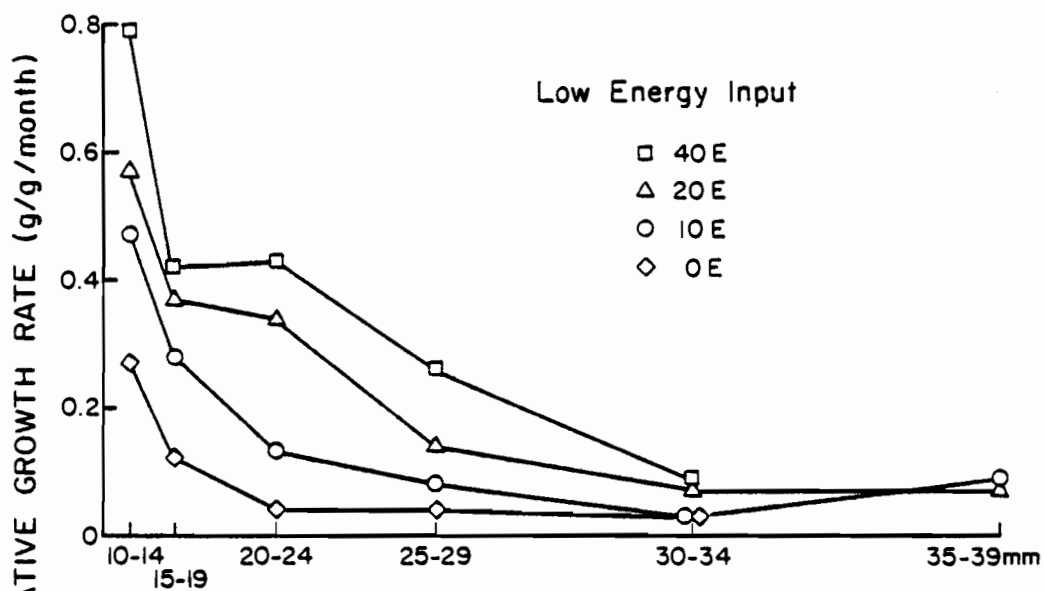
Figure 20.   Guppy size class mean relative growth rate near steady
state as a function of mean population biomass near
steady state. In general, dieldrin (solid symbols) re-
duced the growth rates of males, newborns, immatures
(10-14 mm), and small females up to 24 mm in length
relative to the growth of guppies in the same size popula-
tion prior to dieldrin introduction (open symbols). The
two solid squares for each of the eight size classes
represent mean growth of guppies before extinction, and
then zero growth at extinction of the 40 percent exploita-
tion system (◇ - 0, O - 10, △ - 20, and □ - 40 percent
guppy exploitation). Not all populations had fish in the
35-39 mm size class. Curves were fit by eye.
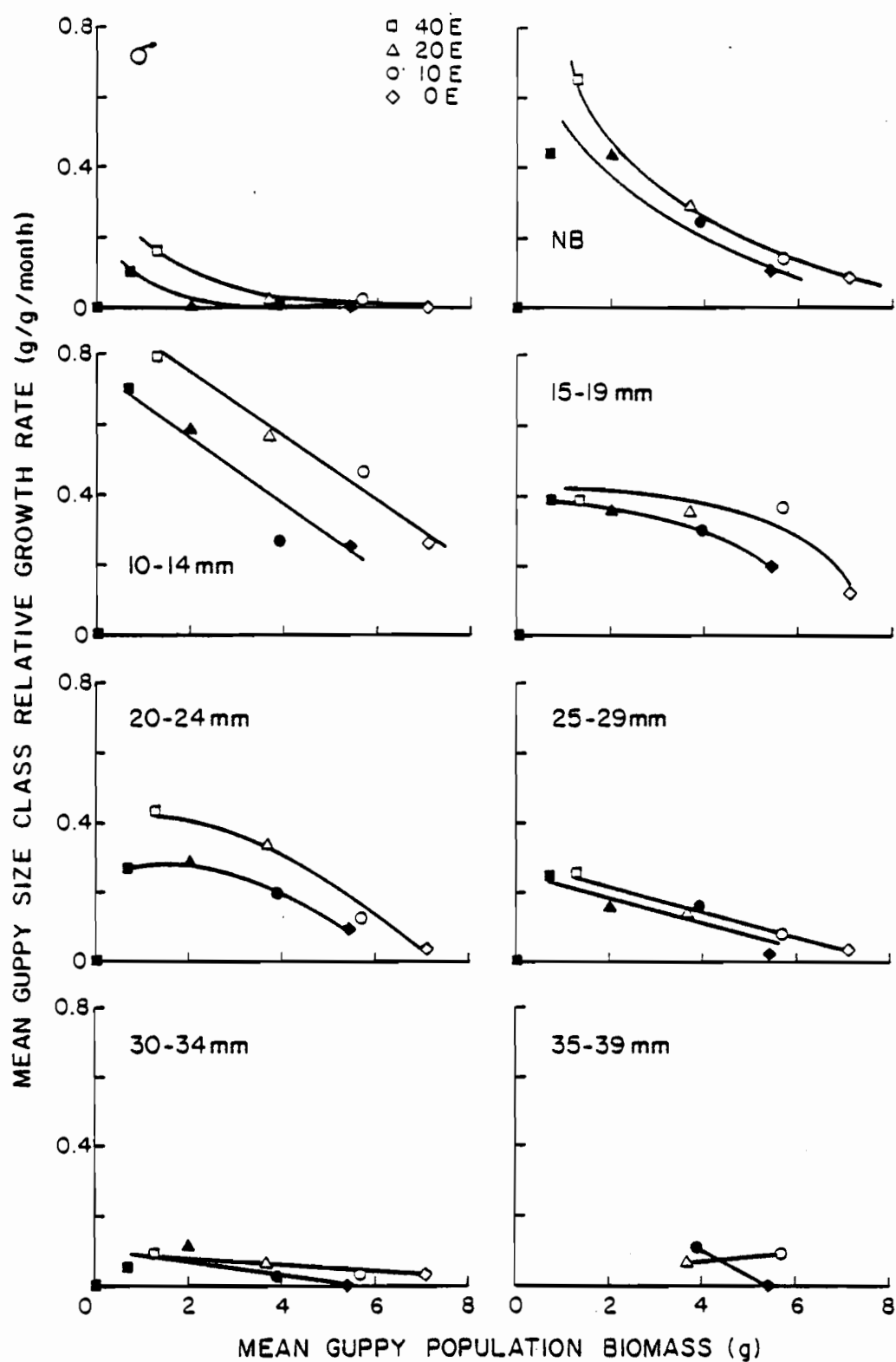
Size specific fecundity, the mean number of oocytes carried by an exploited mature female of given size, was lower in systems with low exploitation, with dieldrin, or with the high level of energy input (Figs. 21, 22, and 23). No oocyte counts were made for females at zero exploitation. Because of the near linear relationship between size and the number of oocytes, linear regression lines were fit to the near steady-state fecundity data for a particular system and set of environmental conditions (r values were between 0.85 and 0.99). Lines were drawn only over the range of sizes of females collected by exploitation (i.e. no extrapolations). There was some overlap in fecundity between low energy input systems at the three exploitation levels. Averaging the fecundity data for the four systems at each exploitation level indicated that size-specific fecundity increased as a function of increasing exploitation rate (Fig. 21). Comparisons of fecundity in the presence and absence of dieldrin and between levels of energy input were made on the basis of data collected before and after particular systems were altered.

Guppy reproductive effort responded in an apparent density-dependent manner to decreases in population biomass occasioned by exploitation. The fecundity of individual fish increased with decreases in population biomass, providing sufficient numbers of offspring for population persistence. Fewer mature females and a smaller percentage of males occurred in such populations. Dieldrin reduced the mean

Figure 21.   Guppy fecundity (mean number of oocytes carried by
             an exploited female of given size) near steady state
             for laboratory ecosystems at low energy input.   In
             general, size specific fecundity increased with in-
             creased exploitation (O - 10, △ - 20, and □ - 40
             percent guppy exploitation).   Inset shows average
             fecundity of the four systems at each exploitation
             rate.   A linear regression line was fit to the data
             for each system (labeled with system number); r
             values were bet ween 0. 85 and 0. 99.   Lines were
             not extrapolated beyond guppy size and oocyte num-
             ber collected by exploitation (range enclosed by ex-
             ploitation symbols O, △, □).
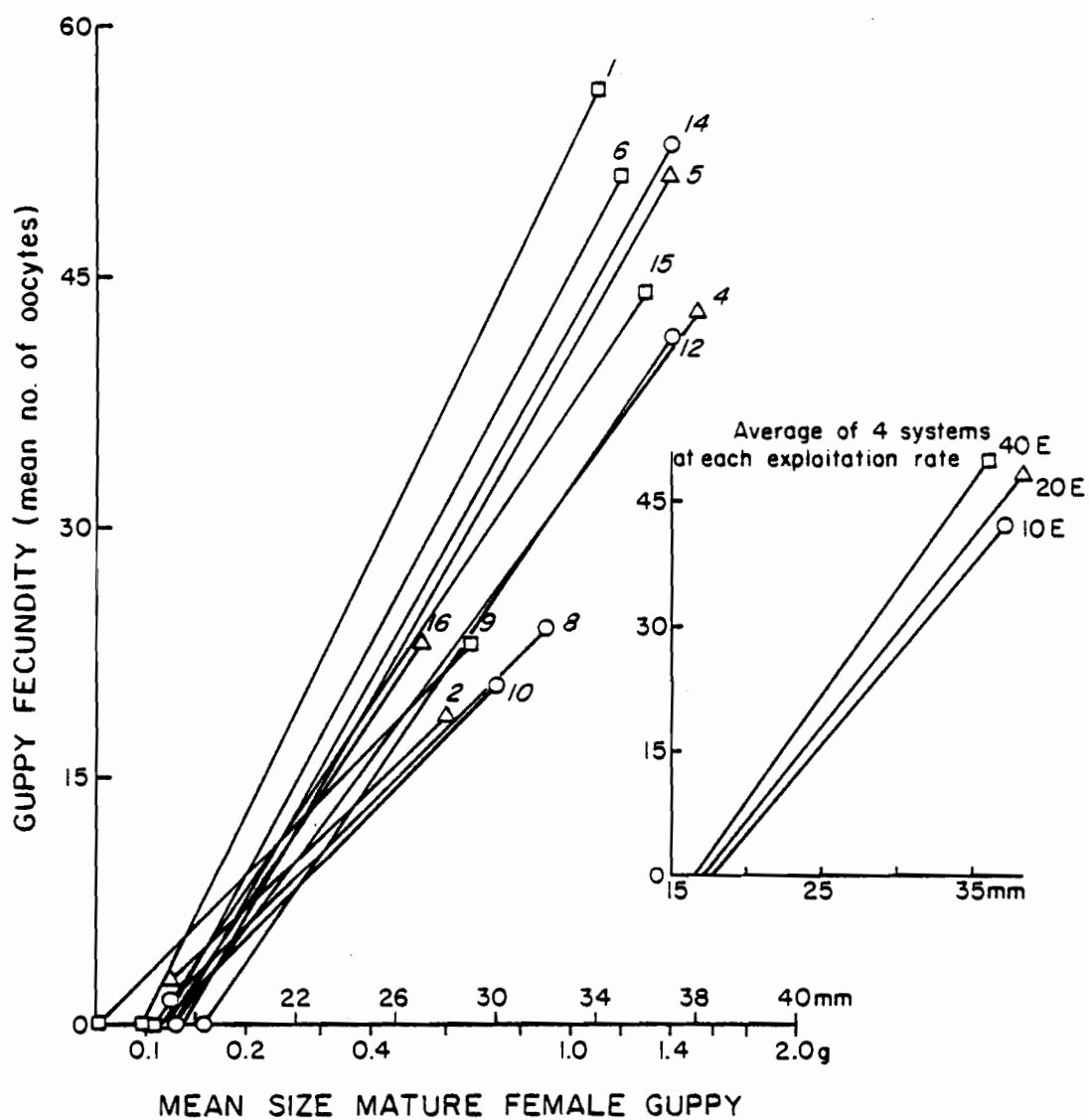
Figure 22.　Guppy fecundity (mean number of oocytes carried by an exploited female of given size) near steady state at low energy input before (open symbols) and after (solid symbols) dieldrin introduction. Dieldrin reduced size specific fecundity by approximately 20 percent; comparisons are made within a particular laboratory ecosystem (i.e. system 1 - 40 E, 4 - 20 E, 14 - 10 E). A linear regression line was fit to the data for each system; r values were between 0.85 and 0.99. Lines were not extrapolated beyond guppy size and oocyte number collected by exploitation (range enclosed by exploitation symbols O, △, □).
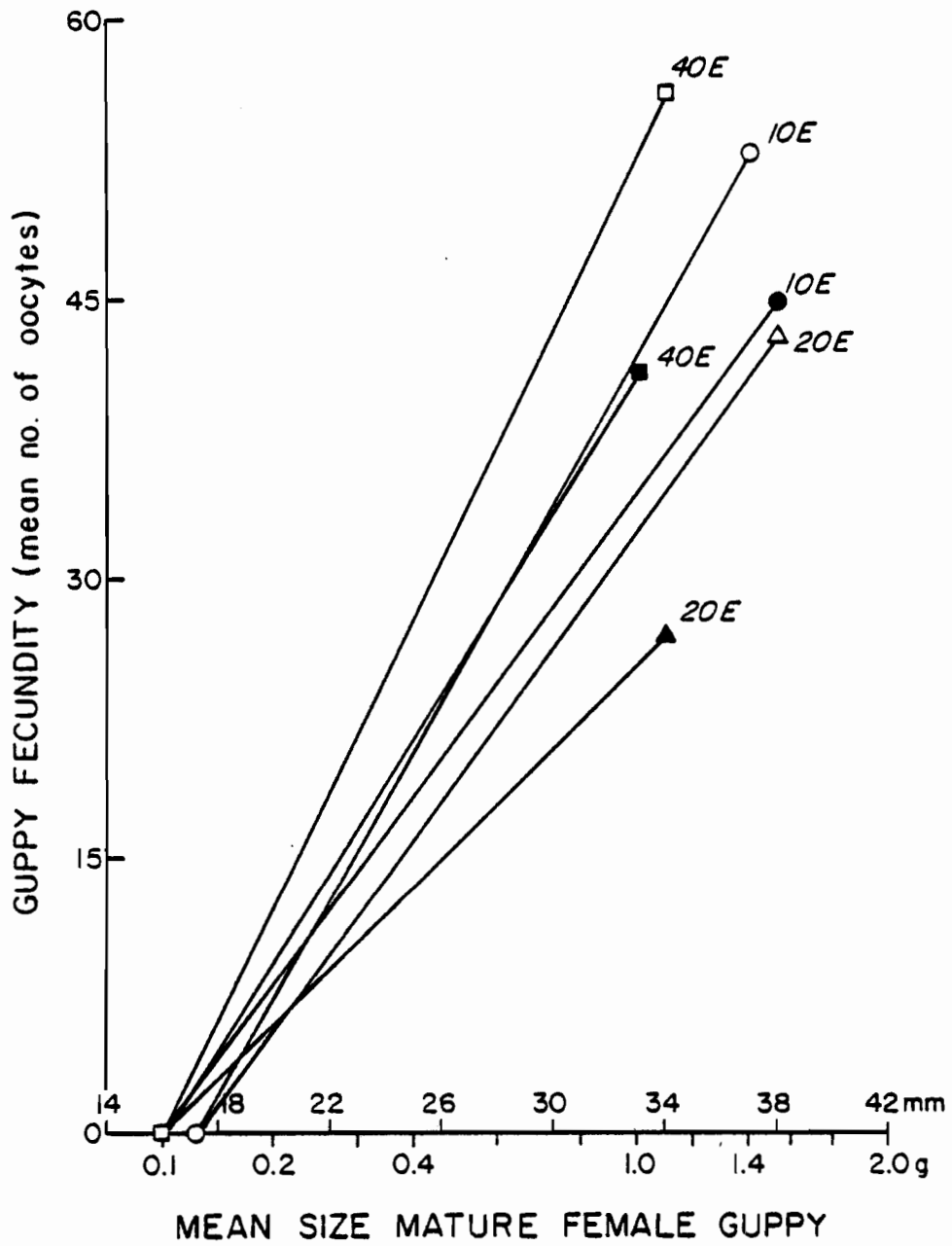
Figure 23. Guppy fecundity (mean number of oocytes carried by an exploited female of a given size) near steady state at low energy input (open symbols) and at high energy input (solid symbols) for a particular system (labeled with system number). Size specific fecundity decreased in systems shifted to high energy input. A linear regression line was fit to the data for each system (identified by system number); r values were between 0.85 and 0.99. Lines were not extrapolated beyond guppy size and oocyte number collected by exploitation (range enclosed by exploitation symbols O - 10, △ - 20, and □ - 40 percent exploitation). The relatively narrow range of large female sizes sampled for some systems (e.g. 8 and 10 at high energy input) tends to reduce the slope of their regression lines.
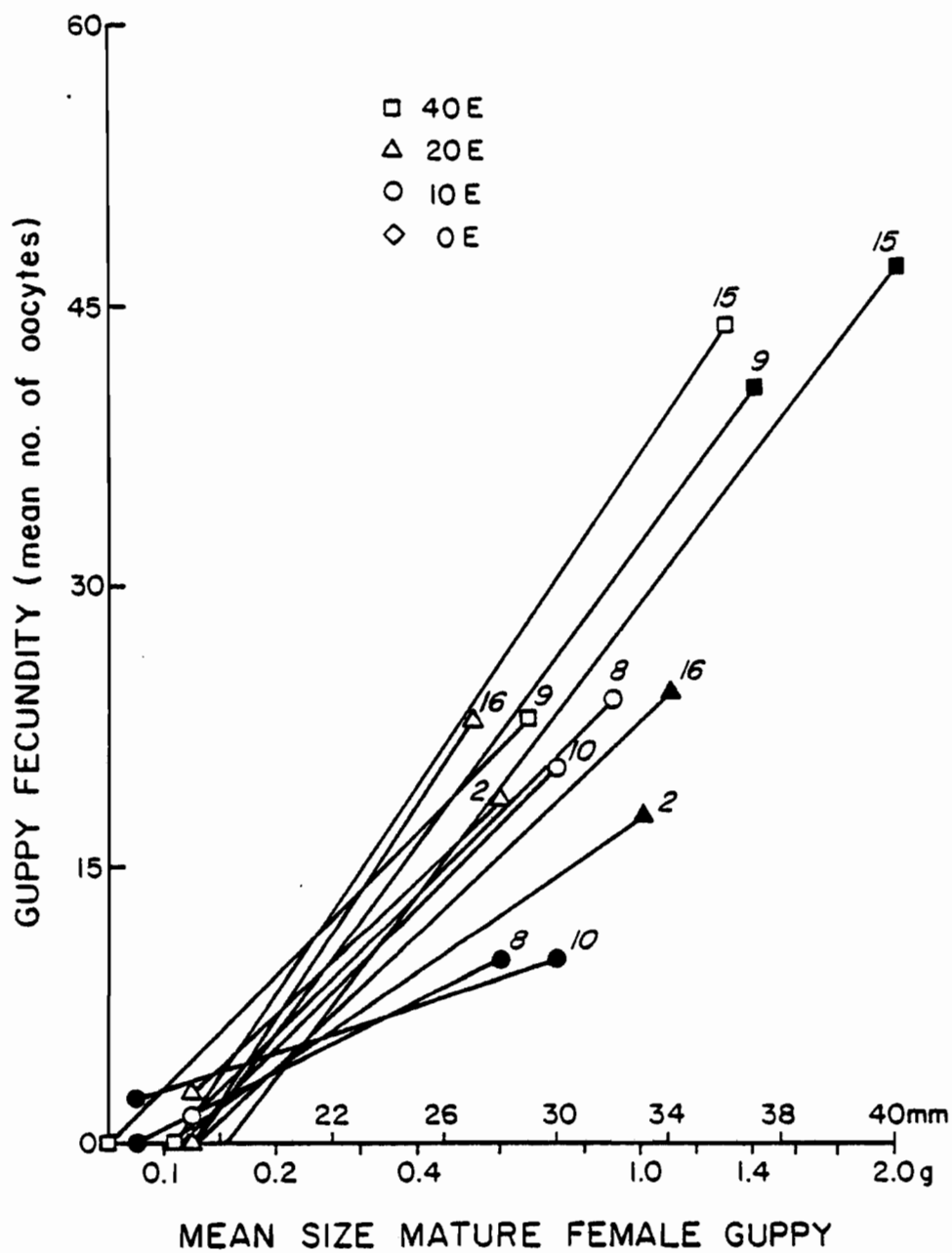
number of oocytes per female by approximately 20 percent, and

accounts for at least a part of the reduction in growth rates of mature

females (Figs. 20 and 22). Reductions in fecundity, relatively poor

survival of newborns to the 10-14 mm size class, and additional physio-

logical responses to dieldrin including delays in development of

oocytes appear to have been in part responsible for the extinction of

the guppy population at 40 percent exploitation. Size specific fecundity

decreased in systems shifted to high energy input. This could possibly

reflect the saturation of space in the tanks and therefore a density-

dependent reduction in reproductive effort by the females (Fig. 23).

The data are insufficient to determine a change in the size at maturity

of the females under different environmental conditions. Extrapola-

tions beyond the sampled size range to the x-axis could introduce a

bias of the linear regression analysis.

Guppy Size Specific Production and
Yield Near Steady State

Size specific production and yield are a summary account of size

specific biomass, growth, reproduction and mortality. For different

levels of environmental conditions, they represent the variation in

adaptive responses of particular components of the population; and

combined, they are the total population biomass response to interac-

tions in the laboratory ecosystems. The sum of production values or

yield values for the eight size classes of a particular population equals the total population production or total population yield in Figure 17.

Maximum tissue elaboration occurred near the 20 percent exploitation level for all size classes, with or without dieldrin (Fig. 24). Production rates for individuals in the 40 percent exploitation system were on the ascending limb of the curve, at a relatively low biomass but a high relative growth rate. Production rates for the 10 and 0 percent exploitation systems were on the descending limb of the production curve, characteristic of relatively high biomasses and low relative growth rates. The decrease in total population production following the introduction of dieldrin was accounted for primarily through reductions in production of males, newborns, and the 10 to 14 and 15 to 19 millimeter size classes.

Dieldrin reduced the guppy population biomasses through its effects on growth and reproduction and on mortality at zero exploitation. This biomass reduction near steady state then accounts for the loss in size specific yields (Fig. 25). The mean yield of a size class does not necessarily equal its mean production. Tissue production occurs (and the calculations were adjusted) over all the size classes through which a fish has passed up to the time it dies or is exploited; biomass yield is attributed only to the size class from which the fish is removed. However, the total yield (plus any additional mortality) of the eight size classes for a given system equalled their total

production, and resulted in a total population mean biomass being near
steady state according to prevailing environmental conditions.

Figure 24.   Guppy size class mean production near steady state as
a function of mean population biomass near steady state.
In general, dieldrin (solid symbols) reduced the pro-
duction rates of males, newborns (NB), immatures (10-
14 mm), and females in the 15-19 mm size class rela-
tive to guppies in the same size population prior to
dieldrin introduction (open symbols). The two solid
squares for each of the eight size classes represent
mean production of guppies before extinction, and then
zero production at extinction of the 40 percent exploita-
tion system (◇ - 0, O - 10, △ - 20, and □ - 40 percent
guppy exploitation). Not all populations had fish in the
35-39 mm size class. Curves were fit by eye.
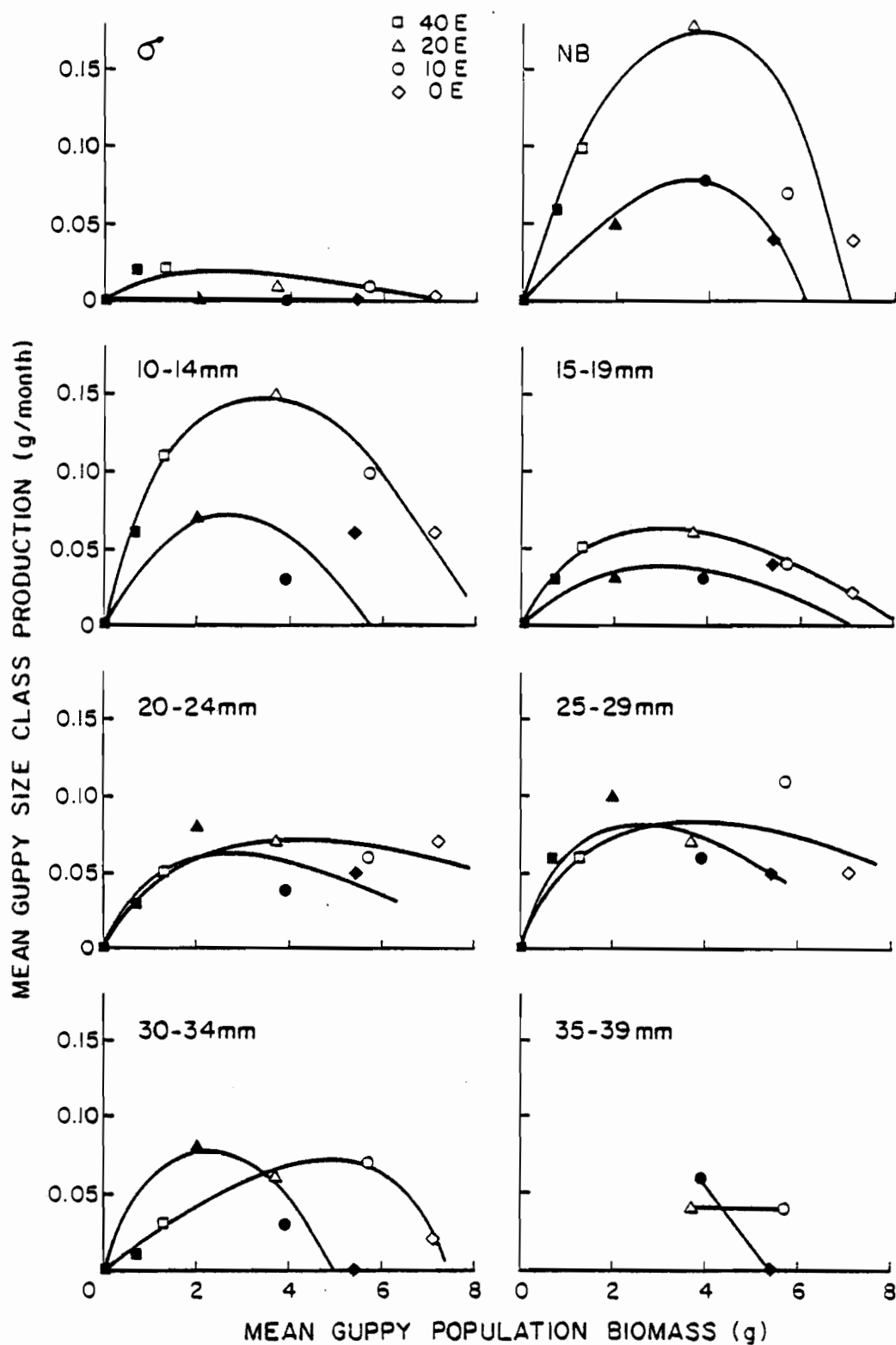
Figure 25.   Guppy size class mean yield near steady state as a function of mean population biomass near steady state. In general, dieldrin (solid symbols) reduced the yields of males, newborns (NB), immatures (10-14 mm), and females up to 29 mm in length relative to guppies in the same size population prior to dieldrin introduction (open symbols). The two solid squares for each of the eight size classes represent mean yield of guppies before extinction, and then zero yield at extinction of the 40 percent exploitation system ($\diamondsuit$ - 0, O - 10, $\triangle$ - 20, and $\square$ - 40 percent guppy exploitation). Not all populations had fish in the 35-39 mm size class. Curves were fit by eye.
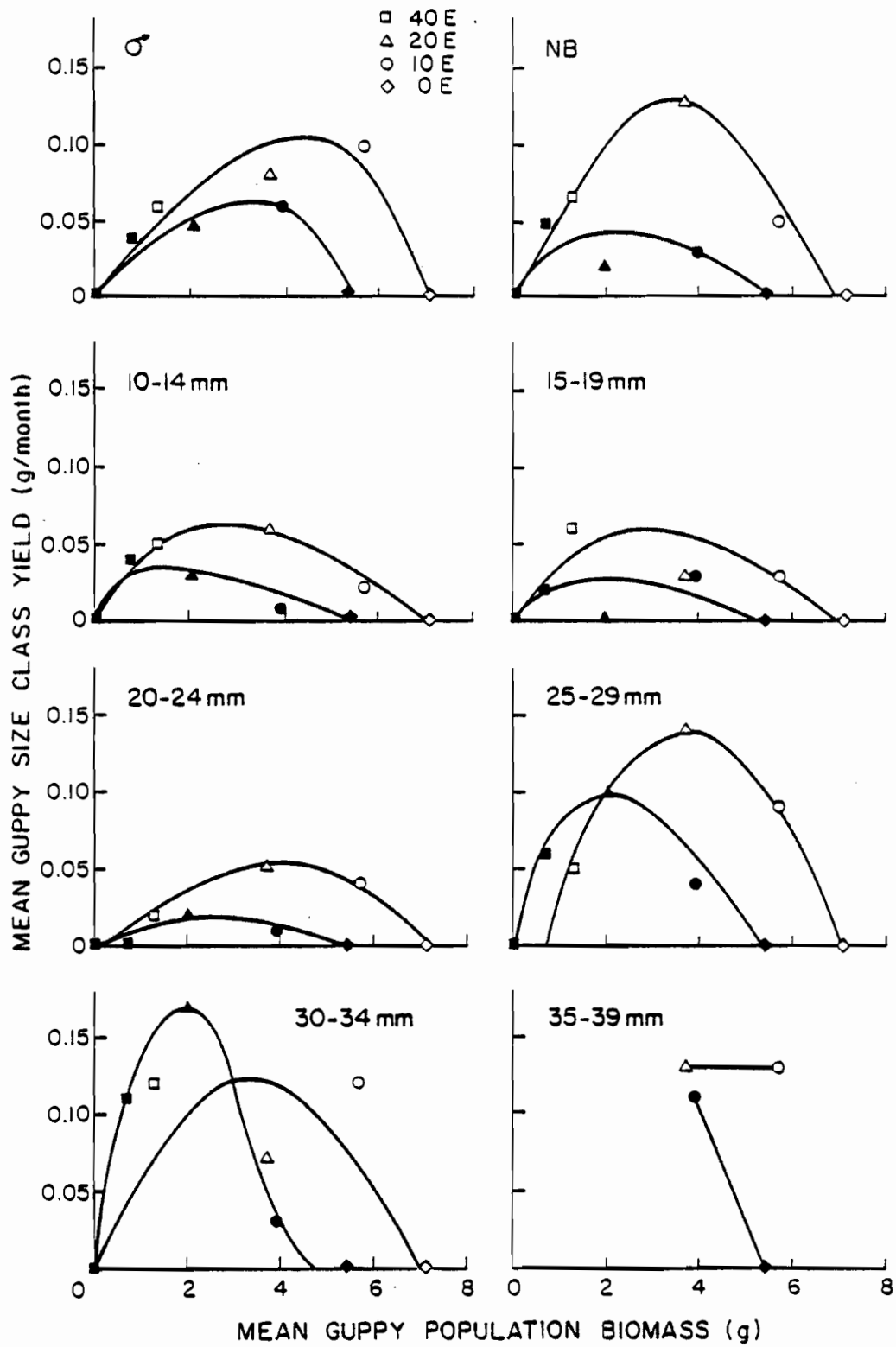
IV. DISCUSSION

The objective of this laboratory study has been to demonstrate
and explain aspects of the organization and adaptation of organismic
systems at the ecosystem level of biological organization. Such an
account would begin to detail the incorporation and concordance of
community, population, and individual organism capacities and per-
formances. Any performance of an organismic system can be under-
stood as the consequence of the system's capacity and of its environ-
ment at a particular time. How those observed performances come
about entails the total organization (including trophic, habitat, and
life history organization) of the system. Here, I would hope to infer
a synthesis of generalizations that would help in drawing out and
interrelating empirical experience of ecological systems. Empirical
generalizations from ecological theory, productivity theory, and fish-
ery exploitation theory were presented in the introduction and will be
incorporated here to account in part for such performances as de-
velopment, structure, and persistence of the laboratory ecosystems,
their communities, populations, and individual organisms.

The 16 laboratory ecosystems were established with similar
capacities for community development, structure, and persistence.

Their capacities were entailed in the possibilities for interactive performances of the introduced species, which were to be at least partially expressed according to the physical and chemical dimensions of the laboratory environment. Community organization and its expression in community development, structure, and persistence involved the adaptation of species populations to each other, to available energy, to habitat, to "climatic" conditions including water quality and temperature, to exploitation, and to the introduction of a toxicant. Manipulating energy and habitat availability, exploitation levels, and toxicant presence altered near steady-state community, population, and individual level performances. In these responses to environmental conditions, there is a certain concordance of community, population, and life history patterns that constitutes adaptation of the community and its subsystems.

Competition among the guppy, amphipod, and snail populations for the sediment food resource was important in determining community structure. The dynamic (developmental) and near steady-state biomasses of these three populations also reflected their relationship to exploitation of the guppy population, to habitat availability, and to toxicant presence. Guppies appeared to dominate in the utilization of the sediment resource, perhaps because of their mobility, pelagic

habitat, and predator relationship with amphipods, one of their prime competitors. Exploitation directly affected the size of the guppy populations and indirectly affected the size of the snail and amphipod populations, which responded to competition and/or predation from guppies (Fig. 6). Habitat utilization patterns suggested that amphipods had a competitive advantage over snails for the sediment food resource at the low energy and habitat levels. Release of amphipods from competition and predation from guppies with the loss of the guppy population in system 1 may have prevented an increase in snail biomass (Fig. 15). It was apparent that guppy predation on amphipods favored higher snail populations by largely restricting amphipod movements and habitation to the rock nests.

Population interactions were different at the high energy and habitat level. High cover substantially released amphipods from predation and interference competition from guppies. Amphipods apparently also benefited by some release from snail competition, again because of their ability to better enter and utilize resources in the rock substrate. Snails were largely released from amphipod competition when predation by planaria greatly reduced or eliminated amphipods. In the systems where planaria were eventually removed, amphipods regained their sediment resource apparently because of a competitive (i. e. mobility) advantage and snail population biomass declined to previous levels (Fig. 13). An increase in total energy available to the systems

allowed an increase in population size for some of the species, but some species of microorganisms in the substrate were greatly reduced (Finger 1980).

Adaptive foraging strategies and the availability of alternative prey, algae in addition to sediments for snails, and amphipods and sediments for guppies, allowed both species to persist when one food resource was monopolized by a competitor(s). The predation advantage of the planaria over guppies for amphipods as food would have resulted in the loss of guppy populations in the presence of planaria at high energy input, if the guppy were a foraging specialist. Likewise, the presence and utilization of algae helped snails to maintain small populations at low energy and habitat levels, when guppies and amphipods monopolized sediment resources. The laboratory systems were characterized by trophic and habitat resource partitioning. Niche utilization of the interacting species expanded and contracted as the entire community adapted to changes in its environment. No single aspect of the environment and no single kind of organismic response accounted for the observed community structure; rather it was an outcome of individual, population, and community incorporated responses to level specific environmental conditions set in motion by the "external" environment of energy and habitat availability, exploitation, and toxicant presence.

A system of isoclines on a series of interrelated resource-utilizer and competition phase planes can be employed in explanation to gain a better understanding of the structure and apparent organization of the laboratory systems. Booty (1975), Liss (1977), and Warren and Liss (1977) have developed and used a formal graphical calculus to explicitly couple the dynamics of interrelated populations to one another and to prevailing environmental conditions. On each resource-utilizer phase plane, prey biomass is plotted on the x-axis and predator biomass on the y-axis. One of two competitors is plotted on each of the axes of a competition phase plane. A phase plane entails all possible combinations of biomass of two interacting populations.

Descending lines on a predator-prey phase plane are prey isoclines and represent the set of predator and prey biomasses for which the rate of prey biomass change with time is zero. Prey isoclines are identified or parameterized by and vary according to factors that determine resource levels for the prey and the predator. For the laboratory ecosystems, such factors included levels of energy and material input and levels of competitors for those resources. Ascending lines on a predator-prey phase plane are predator isoclines. These are formed by sets of predator and prey biomasses for which the rate of predator biomass change with time is zero. Predator isoclines are identified or parameterized by and vary according to factors that determine predator biomass. Levels of exploitation on predators, toxicant

levels, and levels of alternative prey identify predator isoclines for the laboratory systems.

Each intersection of a predator and a prey (or of two competitor) isocline(s) is a possible steady state where the biomass of neither population changes so long as the environmental variables parameterizing the isoclines remain constant. Such a phase plane/isocline system describes a multisteady-state ecological system that has the capacity to develop and persist over a range of structures dependent upon the organization and prevailing environment of the system. The positions and forms of isoclines can be deduced from response functions that represent biomass gains from recruitment and production and biomass losses to predation, exploitation, and other mortality of the interacting populations. A set of predator-prey and competitor-competitor phase planes are here introduced to help explain the near steady-state structures of the laboratory ecosystems (Figs. 26 and 28). The isocline systems were developed as informal or qualitative representations of hypothetical predator, prey, and competitor populations to help identify and interrelate the causally most important elements of the laboratory systems.

Amid the wide range of resource utilization patterns and population sizes of guppies, amphipods, and snails there was apparent a relative invariance of their common food resource, sediments, for a given level of alfalfa input (Fig. 6). Secondly, there was generally

an inverse relationship between competitor biomasses at a series of near steady states, which varied according to level of exploitation on guppies. Apparently, total sediment loss to predation and decomposition was approximately the same for all systems. But the proportion of sediment consumed by a particular population varied according to the density of that population, which ultimately related back to the level of guppy exploitation and to habitat availability.

This and other results of experiments with these laboratory systems can be deduced with a phase plane/isocline system model. Hypothetical biomass gain and loss functions were constructed for guppies, amphipods, snails, and sediments based on a three-way competition and predation interaction, at a single low level of energy input and four levels of guppy exploitation (Appendix V). Resultant systems of isoclines on guppy-sediment, amphipod-sediment, and snail-sediment phase planes interrelate the major system components (Figs. 26A, B, and C). The relative order and spacing of predator or of prey isoclines depends upon the gain and loss response functions which entail the species-species and species-environment interactions. Ordering and spacing on the informal systems presented here are simplistic and are intended to express only relative relations.

The relative positions of the prey isoclines on all three phase planes are dependent upon the levels and interactions of competitors for the sediment resource. The family of prey isoclines at the low

Figure 26. Phase plane and interrelated isocline systems repre-
senting a series of resource-utilizer interactions in the
laboratory ecosystems; guppy-sediment (Fig. A),
amphipod-sediment (Fig. B), and snail-sediment (Fig.
C) interactions. The form and position of predator and
prey isoclines on all phase planes have been informally,
or qualitatively, deduced from hypothetical response
functions that represent the biological characteristics
of each of the populations (see Appendix V). An infinite
family of predator and prey isoclines exists on each
phase plane. Each prey isocline is generated and so
parameterized by factors that determine resource levels
for the prey and the predator (i. e. level of energy input,
and levels of competitors for those resources). Each
predator isocline is generated and so parameterized by
factors that determine predator biomass (i. e. levels of
predation including exploitation; additional mortality
including that from a toxicant and levels W, X, Y, and
Z of unknown mortality factors for snails; and levels of
alternative prey). The four symbols ($\Diamond$ - 0E, O - 10E,
$\triangle$ - 20E, and $\square$ - 40E percent exploitation) on each phase
plane are steady-state points defining the relative pattern
of near steady-state biomasses for sediments, guppies
(G), amphipods (A), and snails (SN) at low energy input
in the laboratory systems. (PL - planaria).

LOW ENERGY INPUT

(A)

4 SN 3 SN 2 SN 1 SN 0 SN
43210 43210 43210 43210 43210 A

GUPPY BIOMASS

0 E
10 E
20 E
40 E
40 E, TOX

LOW ENERGY INPUT

(B)

4 G 3 G 2 G 1 G 0 G
43210 43210 43210 43210 43210 A

AMPHIPOD BIOMASS

1 GUP, NO PL
1 GUP, LOW PL
1 GUP, HIGH PL

2 G
3 G
4 G

LOW ENERGY INPUT

(C)

4 G 3 G 2 G 1 G 0 G
43210 43210 43210 43210 43210 A

SNAIL BIOMASS

W
X, HIGH ALGAE
X, LOW ALGAE
X, NO ALGAE
Y
Z

SEDIMENT BIOMASS
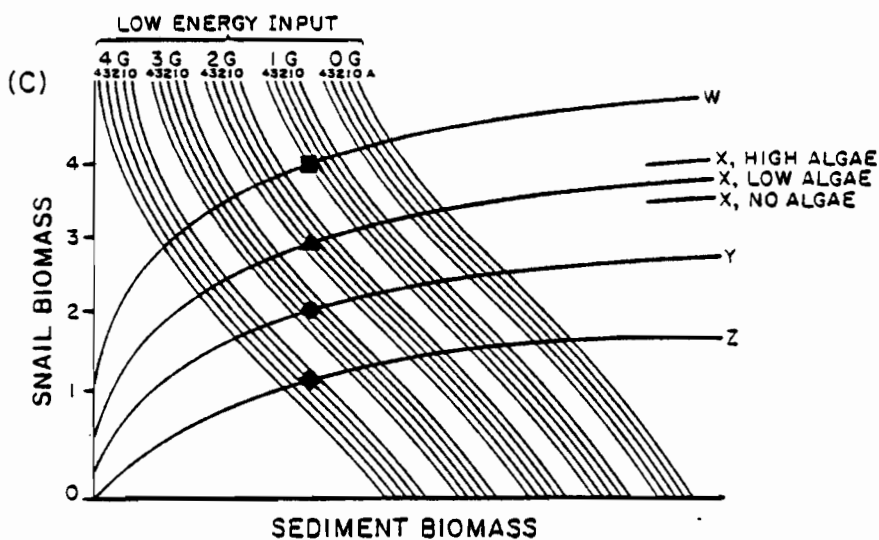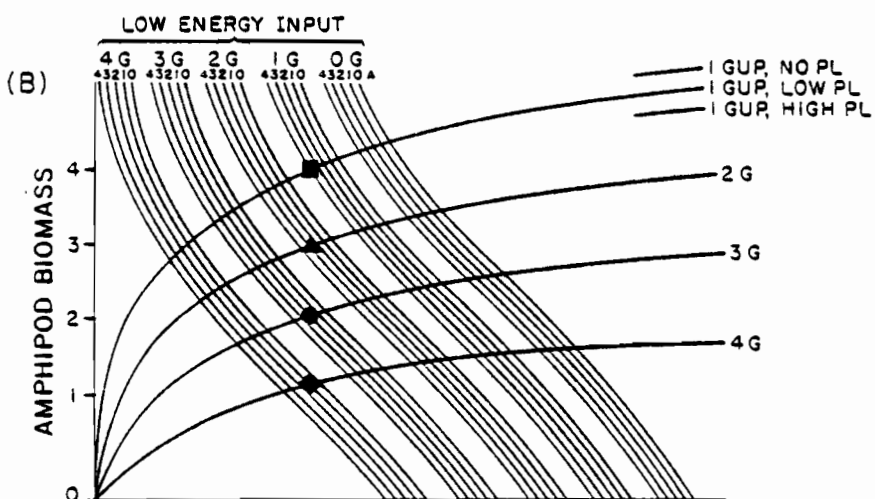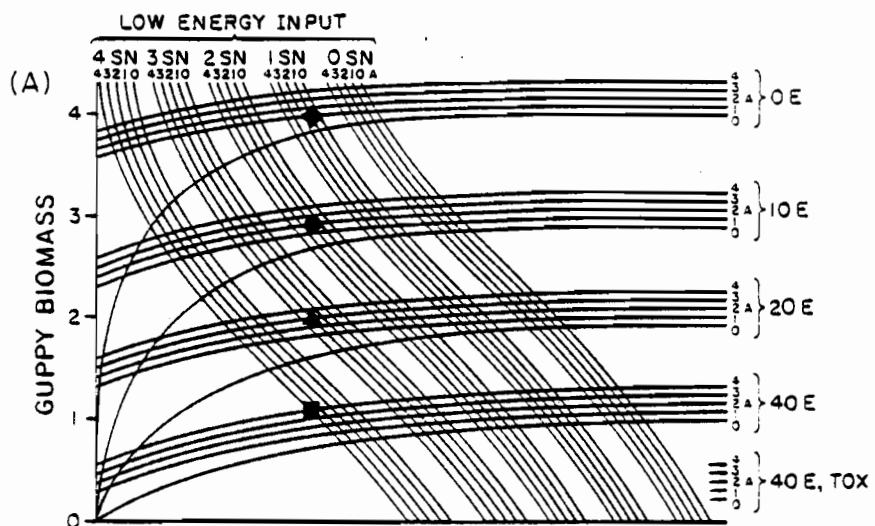
low level of energy input (i. e. 0. 6 gram alfalfa/day) represents possible combinations of competitor population biomasses. The relative positions of the predator isoclines are dependent upon the level and interactions of factors directly changing predator bio- mass. For the guppy, these factors include the level of exploita- tion on the guppy population, the level of amphipods as alternative prey for guppies, and the presence of a toxicant that directly affected guppy biomass (Fig. 26A). For the amphipods, the level of guppy and/or planaria predation parameterize the predator iso- clines (Fig. 26B). And for the snails, the level of algae as an alternative prey for snails, and unknown mortality factors parame- terize the predator isoclines (Fig. 26C).

The relative invariance of sediment densities with changes in the three competitor populations can be explained somewhat as follows. Intersections of predator and prey isoclines were selected on the basis of observed densities of guppies, amphipods, and snails at low energy input in the laboratory systems (Figs. 8 and 11). For example, the steady-state point at low energy input and 40 percent guppy exploitation (Fig. 26A) entails 1 unit biomass of guppies and relatively high, 4 unit, biomasses for amphipods and snails. As exploitation decreases, the steady-state point on the phase plane, and the near steady state structure of the laboratory populations, shifts to higher guppy biomasses and lower snail and

amphipod biomasses. This pattern is identical on all three phase planes and results in a near vertical set of four community steady states relative to sediment density. Thus the relative invariance of sediment densities in the laboratory systems (Fig. 6) is accounted for by systems of isoclines interrelated by population and environmental parameters.

High energy and habitat availability altered the community structure and organization and resulted in increases in sediment density and in guppy, amphipod, snail, and planaria population biomasses (Fig. 6). Presented on the deduced predator-prey phase planes, there would be a family of prey (sediment) isoclines to the right of the low energy input family identified by levels of competitors. And there could be families of predator (guppy, amphipod, or snail) isoclines above those at low energy input if levels of alternative prey were much higher. Some of the population interactions would be different from systems at low energy input (e.g. amphipods affected less by guppy predation and more by snail-guppy competition and by planaria predation). Such differences would be reflected in the shapes and magnitudes of biomass gain and loss functions and thus in the positions and forms of isoclines on the phase planes. Figure 27A illustrates general relationships of a predator-prey interaction as it is affected by increasing energy input and/or exploitation, especially in the relative positions of isoclines and steady state points. For a given level of exploitation, an increase

Figure 27.   Theoretical relationships between the organization,
             environment, and productive capacity of the laboratory
             ecosystems for guppy (predator) production and biomass
             near steady state.   A steady-state production curve
             (Fig. C) is derived from the isocline relationship be-
             tween predator and prey biomasses at a given rate of
             energy input (Fig. A), together with the curve relating
             predator relative growth rate to prey biomass (Fig. B).
             As predator exploitation level (E) increases from 0 to
             40 percent, steady-state predator biomass decreases.
             The co-occurring increase in steady-state prey biomass
             results in an increase in predator relative growth rate.
             Predator relative growth rate is therefore an inverse
             function of predator biomass (diagonal dashed lines on
             C), and the relationship between predator production
             rate and predator biomass is a dome-shaped curve
             (Fig. C).   Each dome-shaped curve represents the
             productive capacity of the system for the predator
             population, and its shape depends upon the level of
             environmental factors including energy input, competi-
             tion, alternative prey, presence of a toxicant, and
             exploitation (i. e. the organization of the system).
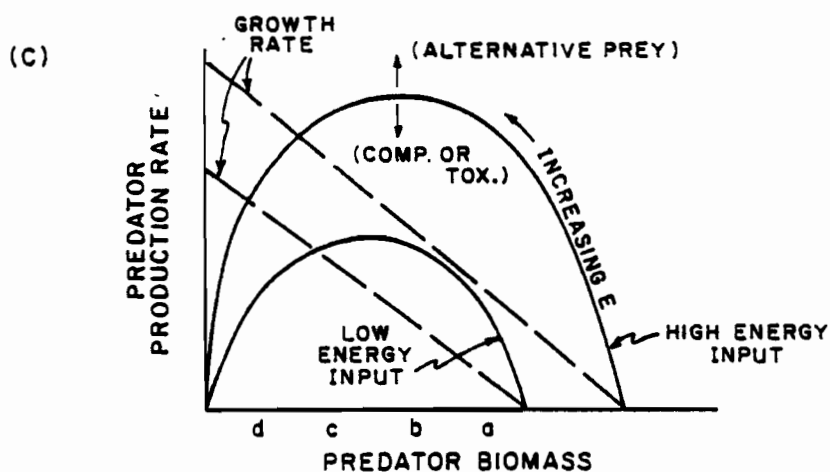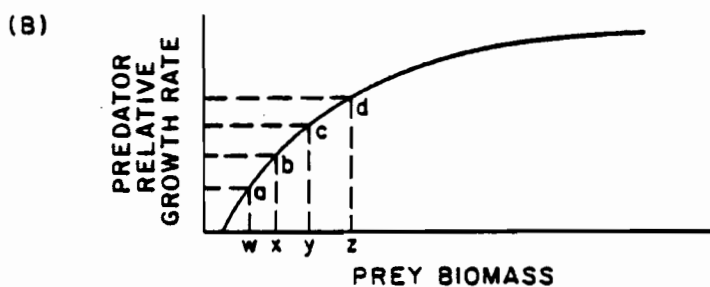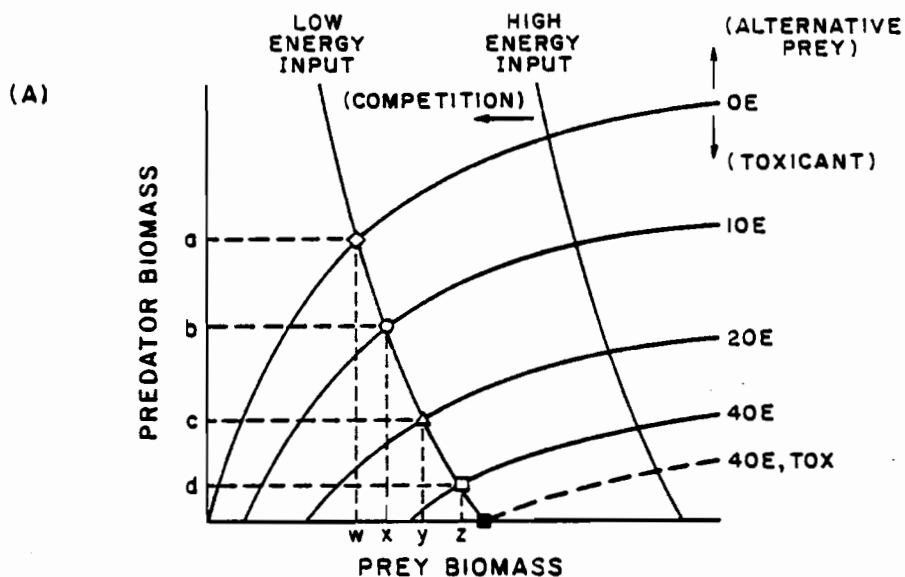
in energy input would result in larger predator and prey populations near steady state. Such near steady-state structures were approached by August 1979 for sediment, guppy, amphipod (without planaria), and snail populations at high energy input in the laboratory systems (Figs. 5, 10 and 12).

Competition phase planes and isocline systems were deduced from guppy-sediment, amphipod-sediment, and snail-sediment isocline systems. The co-occurring biomasses of competitors for every predator-prey isocline intersection (i.e. every possible steady state represented) are plotted on a phase plane with one competitor on each of the two axes. In addition to the levels of environmental factors (e.g. energy input level or exploitation level), levels of the third competitor (e.g. snails on a guppy-amphipod phase plane) identify the resulting competition isoclines. Those intersections of competition isoclines that correspond to steady-state biomasses on the predator-prey phase planes become the steady-state biomasses for competitors under a specified set of environmental conditions. The guppy-amphipod competition phase plane with its parameterized isoclines (Fig. 28A) becomes an explanation for the observed inverse pattern of near steady-state biomasses of guppies and amphipods in the laboratory systems at low energy input (Fig. 8). Similarly, the guppy-snail competition phase plane with its parameterized isoclines (Fig. 28B) becomes an explanation for the inverse near steady-state biomasses

Figure 28. Phase plane and interrelated isocline systems repre-
senting competition interactions between two utilizer
populations, guppies and amphipods (which are also
predator and prey, Fig. A) and guppies and snails
(Fig. B) for a common food resource, sediments,
in the laboratory ecosystems. The form and posi-
tion of competition isoclines on both phase planes
were deduced from their corresponding resource-
utilizer isocline systems. The co-occurring bio-
masses of competitors for every predator-prey
isocline intersection (i.e. steady state) represented
in Figure 26 are plotted on the competition phase
plane and become the competition isoclines for a
given level of parameterizing factors which now
include the level of the third competitor population.
The four symbols ($\diamondsuit$ - 0E, O - 10E, $\triangle$ - 20E, and
$\square$ - 40E, percent exploitation) on each phase plane
are steady state points defining the relative pattern
of near steady-state biomass for guppies (G), amphi-
pods (A), and snails (SN) at low energy input in the
laboratory systems. (W, X, Y, and Z are levels of
unknown mortality factors for snails.)
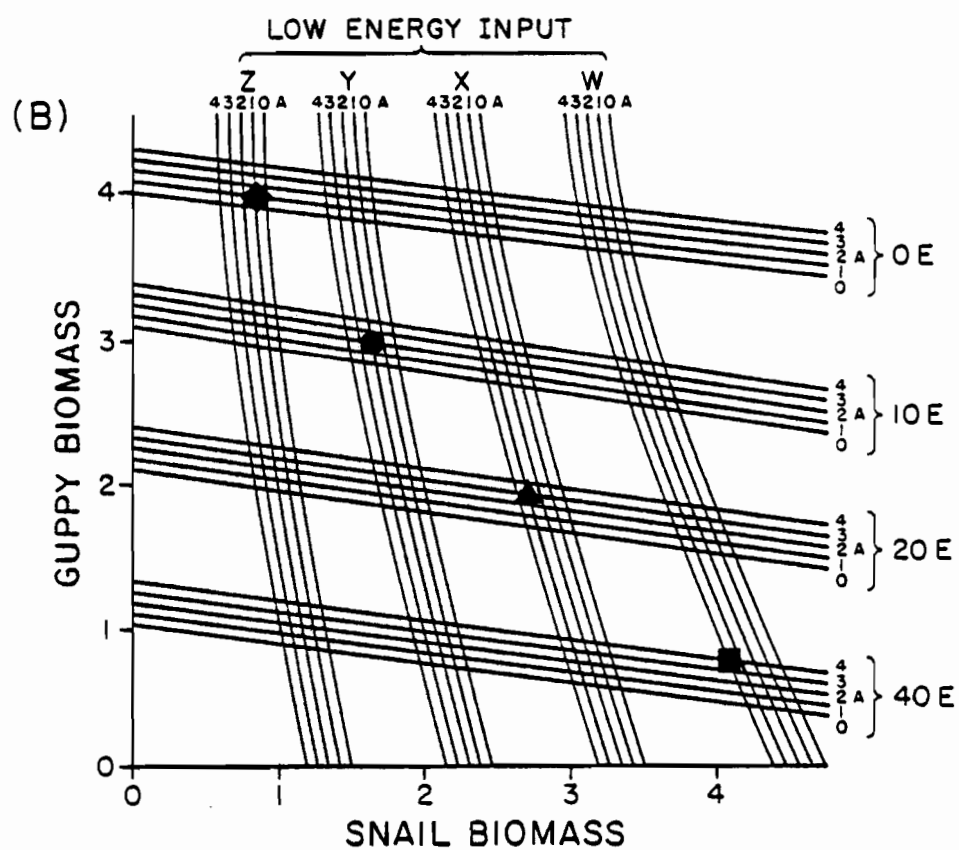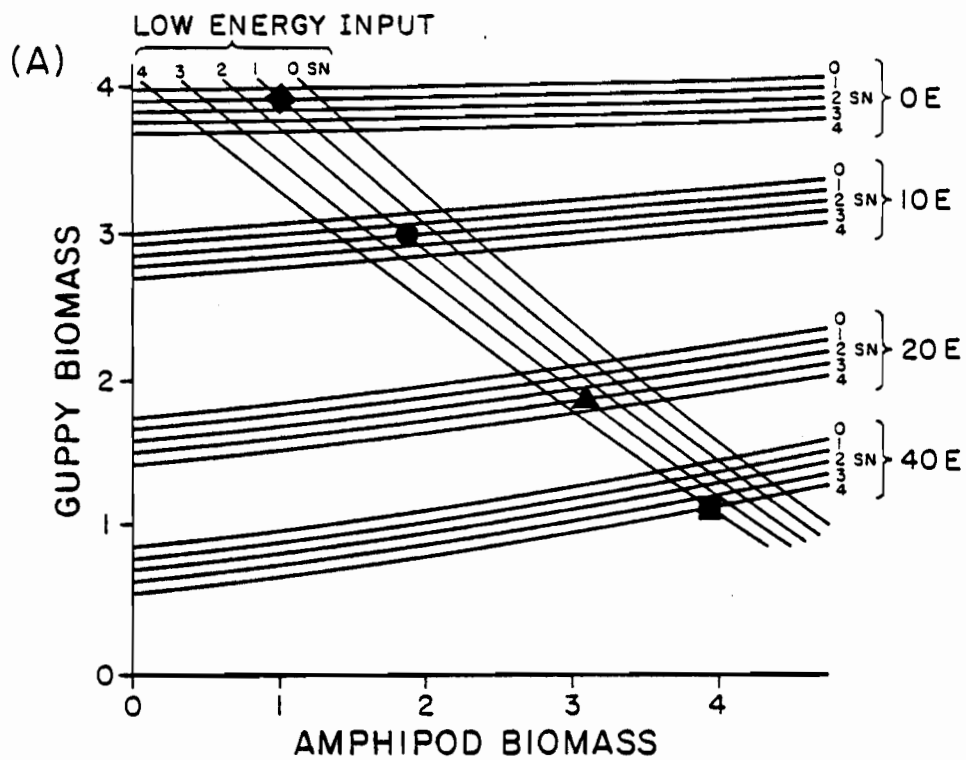
of guppies and snails in the laboratory systems (Fig. 11). Competition isoclines and steady states at high energy input would again vary according to the steady-state patterns established on predator-prey (sediment) phase planes for high energy/habitat availability.

Trophic and habitat organization accounted in part for the observed patterns of population density and interactions, and for the resultant community structure of the laboratory systems. In the above presentation, the explanation of a particular population's structure was approached as the result of its function or role in the encompassing community. An operational explanation is needed to account for the apparent adaptive changes at the population and individual organism levels that were necessary for the populations to respond to manipulations of the environmental system and to persist. Operationally, a population's biomass entails the performances of its subsystems. Patterns of individual organism growth, reproduction, behavior, and survival are adapted to, and need to be viewed within the context of, population density and size distribution, community structure, and the environment of the system. Concordant changes in life history patterns that result from changes in the environment of the community (e. g. energy input, exploitation, toxicant perturbation) determine the kind of changes in population density and community structure that occur.

Productivity theory proposes that the organization of an

ecological system and the level of energy initially available to that system determine the system's capacity to produce a product of interest (e. g. a population). Guppy population biomass in the laboratory systems was the outcome of size specific biomass gains from production (growth and reproduction, Fig. 24), and size specific biomass losses from yield to exploitation (Fig. 25) and from other mortality, which was minimal at low energy input. Production, yield, and other mortality were in turn functions of trophic, habitat, and life history organization that relates a population's structure (e. g. guppy biomass) to the density of its resources, predators, and competitors, as well as to its own adaptive capacity (i. e. developmental and evolutionary plasticity), and to prevailing climatic environmental factors.

A predator-prey phase plane and isocline system can partially illustrate the relationship between the organization, environment, and productive capacity of the laboratory systems for the production, yield, and biomass of the guppy. As was seen in the laboratory systems and in their phase plane representations, prey isoclines are shifted to the left, effectively decreasing both predator and prey biomasses at steady state, with decreasing energy input or with increasing competition for the prey. Predator isoclines are shifted up with alternative prey, or down with increasing exploitation or the presence of a toxicant acting directly on the predator population (Fig. 27A).

Predator (e. g. guppy) production rate (which in the laboratory

systems included reproduction) is the product of the relative growth rate and the biomass of the predator. A steady-state production curve (Fig. 27C) can be derived from the isocline relationship between predator and prey biomass at a given rate of energy input (Fig. 27A) together with the curve relating predator relative growth rate to prey biomass (Fig. 27B). In general, for a given rate of energy input, increased exploitation on a predator results in a decline in predator biomass and an increase in prey biomass (Fig. 27A). As prey biomass increases, the relative growth rate of the predator increases (Fig. 27C). Predator relative growth rate is therefore an inverse function of predator biomass, and the relationship between predator production rate and predator biomass is a dome-shaped curve (Fig. 27C). Each rate of energy input defines an isocline relationship between predator and prey biomass and therefore a production curve given a relationship between prey density and predator relative growth. Such an isocline and growth function define the productive capacity of the system under a set of environmental conditions (Warren and Liss 1977). Changes in community organization including alternative prey for a predator or competition for a prey resource and changes in environmental conditions including increased energy input or toxicant perturbation can affect predator-prey interactions and/or the predator growth response and thus change production relationships and productivity (Fig. 27C). Yield is a function of predator biomass

and the level of exploitation on the predator. At steady state, losses in biomass to yield (and to other mortality) are balanced by gains owing to production (growth and reproduction). Organizational factors affecting population biomass affect yield relationships as they affect production relationships, and families of steady-state production and yield curves are affected similarly by changes in the organization and environment of biological communities (Fig. 27C). Trophic, habitat and life history organization and the level of energy available determined the productive capacity (productivity) of the laboratory systems not only for the guppy but for other populations in the laboratory systems.

Exploitation theory implies that a change at one level of organization in an ecological system will alter the system's responses at other levels. For example, the periodic removal of a portion of a fish population may result in increased growth and reproduction and decreased natural mortality of the exploited population. Such a change in population density will also change community structure and organization through interactions of resource, competitor, and predator populations (Larkin 1963; Liss and Warren, in press; May et al. 1979; Silliman 1975). Thus changes in individual organism responses, changes in life history patterns, are related to and concordant with changes in population density and community structure.

The structure of the guppy populations, including total and size specific biomasses, and that of the laboratory communities developed

in response to manipulation of environmental factors through adaptive changes in the biological characteristics of individual organisms. Two major components of the guppy's life history pattern, size specific growth and size specific fecundity, were observed to vary according to prevailing levels of exploitation, energy input, and dieldrin presence. The guppy populations that persisted had the capacity to adapt (i. e. developmental and evolutionary plasticity) to levels of energy input, exploitation, toxicant, and new community structures. Such adaptation must have involved concordance of the entire life history complex with population, community, and external environmental conditions. Increased growth rates, size specific fecundity, and percent females and a younger age and larger size at first reproduction were life history adaptations of guppies to increased food availability in ancillary individual organism experiments at this laboratory (Kulbicki 1979). Persistence of exploited guppy populations in the laboratory systems must have depended on such adaptive responses of individuals.

Insofar as communities can be thought to come to steady-state structures, their populations must come to steady-state density, age, size, and sex structures. And these must be maintained by steady state distributions of life history patterns within populations. Thus such a steady-state distribution of life history patterns can be thought to occur at and be specific for each steady-state point defined by the intersection of parameterized isoclines. Increases in predator

exploitation levels reduce the steady-state biomass of the predator at a given level of energy input, and result in more prey being available (Fig. 27A). Predator growth and reproduction (combined for the guppies) then increases in response to the increased food availability per individual (Fig. 27B). Guppy relative growth rate (Fig. 19) and fecundity (Fig. 21) were observed to increase as exploitation reduced their near steady-state population biomass. In addition, the percent of females in a population increased with exploitation (i.e. smaller population size).

For a given level of exploitation, increasing the level of energy input to the community would result in a larger prey population through adaptation of prey growth and reproduction. Predators would respond with increases in growth, reproduction, and survival. Larger steady-state predator and prey populations would thus result (Fig. 27A). Guppy biomass increased considerably in response to sediment increases in high energy input systems. Increased individual growth and survival were probably largely responsible. Guppy fecundity was observed to decrease at high energy input (Fig. 23), possibly in response to crowding, which has been shown to increase aggression and to decrease courting behavior and fecundity in guppies even when food resources are not limiting (Warren 1973).

Toxicant perturbation of established communities provided an additional opportunity to demonstrate the concordance of community,

population, and life history patterns and to observe a wide range of the adaptive capacity of the guppy populations in the laboratory systems. The response of the laboratory ecosystems to dieldrin perturbation was determined by the levels of prevailing environmental factors as well as by the system's organization and the capacity of the populations to adapt and to persist. Population size and the relative condition of individuals because of food availability were the major differences between guppy populations at low energy input prior to dieldrin exposure. There were both density-dependent and time-dependent components to the response of the systems to toxicant perturbation. The system at zero exploitation (system 3) had an immediate loss of guppy biomass because of the relatively poor condition of the fish. Nevertheless, the large population size, the adaptive developmental plasticity of guppies for increased growth (Fig. 20) and reproduction, and the apparent tolerance (a kind of evolutionary plasticity) of survivors to the toxicant were together instrumental in the eventual guppy population recovery. Amphipods in this system, as well as in the 10 percent (system 14) and 20 percent (system 4) exploitation systems, responded to the decrease in predation/competition with increased population sizes. As the guppy population recovered in system 3, the amphipods returned to their previously low levels of biomass (Fig. 15).

The 40 percent exploitation system (system 1), with relatively

few individuals in good condition from high food availability, had an apparent reduction in relative growth rate (Fig. 20) and reproduction (Fig. 22) of guppies that resulted in the eventual loss of the population, after 15 months of exposure. On a phase plane representation, this result corresponds to the predator and prey isoclines for 40E and low energy input crossing the prey axis but not intersecting each other (Fig. 27A). Thus, theoretically, no steady state existed for these conditions. This laboratory population apparently did not have the capacity to make sufficient developmental and evolutionary changes in its life history patterns to persist under the combined stress of dieldrin and heavy exploitation. The capacity and the organization of the system were different following extinction of the guppy population. Amphipods and snails adapted through changes in life history patterns, behavior, and population density to the new environment, which resulted in a new community structure.

Based on the relatively high productivity of the laboratory system for guppies at high energy input and on the developmental plasticity of the guppy observed at low energy input, one might predict the ability of the guppy population at 40 percent exploitation and high energy input to persist when perturbed with 1 ppb dieldrin. The phase plane representation reflects this probable result with the intersection of predator and prey isoclines at 40E, high energy input, and toxicant (Fig. 27A). The implications of such a result, and of the observed structure,

development, and persistence of the laboratory systems, are relevant
to problems in environmental toxicology and resource management.
The organization, capacity, and prevailing environment of an ecological
system together determine its response, at each level of organization,
to perturbation. The extent to which the adaptive capacity of the sys-
tem is altered will in effect determine the possible future perform-
ances of the system, including its ability to recover, within the con-
text of its new environment.

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APPENDICES

APPENDIX I.   SEDIMENTS AND ASSOCIATED MICROORGANISMS

System	Total Sediments in September 1976	% Organic at Low Energy Input	% Organic Following Heavy Rains (Winter 77–78) and High Energy Input	% Organic Nitrogen Low Energy Input	% Organic Nitrogen Following Heavy Rains (Winter 77–78) and/or High Energy Input	Mean Organic Sediments Low Energy Input	Mean Organic Sediments Following Heavy Rains (Winter 77–78) and/or High Energy Input
1	10.4	95	66	3.4	3.2	11.8	11.8
2	11.0	95	72	3.2	2.8	11.9	54.8
3	12.4	95	69	3.4	3.3	12.3	15.6
4	16.5	93	68	3.1	3.3	15.0	12.8
5	15.5	94	64	3.5	3.1	14.1	16.5
6	12.0	96	63	3.3	3.2	12.1	16.4
7	12.9	92	64	3.3	3.0	12.5	12.1
8	15.5	93	72	3.4	2.7	13.9	51.2
9	23.1	93	73	3.4	2.9	22.2	55.4
10	16.4	93	74	3.3	2.9	16.3	53.7
11	12.4	95	75	3.3	2.9	12.3	52.5
12	13.9	94	64	3.5	3.0	13.8	--
13	13.8	94	73	3.3	2.7	13.5	44.8
14	15.1	94	64	3.6	3.1	14.5	14.9
15	11.0	97	73	3.6	2.6	11.5	58.2
16	10.4	97	70	2.8	2.6	11.1	50.8

APPENDIX II. POPULATION DENSITIES NEAR STEADY STATE AT LOW ENERGY INPUT

System	Near Steady State	Number of Months	Percent Exploitation	Guppy	Snail	Amphipod	Organic Sediment	Planaria	Mean footcandles	Attached Algae
1	Sept. 76-Apr. 78	20	35 ±19	1.3g	---	.22g	11.8g	~20	17[b]	L[c]
2	Apr. 77-Mar. 78	12	17 ±7	3.1	---	.05	11.9	20	20	L
3	Feb. 77-Apr. 78	15	0	7.1	---	.02	12.2	5	20	H
4	May 77-Apr. 78	12	18 ±10	3.7	---	.04	15.0	30	18	M
5	June 77-Aug. 79	27	21 ±16	2.3	7.1[a]g	.22	14.1	25	20	L
6	May 77-Aug. 79	28	34 ±17	1.6	4.5	.16	12.1	15	21	L
7	Jan. 77-Aug. 79	32	0	7.6	2.6	.07	12.5	5	15	L
8	Jan. 77-Feb. 78	14	9 ±5	5.4	---	.05	13.9	5	21	L
9	Mar. 77-Mar. 78	13	38 ±10	1.9	---	.09	22.2	50	23	L
10	Sept. 77-Mar. 78	7	11 ±6	4.8	---	.04	16.3	5	23	H
11	Jan. 77-Mar. 78	15	0	8.1	---	.05	12.3	5	21	M
12	Mar. 78-Mar. 79	13	11 ±7	4.6	---	.00	13.8	--	17	L
13	Feb. 77-Mar. 78	14	0	8.3	---	.03	13.5	5	21	L
14	Feb. 77-Mar. 78	14	10 ±8	5.7	---	.07	14.5	5	23	L
15	Apr. 77-Mar. 78	12	38 ±11	1.9	---	.11	11.5	5	23	L
16	Apr. 77-Feb. 78	11	15 ±5	3.1	---	.04	11.1	5	20	L

[a] Snail census began October 1978.

[b] Light intensity average for water surface and tank bottom.

[c] Light (L), medium (M), heavy (H) algal cover on tank sides and bottom, and on gravel substrate; observations recorded at six month intervals.

APPENDIX III. POPULATION DENSITIES NEAR STEADY STATE AT LOW ENERGY INPUT
WITH DIELDRIN, OR AT HIGH ENERGY INPUT

System	Near Steady State	Number of Months	Percent Exploitation	Guppy	Amphipod	Snail	Organic Sediment	Planaria	Mean Footcandles	Attached Algae
1	May 78-July 79	15	36 ±21	0.7g	.56g	10.5g	11.8g	~70	17[a]	M[b]
2	Aug. 78-Aug. 79	13	20 ±6	9.8	.02	70.0	54.8	350	20	L
3	July 78-July 79	13	0	5.5	.03	4.6	15.6	1	20	H
4	Aug. 78-July 79	12	20 ±17	2.0	.07	13.0	12.8	10	18	H
5	--------------	--	------	---	---	----	----	--	--	-
6	--------------	--	------	---	---	----	----	--	--	-
7	--------------	--	------	---	---	----	----	--	--	-
8	Apr. 79-Aug. 79	5	11 ±2	15.4	.01	44.0	51.2	570	21	M
9	May 78-Aug. 79	16	38 ±11	3.9	.01	78.0	55.4	520	23	M
10	May 79-Aug. 79	4	10 ±2	16.9	.80	54.0	53.7	10	23	H
11	May 79-Aug. 79	4	0	23.7	0	34.0	52.5	970	21	H
12	--------------	--	-----	----	---	----	----	---	--	-
13	May 79-Aug. 79	4	0	23.3	1.30	26.0	44.8	30	21	L
14	June 78-Aug. 79	15	11 ±13	3.9	.12	4.7	14.9	1	23	L
15	Feb. 79-Aug. 79	7	36 ±11	6.5	.20	58.0	58.2	1	23	L
16	Nov. 78-Aug. 79	10	20 ±5	9.7	.60	52.0	50.8	10	20	M

[a]Light intensity average for water surface and tank bottom.

[b]Light (L), medium (M), heavy (H) algal cover on tank sides and bottom, and on gravel substrate; observations recorded at six month intervals.

APPENDIX IV.   DIELDRIN SUMMARY--TISSUE[a] AND WATER ANALYSIS

Sample	Date	System	Dry Weight	Dieldrin	Sex
Fish					
	5/78	C[b]	0.07 g	6.8 ppm/g	C[c]
	6/78	C	0.13	12.9	C
	7/78	C	0.06	8.8	C
	7/78	C	0.15	23.7	31 mm ♀
	8/78	C	0.23	8.6	C
	9/78	C	0.14	6.1	C
	10/78	C	0.15	12.8	♀
	10/78	C	0.08	8.5	C
	11/78	C	0.22	8.9	C
	12/78	C	0.05	9.1	3 ♂
	1/79	14	0.45	45.0	38 mm ♀
	1/79	14	0.07	4.3	♀
	1/79	4	0.24	29.0	34 mm ♀
	1/79	5	0.51	0.4	38 mm ♀
	2/79	1	0.27	32.6	34 mm ♀
	2, 3&4/79	C	0.08	20.3	4 ♂
	2, 3&4/79	C	0.07	10.4	newborns
	4/79	4	0.16	29.7	28 mm ♀
	4/79	guppy stock	0.29	undetectable[d]	25 mm ♀ 29 mm ♀
	4/79	9	0.44	0.5	37 mm ♀

[a] whole body; including shells for snails.

[b] combined sample from more than one of dieldrin systems (1, 3, 4, 14).

[c] sample combines males, females, newborns, and immature fish.

[d] detection limit was 0.01 ppb.

Sample	Date	System	Dry Weight	Dieldrin	Size
Water			.		
	mean values	1		0.95 ± 0.09 ppb	
	4/78	3		0.98 ± 0.11	
	through	4		0.96 ± 0.08	
	8/79	14		0.96 ± 0.08	
	1/79	5		undetectable[d]	
	4/79	9		undetectable	
	4/79	guppy stock		undetectable	
Snails			.		
	4/79	3&14	0.19 g	1.00 ppm/g	medium
	4/79	3&14	0.16	1.16	small
	4/79	1&4	0.26	0.72	medium
	4/79	1&4	0.16	1.07	small
	4/79	1&4	0.48	0.40	large
Ceratophyllum					
	8/78	1	0.35 g	5.0 ppm/g	
	8/78	3	0.30	4.8	
	8/78	4	0.32	4.9	
	8/78	14	0.31	5.2	
Sediments and Microorganisms					
	8/78	1	0.17 g	5.0 ppm/g	
	8/78	· 3	0.14	2.8	
	8/78	4	0.20	5.0	
	8/78	14	0.15	6.3	
	4/79	1	0.18	12.3	
	4/79	3	0.17	11.8	
	4/79	4	0.19	6.5	
	4/79	14	0.23	10.1	

[d] detection limit was 0.01 ppb.

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APPENDIX V.

Hypothetical biomass gain and loss functions for sediment (SED),
guppy (G), amphipod (A), and snail (SN) populations from which the
predator-prey isocline systems were derived. Total biomass gains
from production and reproduction (combined for the laboratory systems)
or from alfalfa ration for the sediments, are graphically summed with
total biomass losses to predation, exploitation, and non-predatory
mortalities. Each gain or loss curve is identified by a particular level
of energy and material input or level of predator, exploitation, or other
mortality factor. The intersections of total gain and total loss curves
for the sediments are the biomasses of that resource and the utilizer
populations at which the rate of sediment change with time is zero (i. e.
prey isocline). The intersections of total gain and total loss curves
for the guppy (or for the amphipods or snails) are the biomasses of
the sediment resource and the utilizer population (guppy, amphipod,
or snail) at which the rate of change in the utilizer biomass with time
is zero (i. e. predator isocline). These predator and prey isoclines are
then plotted on a resource-utilizer phase plane and are identified by
their corresponding levels of environmental factors (energy input,
alternative prey, competitors, predators, and exploitation). See
Warren and Liss 1977 for detailed procedure.

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