

AN ABSTRACT OF THE THESIS OF

William John Liss for the degree of Doctor of Philosophy
in Fisheries and Wildlife presented on March 2, 1977

Title: TOWARD A GENERAL THEORY OF EXPLOITATION OF FISH
POPULATIONS

Abstract approved: Redacted for Privacy
Charles E. Warren

A possible form of a theory of exploitation of fish populations was examined. The exploitation theory was derived from a theory of community dynamics that represents the interactions between populations in a biological community with complex interrelated systems of isoclines on phase planes. The isocline systems are deduced, with a graphical calculus, from response functions that represent the biological characteristics of each of the interacting populations. The time-invariant systems of isoclines and the response functions from which they are deduced underlie, determine, and so explain time-variant population performances.

A fish population was defined as a member of a simple community. Isocline systems were deduced to represent and provide an integrated explanation of the effects of the following factors on the dynamics and persistence of the

fish populations: changes in the levels of environmental factors such as light energy and fishing effort, competition for food with another fish population, and foraging by the fish population on two prey species. The impact of these factors on the magnitude and form of the recruitment, production, and yield curves of the fish population was also determined. In general, increases in light energy input rate and other environmental factors such as plant nutrients, and the addition of another prey species to the diet of the fish population, were found to increase the magnitude of these curves. Competition reduced their magnitude.

With the theoretical approach developed here, causal-deterministic explanations of the dynamics of exploited fish populations can be developed. These explanations couple the dynamics of the fish population to the dynamics of other populations in the biological community and to external environmental factors. This approach thus permits broad understanding of the performances of exploited fish populations as they interact with their co-extensive environmental systems.

Toward a General Theory of
Exploitation of Fish Populations

by

William John Liss

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1977

APPROVED:

[Handwritten Signature]
Redacted for Privacy

Professor of Fisheries
in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

[Handwritten Signature]
Redacted for Privacy

Dean of Graduate School

Date thesis is presented March 2, 1977

Typed by Deanna L. Cramer for William John Liss

ACKNOWLEDGEMENTS

I wish to express, to Dr. Charles E. Warren, my most sincere appreciation for advice, assistance, and encouragement so generously given throughout the course of this research.

For their interest and many helpful suggestions, I would like to thank the staff and students of Oak Creek Laboratory of Biology, particularly Dr. Gary L. Larson and Mr. W. Micheal Booty. I shall always be grateful for the many years of friendship and wise counsel provided by Dr. LaVern J. Weber.

My wife, Evelyn, deserves special thanks for her patience and understanding.

This thesis is based in part on research carried out as part of the Oregon State University Sea Grant College Program, cooperatively supported by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce, by the State of Oregon, by participating local governments and private industry, and by the people of Oregon.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
EXPLANATION OF THE DYNAMICS, STABILITY, AND TIME-VARIANT BEHAVIOR OF EXPLOITED FISH POPULATIONS.	10
Representation and Explanation of the Dynamics of an Exploited Fish Population in a Simple Community.	10
Representation and Explanation of the Stability of Exploited Fish Populations.	37
Representation and Explanation of the Time-Variant Behavior of Exploited Fish Populations under Periodic Exploitation	43
REPRESENTATION AND EXPLANATION OF THE DYNAMICS OF INTERSPECIFIC COMPETITION BETWEEN EXPLOITED FISH POPULATIONS	52
REPRESENTATION AND EXPLANATION OF THE DYNAMICS OF AN EXPLOITED FISH POPULATION FEEDING ON TWO PREY SPECIES	70
DISCUSSION	88
BIBLIOGRAPHY	98

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Kinetic representation of some important classes of interactions between populations in a biological community	6
2	Phase planes and interrelated isocline systems representing a sequence of predator-prey interactions in a simple community	11
3	Derivation of prey isoclines on the C-H phase plane by graphical summation of herbivore gain and loss response functions. . .	16
4	Derivation of the herbivore production gain response functions used in constructing the prey isoclines on the C-H phase plane	19
5	Derivation of predator isoclines on the C-H phase plane by graphical summation of carnivore gain and loss curves.	25
6	Derivation of the carnivore production gain response functions used in constructing the predator isoclines on the C-H phase plane . . .	27
7	System-determined carnivore equilibrium recruitment, production, and yield curves . . .	33
8	The effect of two different forms of the yield response function on the scope for persistence of a carnivore-herbivore system . .	40
9	Steady-state trajectores of biomasses of C and H generated by different fishing regimes	45
10	Phase plane representation of competition between two carnivore populations, C and C ₂ , for a common food resource, herbivore H . .	54
11	Competition phase plane used to determine equilibrium carnivore biomasses that result from the competitive interaction of carnivore populations C and C ₂ at each rate of light input and level of fishing effort	58

List of Figures -- continued

<u>Figure</u>		<u>Page</u>
12	The influence of competition on the magnitude and form of the system-determined C equilibrium recruitment, production and yield curves at each rate of light input . . .	64
13	Equilibrium yield curves of carnivore C and carnivore C ₂ , and the curve representing total equilibrium yield to the fishery is shown for two rates of light input.	67
14	The feeding strategy of carnivore C preying upon herbivore H and herbivore H ₂ is represented by the predation loss response functions of herbivore H and herbivore H ₂ at carnivore biomass 1C.	72
15	Phase plane representation of the interaction between carnivore C, an exploited fish population, and its prey species, herbivore H and herbivore H ₂	75
16	Two sets of curves representing the relationship between the relative growth rate of the carnivore and the biomass of its prey species, herbivore H and herbivore H ₂	78
17	Foraging phase plane used to determine, for each rate of light input and level of fishing effort, the equilibrium biomasses of herbivore H and herbivore H ₂ that result when both are preyed upon by carnivore C.	83
18	The effect of the addition of prey species H ₂ on the magnitude and form of the system-determined carnivore equilibrium recruitment, production, and yield curves	86
19	Changes in position of the predator and prey isoclines on the C-H phase plane and changes in magnitude of the carnivore equilibrium recruitment, production, and yield curves that result from changes in plant nutrient concentration N, introduction of a competitor C ₂ and addition of another prey species to the diet of C.	95

LIST OF TABLES

Table

Page

1	Total carnivore yield obtained under each fishing regime	49
---	---	----

TOWARD A GENERAL THEORY OF EXPLOITATION OF FISH POPULATIONS

INTRODUCTION

An objective of fisheries science has traditionally been to explain the response of fish populations to exploitation. The accomplishment of such an objective by fisheries biologists first requires some understanding of what such an explanation entails, what the form of the explanation might be, and what criteria can be used to evaluate any proposed explanation.

A population has a capacity to respond in different ways to conditions in its environment. The response, or performance, of the population at any particular time is determined by both its capacity and environmental conditions (Warren, Allen, and Haefner, MS). Changes in environmental conditions, even without a change in the population's capacity, lead to a change in its performance.

An adequate explanation of the response of fish populations to exploitation would therefore entail a reconstruction or representation of all those conditions in the environment of a fish population that determine, under different fishing regimes, the magnitude of fish population performances such as population biomass, recruitment, production, yield, and other forms of mortality. If such a

reconstruction were both time-invariant and general, it would be a universal explanation (Campbell, 1920) of the response of fish populations to exploitation. The reconstruction would be time-invariant if it represents what underlies, determines, and so explains the time-variant behavior of population performances. And it would be general if it applied over a broad natural domain.

The most universal explanations in science are achieved by theories. A theory will be defined here as a scientific deductive system employing, as initial premises, abstract concepts (Braithwaite, 1953) or theoretical propositions. From the initial theoretical concepts or propositions -- the assumptions -- theorems are deduced with an abstract calculus. The theoretical propositions can be variously interpreted so as to make their explanatory coverage very great.

We cannot suppose that such universal explanations can easily be achieved. There must be some criteria for evaluating the adequacy of any proposed theory, or explanation, of the response of fish populations to exploitation (Warren and Liss, MS). All good theories should be internally (logically) consistent and externally adequate. If an explanation is to be externally adequate, it must be dimensionally, dynamically and empirically sufficient (Lewontin, 1974) to explain the performances of exploited fish populations within the context of their environmental

systems. An explanation is dimensionally sufficient if it adequately accounts for and represents the dimensions of the environmental system that determine population performances. Furthermore, the explanation should adequately explain the dynamic behavior of populations and, thus, account for, in a causal-deterministic manner, the continual change in magnitude of population performances observed in nature. The explanation should therefore be dynamically and empirically sufficient. Finally, an adequate explanation of the responses of exploited fish populations should have heuristic (discovery) power and explanatory power, which includes visualizability, communicability, and aesthetic satisfaction.

The criterion of dimensional adequacy is paradoxical. Theories which include too few dimensions are representationally inadequate for explanation of complex population performances, as Lewontin (1974) was aware. But if theories or models attempt to attain the complex dimensionality of natural systems by simple addition of dimensions, the theory or model eventually must become conceptually and methodologically intractable. These theories would lose much of their visualizability and heuristic power and would instead be mere reflections of nature rather than explanations. As Holling and Ewing (1971, p. 212) observe: "...with so many dimensions...it becomes difficult to condense our insight."

Fisheries biologists since Baranov (1918) have been engaged in developing models that explain the impact of exploitation on the biomass, recruitment, production, and yield of fish populations (Graham, 1935; Ricker, 1954; Schaeffer, 1954, 1957; Beverton and Holt, 1957; Fox, 1970; Walters and Hilborn, 1976). Although these models have increased our understanding of the dynamics of exploited fish populations and have been useful in fisheries management, they have not explicitly coupled the dynamics of exploited fish populations to the dynamics of other populations in the community or to environmental factors.

A particularly visualizable and heuristic approach for articulating population interactions within a community has been developed by Booty and Warren (MS). They have utilized a graphical calculus to develop a theory of community dynamics and productivity. The initial propositions of the theory take the form of response functions that represent the biological characteristics of each interacting population in a biological community. With the graphical calculus, interrelated time-invariant systems of isoclines that represent the interaction between populations and external environmental factors can be deduced.

Ecologists have used isocline theory to represent, with a single pair of isoclines, the interaction between a single predator and a single prey population or the interaction between two competing species. Rosenzweig (1973)

was able to construct a three-dimensional isocline model of a carnivore-herbivore-plant community. Furthermore, Rosenzweig (1971a,b) was aware that the position and form of isoclines on phase planes could be affected by environmental factors. In general, however, extant isocline theory in ecology is limited to representation of the interaction between at most three populations, competition interactions are uncoupled from predation interactions, and utilization of more than one prey by a predator has not been considered.

Although representation of the complex dimensionality of natural systems remains a problem, the graphical calculus developed by Booty and Warren (MS) allows a substantial increase in the dimensionality of graphical representations and explanations of community dynamics. Utilizing this graphical calculus, a theory of exploitation of fish populations that seems to satisfy many of the criteria for explanatory adequacy set forth above can begin to be developed. With this theoretical approach, the dynamics of exploited fish populations can be coupled to the dynamics of other populations in the community and to environmental factors, thus providing a logical unification of population interactions within the context of an environmental system.

To illustrate the scope and objectives of this theoretical approach, a kinetic representation of some general classes of interactions between populations in a biological community are presented in Figure 1. A group of interacting

Figure 1. Kinetic representation of some important classes of interactions between populations in a biological community. The defined system enclosed by the dashed line is composed of light intensity (R), plants (P, P₁), herbivores (H, H₂) and carnivores (C, C₁, C₂). Numerical subscripts denote different populations on a given trophic level. Carnivore C is the exploited fish population of primary interest. The environment of the defined system is composed of light input rate (I), fishing effort (E) and plant nutrients (N). Organisms on all trophic levels contribute organic matter (OM) which is converted by decomposers (D) to plant nutrients. The classes of population interaction represented are predator-prey interactions (+,-), commensalism (+,0) and mutualism (+,+). Competition between C and C₂ occurs through utilization of a common prey H. The sign in the direction of the arrow characterizes the effect of one population on another as positive if the other increases as a result of the interaction, negative if the other decreases, and neutral if the other is unaffected. The numbered interactions will be represented and explained with interrelated systems of isocline on phase planes.

ENVIRONMENT OF THE
DEFINED SYSTEM

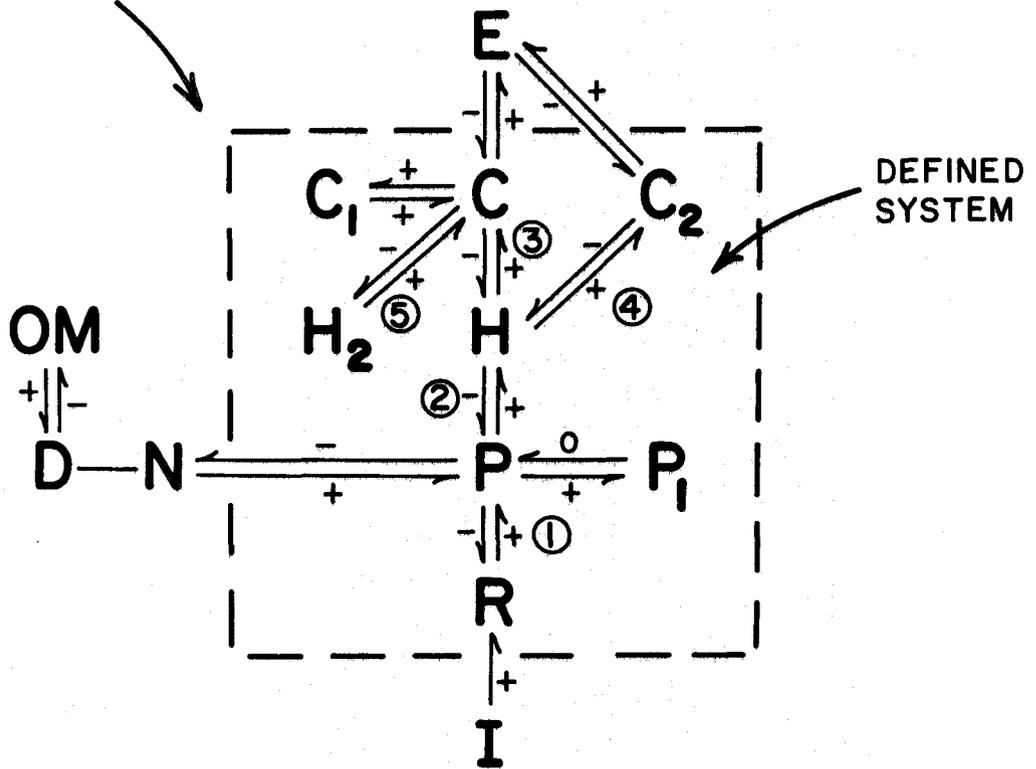


Figure 1

populations including carnivore C, the exploited fish population, compose the defined system. Fishing effort E, light input rate I, and plant nutrients N are variables external to the defined system and constitute the environment of the defined system.

The first objective is to represent and explain the impact of external environmental factors, specifically I and E, on the dynamics and stability of the exploited fish population carnivore C as a member of a simple food chain. This will be accomplished by deducing interrelated systems of isoclines on phase planes that represent the sequential predator-prey interactions between C, H, P and R (interactions 1, 2, 3). The effect of changes in I and E on the recruitment, production, and yield performances of carnivore C will then be determined. The impact of periodic exploitation on the performances of carnivore C will also be examined.

The second objective is to represent and explain the dynamics of interspecific competition between exploited fish populations. To accomplish this, another dimension of the community, carnivore C_2 , will be introduced as a competitor of carnivore C (interaction 4 will be included in the explanation). The effect of competition on the recruitment, production, and yield of carnivore C will be determined.

The third objective is to represent and explain the dynamics of carnivore C, the fish population, when it feeds on two prey species with a particular foraging strategy. Herbivore H_2 will be introduced as an additional prey (interaction 5) of carnivore C. The recruitment, production, and yield of carnivore C when additional prey are included in its diet will be examined.

External environmental variables I and E will be formally introduced into the explanation of all population interactions. Plant nutrient N will only be considered informally. Commensalism and mutualism are other classes of population interactions that could be explained with this theory of exploitation, but will not be examined here.

EXPLANATION OF THE DYNAMICS, STABILITY, AND TIME-VARIANT BEHAVIOR OF EXPLOITED FISH POPULATIONS

Representation and Explanation of the Dynamics of an Exploited Fish Population in a Simple Community

Phase planes and isocline systems representing a sequence of predator-prey interactions in a simple community (interactions 1, 2, and 3 in Figure 1) are presented in Figure 2. On each phase plane in Figure 2, prey biomass (or resource level) is plotted on the x-axis and predator biomass (or utilizer level) on the y-axis. The descending curves parameterized by light input rate (low I, med I, high I) on each phase plane are the prey or resource isoclines. Each prey isocline is a set of points, or biomasses (or level) of predator and prey, at which the rate of change of prey biomass with respect to time is zero ($dR/dt = 0$ on the P-R phase plane, $dP/dt = 0$ on the H-P phase plane, $dH/dt = 0$ on the C-H phase plane). The ascending curves on each phase plane are predator or utilizer isoclines. Each predator isocline is a set of points, or biomasses (or levels) of predator and prey, where the rate of change of predator biomass, with respect to time is zero ($dP/dt = 0$ on the P-R phase plane, $dH/dt = 0$ on the H-P phase plane, and $dC/dt = 0$ on the C-H phase plane). The predator isoclines are parameterized by herbivore biomass on the P-R phase plane, by carnivore biomass on the H-P phase plane

Figure 2. Phase planes and interrelated isocline systems representing a sequence of predator-prey interactions in a simple community are shown in A, B, and C. The form and position of predator and prey isoclines on all phase planes have been deduced, with a graphical calculus, from response functions that represent the biological characteristics of each of the populations. An infinite family of prey isoclines exists on each phase plane. Each prey isocline is generated and so parameterized by a particular rate of light input I . The prey isoclines generated by three rates of light input, low I , med I , and high I , are shown on each phase plane. The dashed prey isocline on the C-H phase plane would be generated by a very low light input rate. An infinite family of predator isoclines also exist on each phase plane. Predator isoclines are generated and thus parameterized by particular herbivore biomasses (OH, 1H, 3H, 5H) on the P-R phase plane; by particular carnivore biomasses (OC, 1C, 3C, 5C) on the H-P phase plane; and by particular levels of fishing effort (OE, 30E, 90E, 150E) on the C-H phase plane. The rates of change of the variables R, P, H, and C can be represented by a series of functional equations as in D.

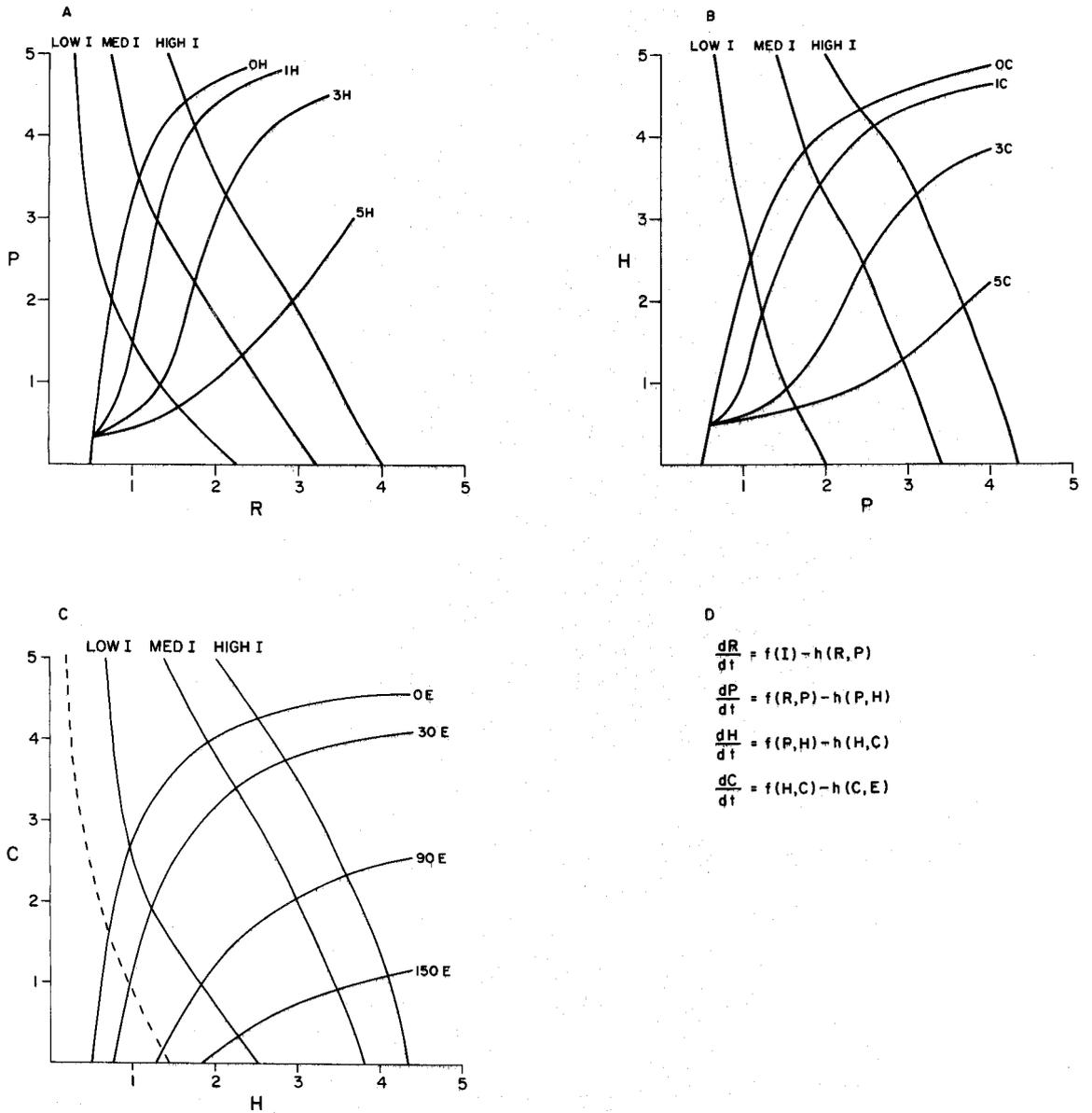


Figure 2

and by level of fishing effort on the C-H phase plane. Each intersection of a predator and prey isocline, where the rate of change of both predator and prey biomass with time is zero, is an equilibrium point.

The form, position, and identity of all isoclines on the phase planes in Figure 2 have deduced, by a graphical calculus, from response functions that represent the biological characteristics of the interacting populations. But before turning to the graphical deduction of the isoclines, it will be helpful to examine in some detail the density-dependent shifts in equilibrium points on all phase planes that result from changes in the external variables I and E. Although Rosenzweig (1971a,b) was aware that changes in environmental variables would alter the position and form of prey isoclines, shift the equilibrium point, and possibly alter the stability of simple predator-prey interactions, ecologists have not fully utilized graphical techniques to examine the effects of several environmental variables on the behavior of more complex biological systems.

We can begin, on the C-H phase plane in Figure 2C, with the equilibrium point at the intersection of the prey isocline parameterized by med I and the predator isocline parameterized by OE. Progressively higher levels of fishing effort (OE to 150E) at this light input rate lead to lower equilibrium C biomasses and higher equilibrium H biomasses. In a sense, then, increasing fishing effort moves

the equilibrium point downward on the prey isocline identified by med I, reducing C biomass and at the same time allowing the biomass of H, the prey, to increase. Now, on the H-P phase plane at med I (Figure 2B), an increase in equilibrium H biomass leads to a reduction in the equilibrium biomass of P, the equilibrium point shifting upward along the med I prey isocline with declining C biomass. And, finally, in Figure 2A, the reduction in P biomass resulting from increased H biomass leads to an increase in R.

Similarly, at a given level of fishing effort such as 30E (Figure 2C), progressively higher rates of light input (low I to high I) lead to higher equilibrium biomasses of both C and H, the equilibrium point now moving upward along the predator isocline identified by 30E. Increased I causes not only increases in C and H biomasses but also increases in P and R. Thus, because of the density-dependent causal relationships between populations, changes in either I or E result, either directly or indirectly, in changes in the equilibrium densities of all populations in this simple community. Furthermore, for a given rate of light input I and level of fishing effort E, there exists a single equilibrium point on each phase plane defining one possible set of equilibrium biomasses of C, H, P, and R (Booty and Warren, MS). A given set of such equilibrium biomasses can be conceptualized as a four-dimensional community equilibrium point, which is represented by the set

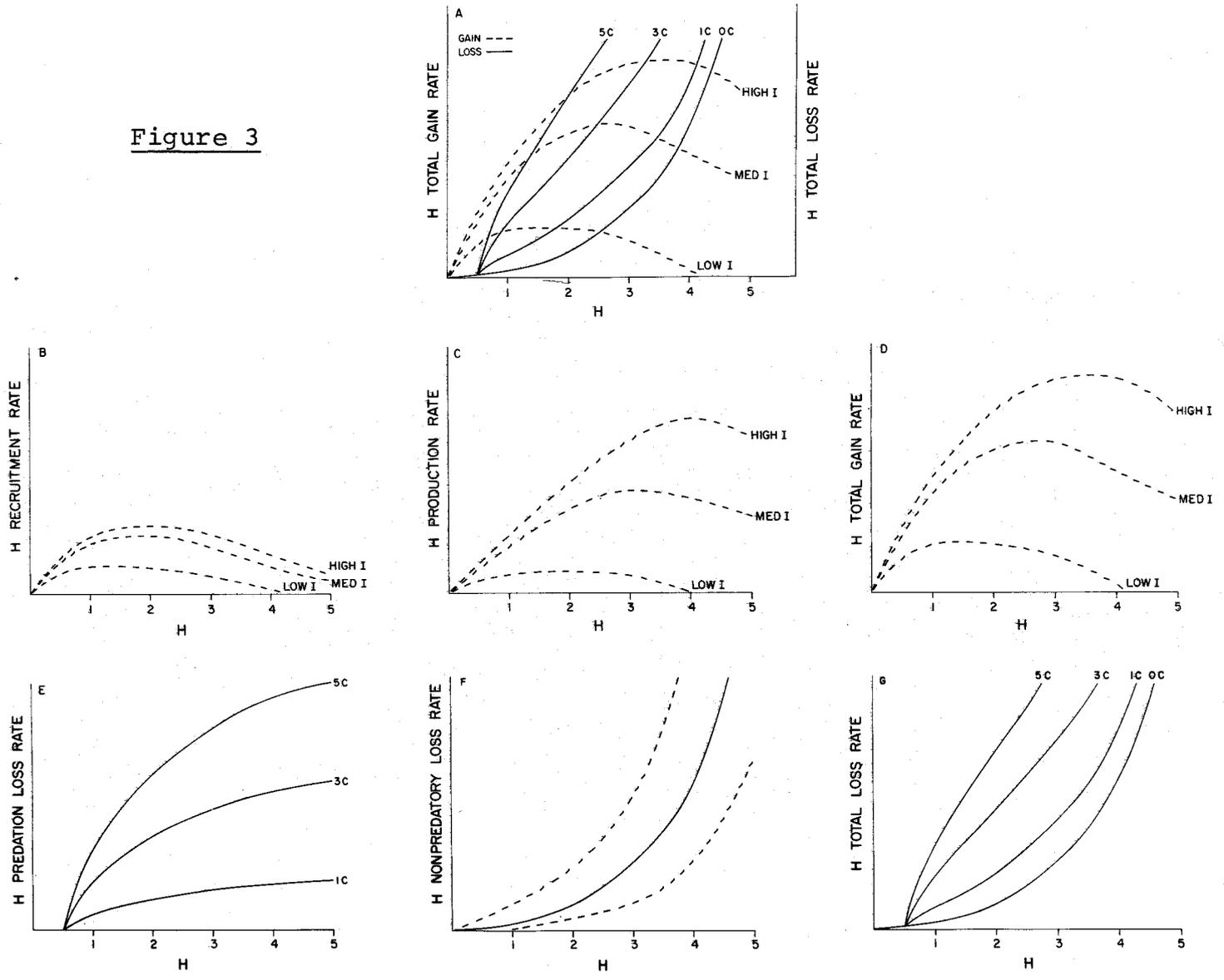
of two-dimensional equilibrium points on the three phase planes in Figure 2. Each two-dimensional equilibrium point is simply one possible projection of the four-dimensional community equilibrium point in hyperspace.

The form and position of the isoclines on each phase plane can be deduced, by a graphical calculus, from systems of curves representing such biological characteristics of populations as recruitment, production, loss to predation, nonpredatory losses, and yield to exploitation. Booty and Warren (MS), beginning with the P-R phase plane, provide a detailed and formal description of the graphical method of determination of predator and prey isoclines on all phase planes. Here only the isoclines on the C-H phase plane will be graphically derived (Figures 3 to 6). In principle, the same argument is used to deduce the forms and positions of isoclines on the P-R and H-P phase planes.

The position and form of the prey isoclines on the C-H phase plane are derived from the biological characteristics of the herbivore population. The rate of change of herbivore biomass with time (dH/dt) is dependent upon the rate that the herbivore population gains biomass and the rate that it loses biomass. The population of herbivores in this simple community gains biomass through recruitment and production and loses biomass through consumption by carnivores (predation losses) and nonpredatory losses such as those owing to emigration and disease (Figure 3). The rate

Figure 3. Derivation of prey isoclines on the C-H phase plane (Figure 2C) by graphical summation of herbivore gain and loss response functions. The prey isoclines on the C-H phase plane are the sets of biomasses of herbivore and carnivore where $dH/dt = 0$. The intersections of the curve representing herbivore total gain rates for a particular rate of light input I , with the series of curves representing herbivore total loss rates for different carnivore biomasses, C , (A) defines the set of herbivore and carnivore biomasses where $dH/dt = 0$. Each rate of light input generates and thus parameterizes a particular prey isocline. The curves representing the total gain rates of the herbivore (D) are constructed by graphical summation of herbivore recruitment (B) and production (C) rate curves for each rate of light input. The curves representing herbivore total loss rates (G) are constructed by graphical summation of the nonpredatory loss rate curve (solid line, F) with each predation loss rate curve (E). Total loss rates at OC represent only nonpredatory losses. The nonpredatory loss rate response could also be represented by a family of curves parameterized by different levels of chemical, physical, or biological factors that would affect nonpredatory loss rate (dashed lines, F).

Figure 3



of change of herbivore biomass with time is zero when the rate of gain of herbivore biomass is equal to the rate of loss of herbivore biomass. Thus to construct prey isoclines on the C-H phase plane we must define and appropriately parameterize gain (recruitment, production) and loss (predation, nonpredatory) functions for the herbivore and then determine, by graphical summation of these curves, the biomasses of herbivore and carnivore at which $dH/dt = 0$.

To illustrate derivation of the gain curves (Figure 3B and 3C) used to determine the prey isoclines on the C-H phase plane, we will begin with herbivore production. Production of a population is simply the total amount of tissue elaborated by the population per unit of time regardless of the fate of that tissue. Production can be computed as the product of relative growth rate and biomass (Chapman, 1968; Warren, 1971). Now the prey isoclines on the H-P phase plane define possible density-dependent relationships between equilibrium herbivore and plant biomasses at different rates of light input (Figure 2B). Furthermore, herbivore relative growth rate can be defined as a curvilinear function of plant biomass, thus associating equilibrium herbivore biomass and herbivore relative growth rate. Relationships of this type have been empirically derived for fish in laboratory stream communities and in lakes (Warren, 1971). A herbivore production gain curve (Figure 4) can thus be determined from each of the density-

Figure 4. Derivation of the herbivore production gain response functions used in constructing the prey isoclines on the C-H phase plane. Herbivore production rate is the product of herbivore relative growth rate and herbivore biomass. Each production gain curve is derived from the density-dependent relationship between equilibrium herbivore and plant biomass at a given light input rate and from the curve relating herbivore relative growth rate to plant biomass. The determination of herbivore production rates from these relationships is illustrated for equilibrium herbivore biomasses 1 and 3 at light input rate $med I$. In general, at a given rate of light input, an increase in carnivore biomass results in a decline in equilibrium herbivore biomass and an increase in equilibrium plant biomass. With an increase in plant biomass, the relative growth rate of the herbivore (g_j) also increases. Herbivore relative growth rate is therefore an inverse function of herbivore biomass and the relationship between herbivore production rate and herbivore biomass is a dome-shaped curve. Each rate of light input defines a unique density-dependent relationship between herbivore and plant biomass and, thus, a unique herbivore production curve.

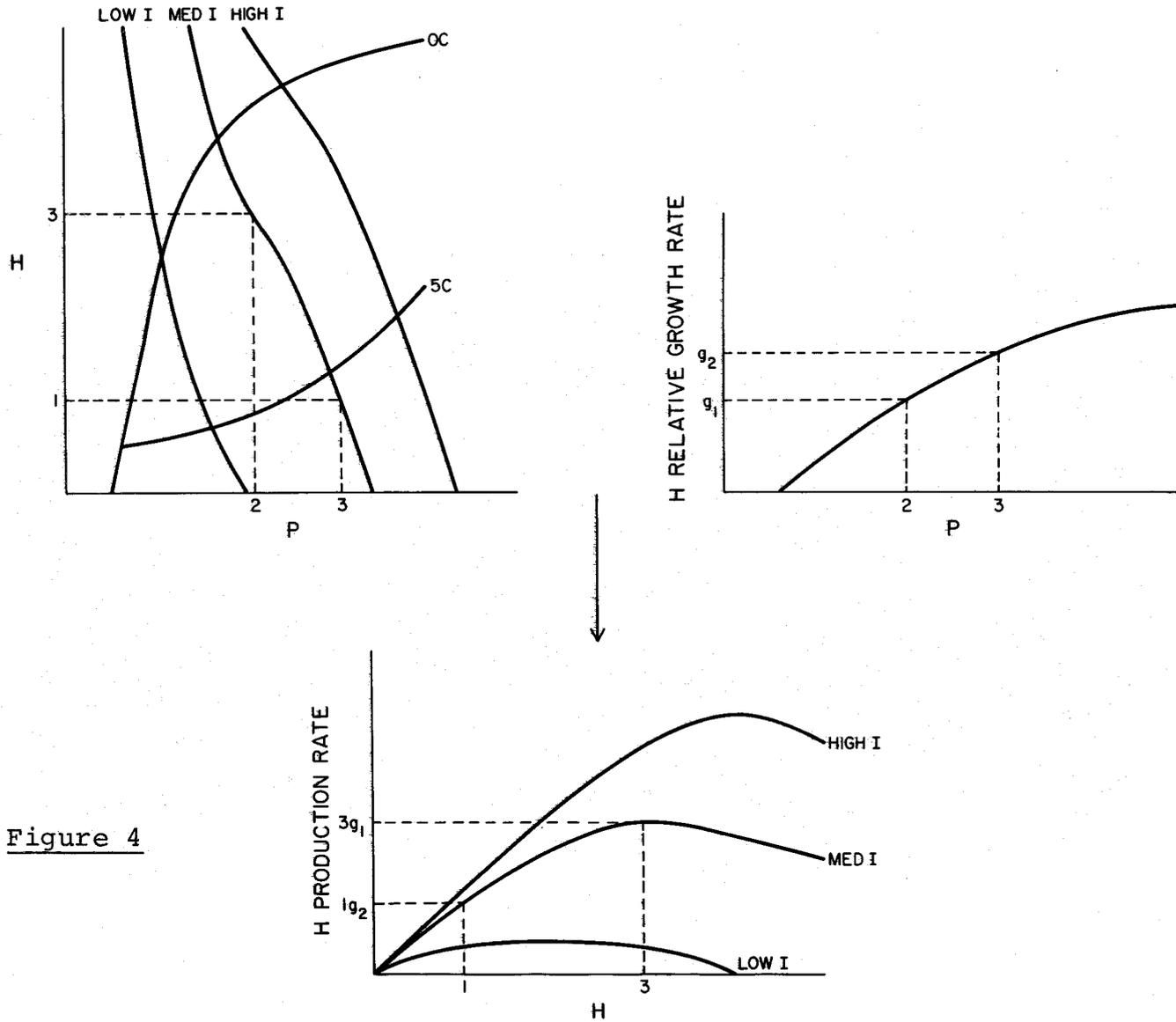


Figure 4

dependent relationships between herbivore and plant biomass, generated by a particular rate of light input, together with the herbivore growth function.

The curve relating herbivore relative growth rate to plant biomass (Figure 4) is taken to be a representation of the "average" relative growth rate of all individuals in the herbivore population at each plant biomass. A unique growth response function exists for each size group or age group of organisms in the population, and the growth response of the population could have been represented as a family of curves, each curve parameterized by a particular size group or age group. For simplicity, a single curve will be utilized here since this will not affect the general conclusions.

The recruitment gain curves of the herbivore are constructed in very much the same manner as the production gain curves, by utilizing once again the prey isoclines identified by particular rates of light input on the H-P phase plane and a set of curves representing herbivore relative recruitment rate as a function of both plant biomass and herbivore biomass. Since there are conceivably an infinite number of particular rates of light input and thus, an infinite number of prey isoclines, an infinite family of recruitment and production curves exist, each curve generated at and identified by a particular rate of light input. The recruitment and production gain curves

of the herbivore for each rate of light input are graphically summed to generate a set of curves representing herbivore total gain rates (Figure 3D).

Herbivore biomass is removed from the herbivore population through consumption of herbivores by carnivores (predation losses) and through nonpredatory losses. The rate of consumption of herbivores by carnivores is represented, in Figure 3E, as a function of both herbivore biomass and carnivore biomass. These curves, similar to Holling's (1959) type 2 predation functional responses, intercept the H axis at a positive value of H. This kind of functional response could result if prey have a refuge that allows a constant biomass of prey to escape predation (Murdoch and Oaten, 1975). The rate of nonpredatory loss of herbivores is taken to be an exponential function of herbivore biomass (Figure 3F, solid line). The nonpredatory loss curve is summed with each predation loss curve to generate a set of curves representing total loss rates of the herbivore (Figure 3G).

The prey isoclines on the C-H phase plane have been defined as the sets of biomasses of carnivore and herbivore at which $dH/dt = 0$. When $dH/dt = 0$, the total rate of gain of herbivore biomass is equal to the total rate of loss of herbivore biomass. If curves representing total gain rates (Figure 3D) and curves representing total loss rates (Figure 3G) are plotted on the same graph (Figure 3A),

the intersections of a gain curve (identified by a particular rate of light input) with a series of loss curves (identified by carnivore biomasses) defines a set of biomasses of carnivore and herbivore at which $dH/dt = 0$. That is, each rate of light input generates and so identifies a prey isocline on the C-H phase plane (Figure 2C).

In general, this procedure is used to derive prey isoclines on all phase planes. Rates of light input are initially introduced as the gain terms of R and so become the identities of prey isoclines on the P-R phase plane. It can be rigorously shown that rates of light input become identities of prey isoclines on all successive phase planes (Booty and Warren, MS). This is a consequence of constructing prey isoclines on any particular phase plane by utilizing recruitment and production gain curves derived from the prey isoclines of the previous phase plane. It is thus evident that rate of light input must be a determinant of the dynamics of all populations in the community. The impacts of changes in rate of light input are clearly visualizable on all phase planes.

Rate of light input is not the only possible parameterizing identity of prey isoclines. Any chemical, physical, or biological factor affecting any of the gain or loss curves of a population would become an additional parameterizing identity of the prey isoclines derived from that population's gain and loss curves and of the prey isoclines

on all successive phase planes. This has great importance, for it permits rigorous incorporation of other dimensions into the explanation of population and community dynamics.

We can now turn to derivation of the predator isoclines on the C-H phase plane (Figure 2C). These isoclines are deduced in much the same way as were the prey isoclines: graphic summation of the carnivore's gain curves (recruitment, production) and loss curves (yield, nonpredatory losses), as shown in Figure 5. The major difference is in the form and identities of the recruitment and production gain curves. The derivation of the gain curves will be illustrated by taking carnivore production as an example (Figure 5C).

In deducing the predator isoclines on the C-H phase plane -- and predator isoclines in general -- production rate relationships are derived solely from a curve relating predator relative growth rate to prey biomass as shown in Figure 6. In this way, linear carnivore production responses are generated for each herbivore biomass (Figure 5C). Similarly, carnivore recruitment gain curves are derived solely from relationships between carnivore relative recruitment rate, herbivore biomass, and carnivore biomass. Such relationships take into account direct effects of carnivore biomass on carnivore recruitment as well as the effects of herbivore biomass on relative recruitment rate.

Figure 5. Derivation of predator isoclines on the C-H phase plane (Figure 2C) by graphical summation of carnivore gain and loss curves. The predator isoclines on the C-H phase plane are the sets of biomasses of carnivore and herbivore where $dC/dt = 0$. The intersections of the curve representing carnivore total loss rates for a particular level of fishing effort, E , with the series of curves representing carnivore total gain rates at different herbivore biomasses, H , (A) defines the set of carnivore and herbivore biomasses where $dC/dt = 0$. Each level of fishing effort generates and so identifies a particular predator isocline. The curves representing the total gain rates of the carnivore (D) are constructed by graphical summation of carnivore recruitment (B) and production (C) rate curves for each herbivore biomass. The curves representing carnivore total loss rates (G) are constructed by graphical summation of the non-predatory loss rate curve (F) with each yield rate curve (E). The problematical yield response curves are determined from $dY/dt = qEC$ where q , the catchability coefficient, was fixed at 0.2. Total loss rates at OE represent only nonpredatory losses.

Figure 5

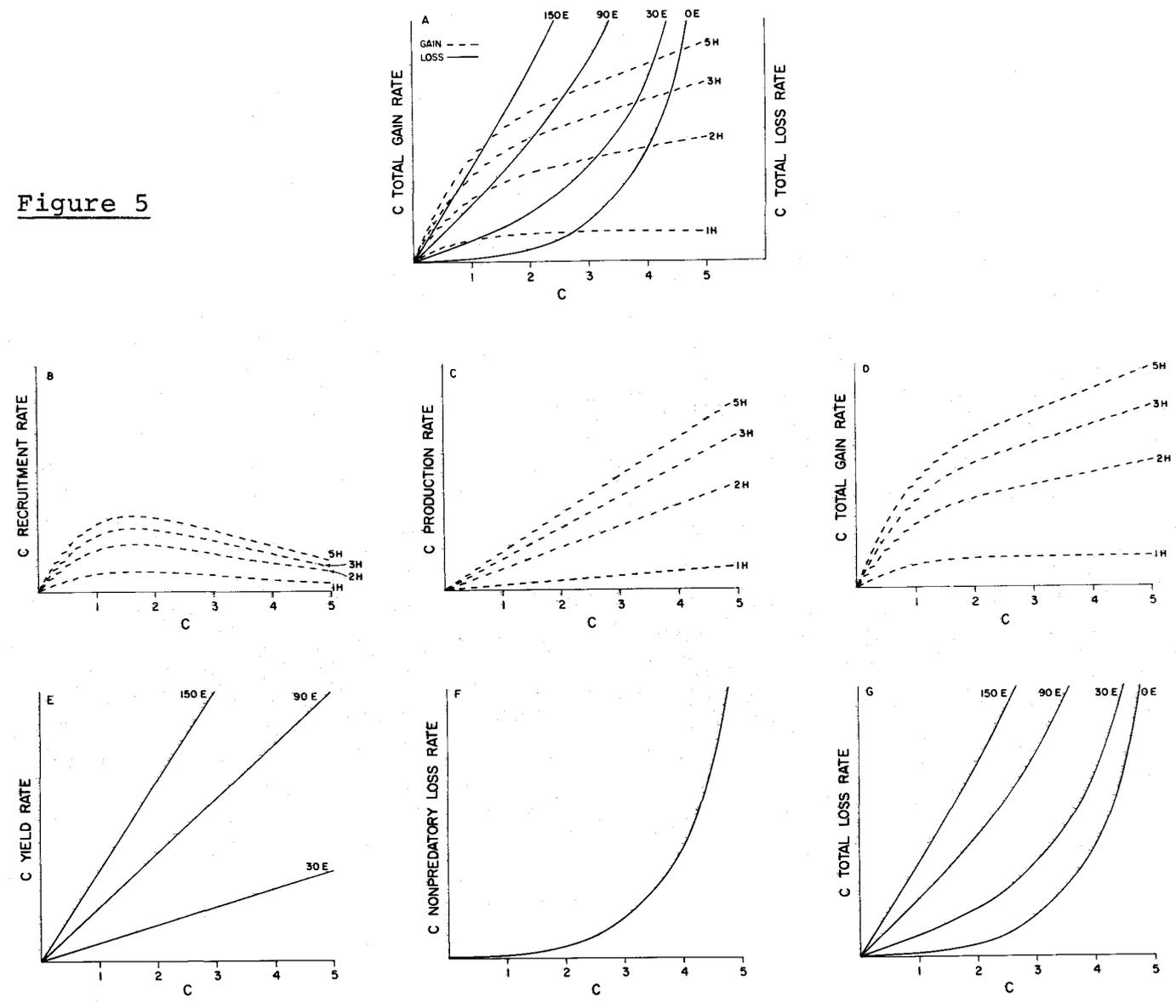


Figure 6. Derivation of the carnivore production gain response functions used in constructing the predator isoclines on the C-H phase plane. Carnivore production rate is derived from the curve relating carnivore relative growth rate to herbivore biomass. If herbivore biomass and, thus, carnivore relative growth rate were capable of being held constant, the relationship between carnivore production rate and carnivore biomass would be linear. Linear production responses can be generated for each herbivore biomass. The procedure is illustrated for herbivore biomasses 2 and 3. Derivation of these problematical carnivore production relationships facilitates construction of predator isoclines. System-determined carnivore production curves can be derived from relationships between carnivore and herbivore biomass defined by the prey isoclines at each light input rate on the C-H phase plane and from the curve relating carnivore relative growth rate to herbivore biomass. The relationship between the linear problematical production responses and the system-determined production curves at three light input rates (dashed curves) is shown.

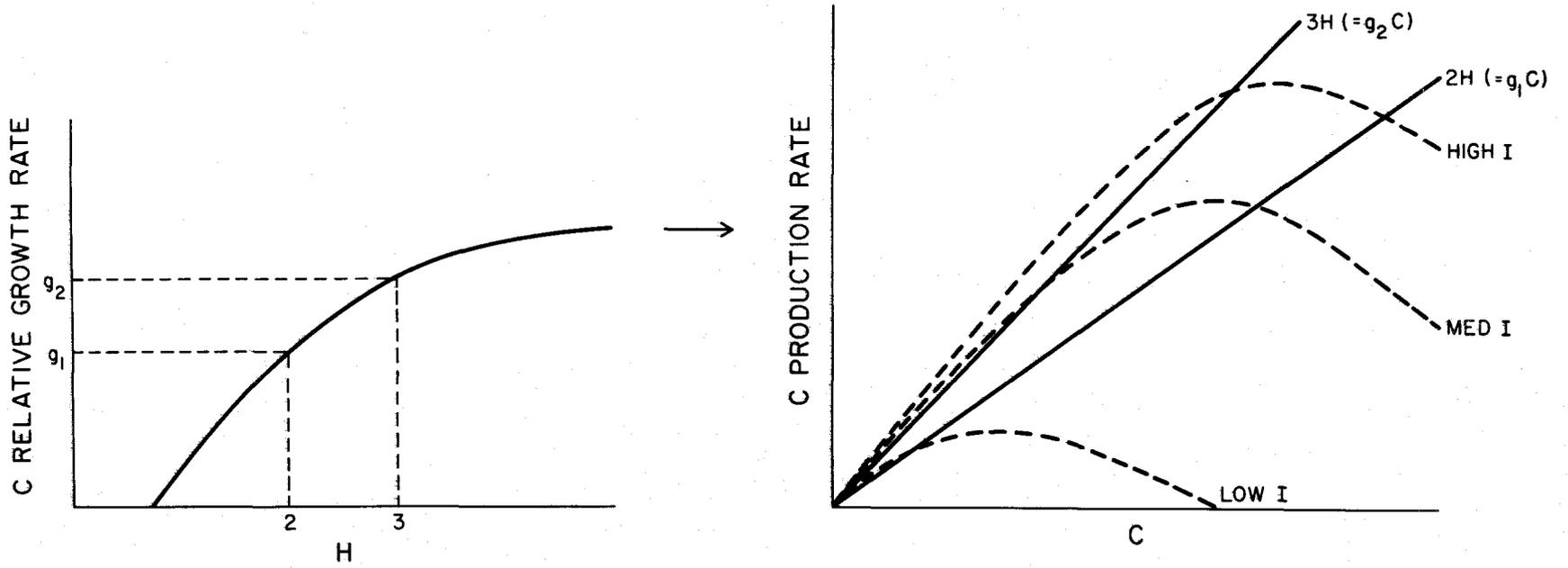


Figure 6

As a result, dome-shaped carnivore recruitment gain curves identified by herbivore biomass are generated (Figure 5B).

Parameterizing these gain curves with prey biomass merely facilitates the construction of predator isoclines. Booty and Warren (MS) refer to curves constructed in this manner as problematically possible responses: that is, curves that express the relationship between a predator response (such as production or recruitment rate) and predator biomass only if the level of the variable (say prey biomass) generating these responses were maintained constant. These curves, then, do not take into account the density-dependent interactions between a predator and its prey, as defined by the prey isoclines. Recruitment and production curves derived from both the prey isoclines and a predator relative recruitment or relative growth rate function are system-determined: that is, they represent predator production and recruitment as equilibrium outcomes of the interactions between predator and prey. System-determined curves of this type will be deduced to explain the recruitment, production, and yield of carnivore C, the fish population.

In deriving the predator isoclines on the C-H phase plane, the problematical recruitment and production gain curves at each H biomass are graphically summed to generate a set of curves representing carnivore total gain rates (Figure 5D). We must now consider carnivore losses, which

are taken to be the rate of yield (Figure 5E) and nonpredatory loss rate (Figure 5F). The problematical relationships between rate of yield and carnivore density are linear and are parameterized by level of fishing effort. The carnivore yield and nonpredatory loss curves are summed to generate a set of curves representing total loss rates of the carnivore (Figure 5G). The curves representing total rate of gain (Figure 5D) and the curves representing total rate of loss (Figure 5G) can now be plotted on the same graph (Figure 5A). The intersections of a loss curve (identified by a particular level of fishing effort) with a series of gain curves (identified by herbivore biomasses) define a set of herbivore and carnivore biomasses at which $dC/dt = 0$. Thus each level of fishing effort generates and therefore identifies a predator isocline on the C-H phase plane (Figure 2C).

Predator and prey isoclines on all phase planes can be constructed by graphical summation of gain and loss curves. The form of these curves, which represent some of the biological characteristics of populations, can be based upon theoretical and empirical knowledge or exploratory hypotheses. The forms of the gain and loss curves that have been employed here seem biologically reasonable and are derived, in part, from extant theoretical and empirical knowledge. And the forms and magnitudes of such gain and loss curves

determine, and so explain, the positions and forms of predator and prey isoclines.

To this point, only the graphical deduction of time-invariant systems of isoclines and the shifts in the equilibrium points at their intersections that result from changes in levels of environmental variables have been considered. But how is the time-variant behavior of interacting populations -- the changes in biomass of populations through time -- to be represented and explained by these isocline systems? When the biomass of a predator, C, and its prey, H, at each point in time are plotted on a phase plane, a trajectory of biomasses is generated.

If the levels of external environmental variables I and E were fixed, a trajectory of biomasses on the C-H phase plane would converge upon the equilibrium point at the intersection of the predator and prey isoclines parameterized by these particular levels of I and E (Booty and Warren, MS). Environmental variables such as I and E are rarely if ever fixed and for each possible pair of values of I and E, a distinct pair of isoclines and a particular equilibrium point at their intersection are defined. If I and E are continually changing, the trajectory of biomasses of C and H are conceptualized as being in constant pursuit of an ever-shifting equilibrium point. By coupling the dynamics of carnivore C, the fish population, to the dynamics of its prey, herbivore H, and thus indirectly to the

dynamics of other populations in the community, the generality of the explanation of changes in fish population abundance has been increased. Furthermore, the abundance of carnivore C and, indeed, the abundance of all populations in the community are related to rate of light input and level of fishing effort. These relationships have been represented as isocline systems on phase planes (Figure 2). These isocline systems and the response functions from which they are deduced are the time-invariant explanation of trajectories of biomasses of the interacting populations.

The influence of different levels of fishing effort and different rates of light input on the system-determined equilibrium recruitment, production, and yield curves of carnivore C, the fish population, can now be examined (Figure 7). These curves are derived in a manner similar to that used to derive the system-determined herbivore recruitment and production curves: that is, from the density-dependent relationships between carnivore and herbivore biomass, defined by the prey isoclines on the C-H phase plane (Figure 2C), and from carnivore relative recruitment and growth rate response functions (Figure 6). Increases in light input rate on the C-H phase plane in Figure 2C shift the prey isocline to the right. This leads to progressively higher curves of carnivore recruitment, production and yield as shown in Figure 7. An infinite family of prey isoclines and thus equilibrium recruitment, production

Figure 7. System-determined carnivore equilibrium recruitment, production, and yield curves. For a given rate of light input on the C-H phase plane, each level of fishing effort generates a particular equilibrium carnivore and herbivore biomass. At each level of fishing effort, carnivore recruitment rate can be determined as the product of carnivore relative recruitment rate and biomass, and carnivore production rate as the product of carnivore relative growth rate and biomass (Figure 6). For a given rate of light input, the yield curves are constructed by solving $dY/dt = qEC$ for each level of fishing effort, E , and corresponding equilibrium carnivore biomass, C , generated by that level of fishing effort. The catchability coefficient, q , is fixed at 0.2. Each rate of light input generates and so identifies a unique prey isocline on the C-H phase plane and, thus, unique carnivore equilibrium recruitment, production, and yield curves.

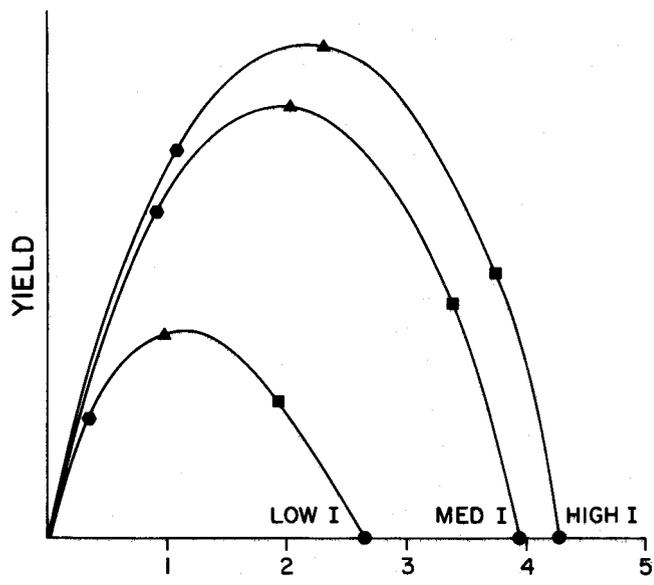
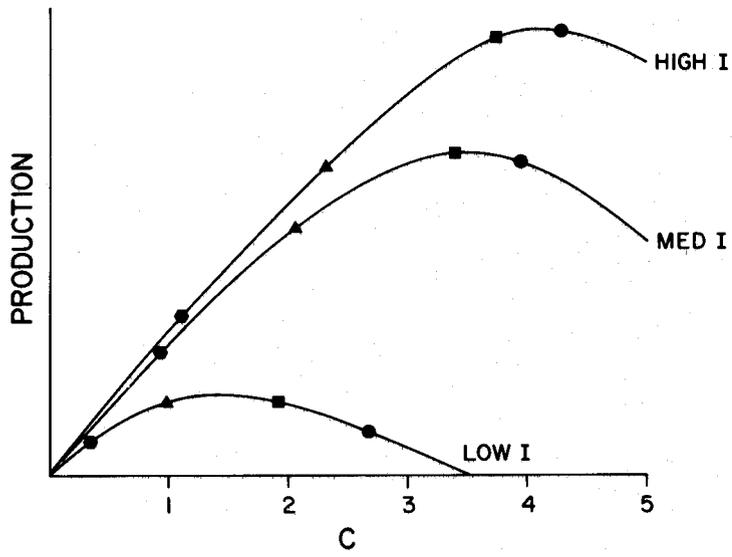
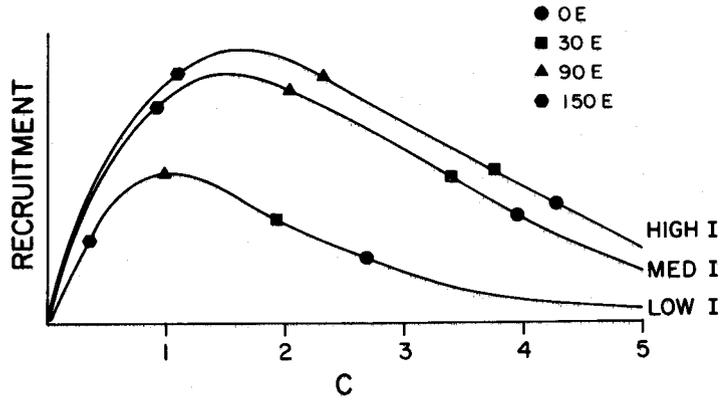


Figure 7

and yield curves exist, in an abstract sense, each generated by some particular rate of light input.

At a given rate of light input, progressively higher levels of fishing effort lead to lower equilibrium carnivore biomasses and higher equilibrium herbivore biomasses. Thus, increasing fishing effort shifts the equilibrium point downward on the prey isocline (Figure 2C) and to the left, toward the origin, along the curves of recruitment, production, and yield (Figure 7). An exploited carnivore population will continue to exist so long as the predator isoclines generated by progressively higher levels of fishing effort intersect a prey isocline and thus form an equilibrium point. But if fishing effort were to remain so high or rate of light input so low that predator and prey isoclines did not intersect to form an equilibrium point, the carnivore population could not persist. This is illustrated in Figure 2C, with a dashed prey isocline (corresponding to a very low light input rate) that does not intersect the predator isocline generated by 150 E. The persistence of the carnivore population, then, is dependent not only on the level of fishing effort but also on the rate of light input.

In general, changes in light input rate result in changes in the form and position of the prey isocline and, thus, in the form and magnitude of the curves of carnivore recruitment, production, and yield. Changes in fishing

effort lead to shifts along a prey isocline and, consequently, along the recruitment, production, and yield curves. As light input rate increases, the peaks of these curves occur at progressively higher carnivore biomasses.

The general form of the curves derived here is similar to other theoretically and empirically derived recruitment (Ricker, 1954), production (Warren, 1971), and yield (Schaeffer, 1954, 1957) curves. But fisheries biologists have not often considered in their explanations the possible existence of families of recruitment, production, and yield curves, even though some have emphasized this (Gulland, 1967; Silliman, 1968; Warren, 1971). Each curve in any such family can be generated by a particular rate of light input and by particular levels of other chemical, physical, and biological factors as well. It seems evident, then, that any reasonably adequate explanation of the observed time-variant behavior of fish populations -- their density, recruitment, production, or yield -- must take into account, either empirically or theoretically, not only fishing effort but also other changes in population environment that determine and thus could explain such time-variant behavior.

Representation and Explanation of the Stability of Exploited Fish Populations

Classically, the stability of ecological systems has been defined as the ability of the systems to return to equilibrium after perturbation. Ecologists have realized, however, that interacting populations composing a system may fluctuate considerably in abundance, never reaching equilibrium, and yet be capable of persisting (Lewontin, 1969; Holling, 1973; Murdoch and Oaten, 1975). Viewed in this context, a system of interacting populations whose densities fluctuate widely is often assumed, or defined to be, less stable than a system of populations exhibiting less fluctuation in density. In order to understand the stability of these systems, however, the magnitude of change of environmental factors that might cause such fluctuations in each system must be taken into account.

The stability of a system of interacting populations will be viewed here as its capacity for persistence (Booty and Warren, MS), that is, the range of values of environmental factors under which the system of interacting populations will persist, regardless of the fluctuations in population densities that may result from changes in the values of environmental factors within this range. This view of stability, then, emphasizes the capacity of systems of interacting populations to persist, that is, the domain of all possible population densities under all possible

environmental conditions. This view of stability is similar to Lewontin's (1969) definition of stability and Hollings (1973) definition of resilience.

Capacity is a theoretical concept (Warren, Allen, and Haefner, MS), and it is not possible to fully evaluate empirically or, at present, even theoretically the capacity of a system to persist under all possible environmental conditions. Thus, only a partial evaluation of this capacity for the C-H system (Figure 2) over a range of values of environmental factors I and E will be undertaken here. This partial evaluation of capacity for persistence will be termed the "scope for persistence" of the C-H system.

Scope for persistence of a system can be determined from the phase planes and isocline systems representing the interaction between populations composing the system and environmental variables. To evaluate the scope for persistence of any system, such as the C-H system in Figure 2, the values of I and E at which the system will persist must be determined. For example, if I and E were fixed at med I and OE (Figure 2C), a trajectory of biomasses of C and H will converge upon the equilibrium point at the intersection of the descending prey isocline parameterized by med I and the ascending predator isocline parameterized by OE. At these values of I and E, then, the C-H system can persist. For some values of I and E, predator and prey isoclines do not intersect and an equilibrium point does not

exist. This is illustrated, in Figure 2C, with a dashed prey isocline generated by very low I and the predator isocline generated by 150E. If light input rate were to remain very low and fishing effort remain at 150E, the carnivore population could not persist and the trajectory of biomasses of C and H would converge upon the point at the intersection of the dashed prey isocline and the H axis.

The position and form of the isoclines on the C-H phase plane are dependent upon the magnitude and form of the response functions representing the biological characteristics of the carnivore and herbivore populations (Figures 3 and 5). If one or more of the response functions characterizing these populations were to change, the position and form of the isoclines representing the interaction between these populations and, thus, the scope for persistence of the C-H system would change. Thus, the scopes for persistence and the stability characteristics of interacting populations with different biological characteristics (different kinds of response functions) can begin to be evaluated. To illustrate this, the scope for persistence of the carnivore-herbivore interaction will be examined by utilizing two forms of the carnivore yield response function.

Two possible forms of the yield response function and the isocline systems generated from each of these forms of the response function are shown in Figure 8. The type 1

Figure 8. The effect of two different forms of the yield response function on the scope for persistence of a carnivore-herbivore system. Carnivores C and C_1 possess the same recruitment, production, and nonpredatory loss response functions. Carnivore C has a type 1 yield response function and carnivore C_1 a type 2 yield response function. Herbivore H has the same response functions in both carnivore-herbivore interactions and, thus, the position and form of the prey isoclines on the C-H phase plane are identical to those on the C_1 -H phase plane. The range of values of I and E over which each carnivore-herbivore system can persist -- the scope for persistence of each system -- is represented on the isopleth diagrams. Isopleths, or contours of equal equilibrium carnivore biomass and equal equilibrium herbivore biomass, are determined from the C_1 -H and C-H phase planes. The area of the isopleth diagram below the OC isopleth for the C-H system, and the area below the OC_1 isopleth for the C_1 -H system represent combinations of I and E at which the respective systems cannot persist. The area above the OC isopleth for the C-H system, and the area above the OC_1 isopleth for the C_1 -H system represent the scope for persistence of the respective systems, that is, the range of values of I and E over which the systems can persist. The C_1 -H system has a greater scope for persistence than the C-H system.

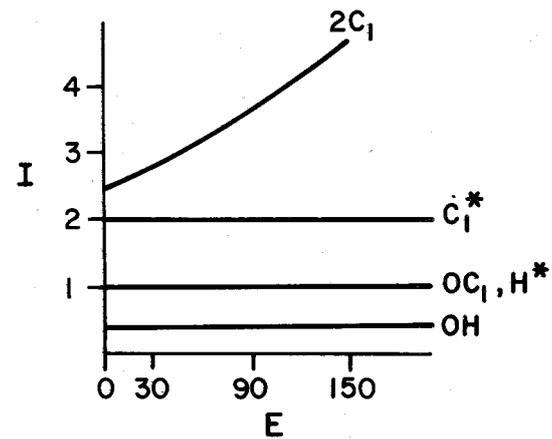
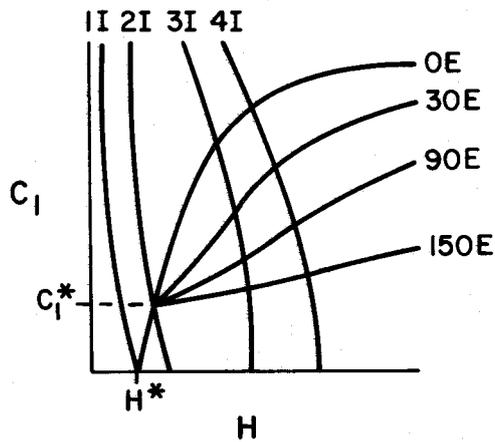
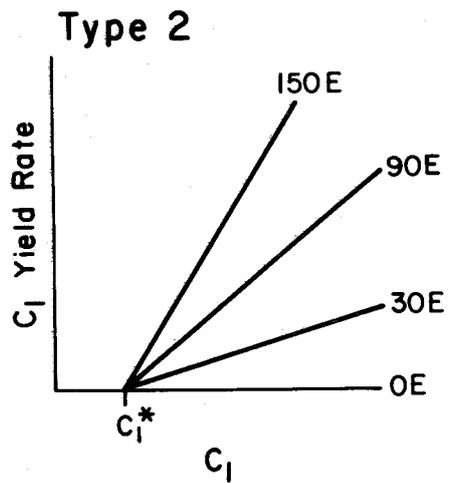
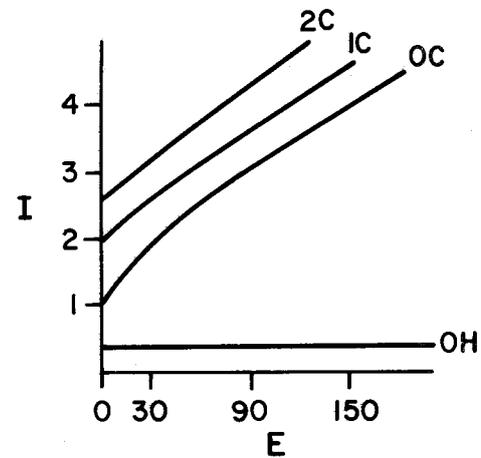
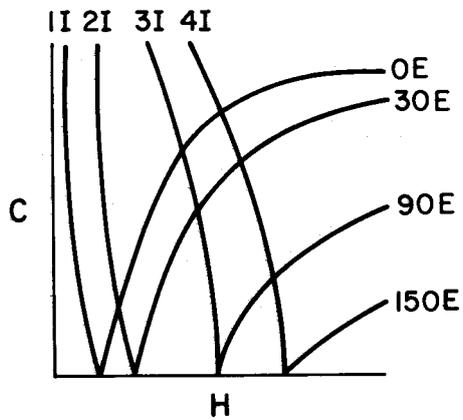
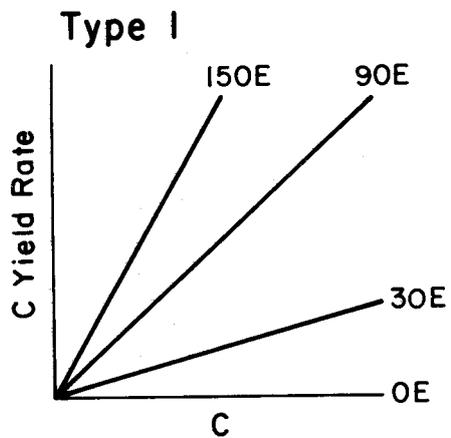


Figure 8

response function is similar to the response function shown in Figure 5E. The type 2 response function could result if the carnivore had a refuge that allowed a constant biomass of carnivore to escape exploitation. In employing the concept of refuge, the type 2 yield response function is similar to the predation loss response function of herbivore H (Figure 3E).

As E increases, the predator isoclines generated with a type 1 response function are shifted downward and to the right, thus intersecting the H axis at progressively higher H biomasses. The predator isoclines generated with a type 2 response function are shifted downward as E increases, but they intersect the predator isocline generated by OE at carnivore biomass C_1^* .

Now, for response function type 1, if E were fixed at $90E$, the C - H system would persist only at values of I greater than $3I$. At values of I less than or equal to $3I$, prey isoclines do not intersect the predator isocline parameterized by $90E$ and carnivore C would not persist. However, for response function type 2, at $90E$, the C_1 - H system is capable of persisting at all values of I greater than $1I$, but cannot persist for values of I less than or equal to $1I$. In general, the C_1 - H system can persist over a greater range of values of I than the C - H system for all values of E greater than zero.

Similarly, if I were fixed at $3I$, the C-H system would persist at values of E less than $90E$, while the C_1 -H system would persist at all values of E . Thus, in the C_1 -H system, fishing effort alone cannot drive the carnivore population to extinction. But, if the value of I were less than or equal to $1I$, the carnivore population in the C_1 -H system could not persist at any value of E .

In general, the C_1 -H system has a greater scope for persistence than the C-H system (Figure 8), that is, it is capable of persisting over a greater range of values of environmental factors I and E .

The stability of exploited fish populations has not been extensively examined by fisheries biologists. The view of stability adopted here provides at least some understanding of how the persistence of exploited fish populations is affected by interaction of environmental factors and fishing effort. Furthermore, this approach provides a rationale for evaluation of the stability characteristics of population response functions, including yield response functions, that may result from different fishing strategies.

Representation and Explanation of the Time-Variant Behavior of Exploited Fish Populations under Periodic Exploitation

Fishing seasons have been established in many fisheries to prevent over-exploitation of fish populations. Many fish populations are therefore subjected to periodic, rather than continuous, exploitation. The effect of periodic

exploitation on the abundance and yield of fish populations can be examined within the framework of this theoretical approach.

The trajectories of biomasses of C and H generated by different fishing regimes (season lengths) are shown in Figure 9. Each trajectory is composed of a series of trajectory vectors. Each trajectory vector represents the change in carnivore and herbivore biomass over one unit of time, and it is constructed by summing component vectors representing change in herbivore biomass and change in carnivore biomass. Booty and Warren (MS) have shown that magnitude (length) and direction of the component vectors are determined from the set of curves representing total gain and loss rates of the herbivore (Figure 3A) and carnivore (Figure 5A).

The trajectories shown in Figure 9 were determined in the following manner. Rate of light input was fixed at med I and a particular fishing regime was specified. The fishing regime used to generate the solid trajectory in Figure 9 will be used as an example. Under this fishing regime, carnivore C was exploited for three successive units of time at 150E and not exploited for nine successive units of time (OE). Initial biomasses of 1C and 1H were arbitrarily chosen as a starting point on the phase plane. At carnivore biomass 1C, the magnitude and direction of the component vector representing change in carnivore biomass over

Figure 9. Steady-state trajectories of biomasses of C and H generated by different fishing regimes. Light input rate was fixed at med I. Each trajectory vector represents the change in biomass of C and H over one unit of time. The solid trajectory was generated when C was exploited for three successive units of time at 150E and not exploited (OE) for nine successive units of time. The dashed trajectory was generated when C was exploited for six successive units of time at 150E and not exploited six successive units of time. The dotted trajectory was generated when C was exploited for nine successive units of time at 150E and not exploited for three successive units of time. The trajectories were determined from the carnivore C and herbivore H gain and loss response functions (Figures 3 and 5).

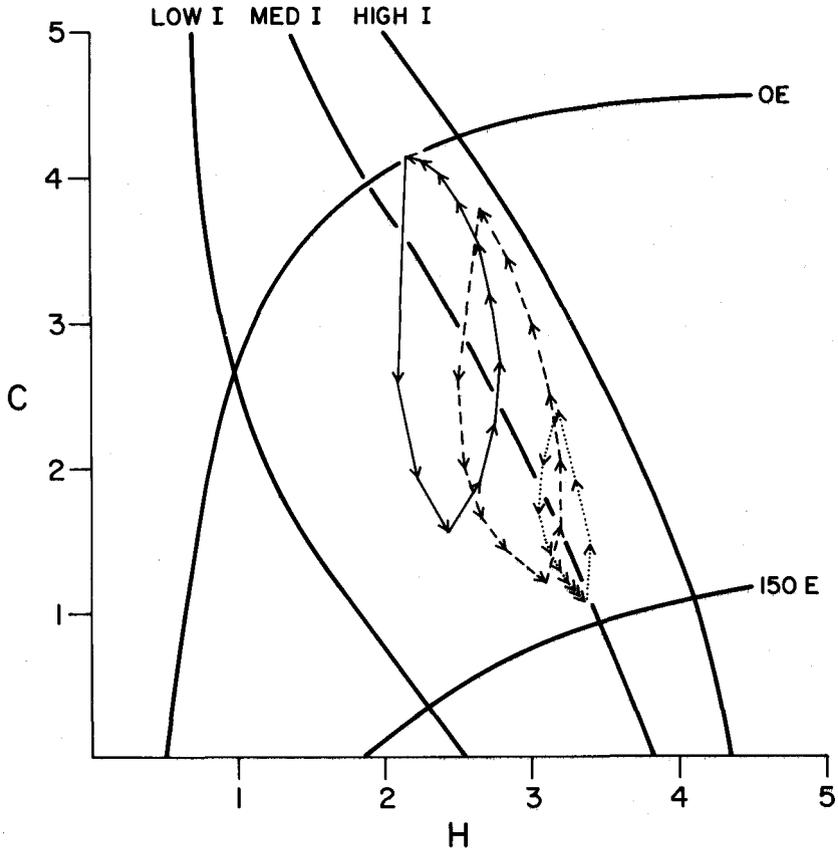


Figure 9

the first unit of time is given by the difference between the carnivore's gain curve at 1H and loss curve at 150E (Figure 5A). Similarly, the magnitude and direction of the component vector representing change in herbivore biomass over the first unit of time is given by the difference between the herbivore's gain curve at med I and loss curve at 1C (Figure 3A). The component vectors were summed to generate a trajectory vector representing the change in biomass of both herbivore and carnivore over the first unit of time.

The trajectory vectors representing the change in carnivore and herbivore biomass over each of the next two units of time were also determined in this manner. Then, after being exploited for three units of time, the carnivore was not exploited over the next nine time units. The carnivore's component vector for each of the nine time units were determined utilizing the loss curve at OE (Figure 5A). The process of exploitation of the carnivore for three successive units of time and cessation of exploitation for nine successive units of time was continued until a regularly repeating trajectory (solid trajectory in Figure 9) was established.

Such a trajectory is a steady-state trajectory. If I is fixed at med I and the fishing regime specified as exploitation of C for three successive units of time and cessation of exploitation for nine successive units of time, trajectories begun at each possible biomass of C and H (at

any point on the phase plane) will eventually converge upon the solid trajectory shown in Figure 9. Now if I or the fishing regime were to change, this steady-state trajectory would be perturbed and the trajectory would begin to follow a new path determined by the new value of I and the new fishing regime. But if I were to later return to med I and C were once again exploited for three units of time and not exploited for nine units of time (the original fishing regime), the trajectory would return to the path described by the solid trajectory in Figure 9.

The trajectories shown in Figure 9 are composed of a descending, exploitation segment and an ascending, recovery segment. The descending segment of the trajectory describes the response of the C-H system to exploitation at 150E, and tracks toward the equilibrium point at the intersection of the prey isocline parameterized by med I and the predator isocline parameterized by 150E. The ascending segment of the trajectory describes the response of the C-H system to cessation of exploitation and tracks toward the equilibrium point at the intersection of the prey isocline parameterized by med I and the predator isocline parameterized by OE. As the length of the fishing season (the number of units of time the carnivore is exploited) is increased, the position of the trajectory is shifted downward along the med I prey isocline.

For each fishing regime, carnivore yield over a particular unit of time, t , was determined from

$$Y_t = qEC_t$$

where Y_t is the yield obtained over time unit t , q is the catchability coefficient, fixed at 0.2, E is fishing effort, and C_t is carnivore biomass at the beginning of time unit t . Total carnivore yield obtained under a particular fishing regime is simply the sum of the Y_t .

Total yield for each fishing regime, including equilibrium yield under continuous exploitation (exploitation for 12 units of time) is presented in Table 1.

Table 1. Total carnivore yield obtained under each fishing regime.

	Number of units of time that the carnivore is exploited			
	12	9	6	3
Yield (units of biomass)	16.6	20.6	19.1	13

Cessation of exploitation for a period of time allows carnivore biomass to increase (the recovery segment of the trajectory). Thus fishing effort can operate on a larger carnivore biomass during the fishing season and, if the season is long enough, the yield obtained by periodic exploitation can be greater than the yield obtained by continuous exploitation (Table 1).

Ecologists have sometimes viewed periodic oscillations in abundance of natural populations like those shown in Figure 9 as stable limit cycles. May (1972), Gilpin (1972), and Tanner (1975) have shown that stable limit cycles can be generated by non-linear mathematical models of predator-prey interactions. A trajectory of densities of predator and prey describes a stable limit cycle when the trajectory continually follows the same path around an equilibrium point but never converges upon the equilibrium point (Gilpin, 1972; Tanner, 1975). If such a trajectory is perturbed, it tends to return to its stable limit cycle. To this extent, then, the trajectories shown in Figure 9 are similar to stable cycles. Limit cycle behavior can be generated with predator-prey models when, for example, the intrinsic growth rate of the prey population is greater than that of its predator (Tanner, 1975). May (1972) suggests that stable limit cycles can be invoked as an explanation, or more precisely a description, of the periodic cycling of natural populations such as lemmings, and lynx and hare populations.

Although the trajectories shown in Figure 9 are similar to stable limit cycles, they have been generated by periodic fluctuations of an environmental factor, fishing effort. If fishing effort and rate of light input were held constant, the trajectory would converge upon the

equilibrium point at the intersection of the isoclines parameterized by the particular values of I and E.

The effects of changes in environmental factors on the time-variant behavior of interacting populations is usually not explicitly considered in models of predator-prey systems. This is particularly true for such environmental factors as light and plant nutrients which may directly affect lower trophic levels and only indirectly lead to periodic fluctuations on higher trophic levels. Caution should therefore be exercised when invoking mathematical models that generate stable limit cycles as explanations of periodic fluctuation in the densities of natural populations.

REPRESENTATION AND EXPLANATION OF THE DYNAMICS
OF INTERSPECIFIC COMPETITION BETWEEN
EXPLOITED FISH POPULATIONS

Any general theory of the dynamics of exploited fish populations will need to be capable of representing and explaining the important kinds of interactions between natural populations. In the previous sections, the relationships between populations in a simple community were represented as a sequence of predator-prey interactions. To increase the dimensional adequacy of this theory of exploitation, interspecific competition between exploited fish populations must be examined.

The classical Lotka-Volterra competition equations, and the competition phase plane derived from them, do not explicitly consider the dynamics of the prey of the competing species, predation, or any other form of loss accrued by the competing species, or the effects of environmental factors on the outcome of competition. Furthermore, explicit biological characterization of the competitors is not possible. Many of the shortcomings of these classical equations can be overcome with the theoretical approach presented here.

Carnivore C_2 can be introduced as a competitor of C in the simple community presented in Figure 1 (interactions 1, 2, 3, 4). Carnivore populations C and C_2 are different species that compete for a common food resource, herbivore

H, and are harvested by a common fishery E. Being different species, C and C_2 have different biological characteristics, and important biological differences between these species can be represented as differences in their respective gain and loss response functions. The forms and magnitudes of the response functions determine the forms and positions of isoclines on phase planes and thus determine the outcome of the competitive interactions between species. Furthermore, the dynamics of the competing species can be coupled to level of fishing effort and rate of light input and, thus, to the dynamics of all populations in the community. In this way, the impact of interspecific competition on the recruitment, production, and yield of the carnivore populations can be deduced.

The phase planes and isocline systems representing the utilization of herbivore H by C and C_2 are shown in Figure 10. On each phase plane, biomasses of the competitor, in addition to light input rates, now parameterize prey isoclines. Thus, in this case, increasing the dimensional adequacy of the explanation of community dynamics and exploitation by including interspecific competition logically has led to the introduction of additional families of prey isoclines (Booty and Warren, MS).

The positions and forms of the predator and prey isoclines on the C-H and C_2 -H phase planes and the outcome of the competitive interaction between carnivores are

Figure 10. Phase plane representation of competition between two carnivore populations, C and C_2 , for a common food resource, herbivore H . C and C_2 are harvested by a common fishery E , but differ in their biological characteristics as reflected in their respective gain and loss response functions and, thus, in the form and position of their predator isoclines. The predation loss responses of herbivore H must now include a set of loss curves due to predation by C_2 as well as those already presented for C (Figure 3E). Consequently, in addition to light input rate I , C_2 biomasses parameterize prey isoclines on the C - H phase plane and C biomasses parameterize prey isoclines on the C_2 - H phase plane. Thus, on each phase plane at a given rate of light input and level of fishing effort, a family of possible equilibrium points exist. The trajectories of biomasses on the C - H and C_2 - H phase planes will finally converge upon only one of these possible equilibrium points. This equilibrium point is determined, for each rate of light input and level of fishing effort, from the competition phase plane (Figure 11). The location of this equilibrium point on the C - H and C_2 - H phase planes at high I , 30E (open circle); low I , 30E (solid circle); high I , 90E (open square); and low I , 90E (solid square) is indicated. At each rate of light input and level of fishing effort, the remaining equilibrium points generated by the instantaneously changing C and C_2 biomasses are merely momentary goals of the trajectory on its path toward equilibrium.

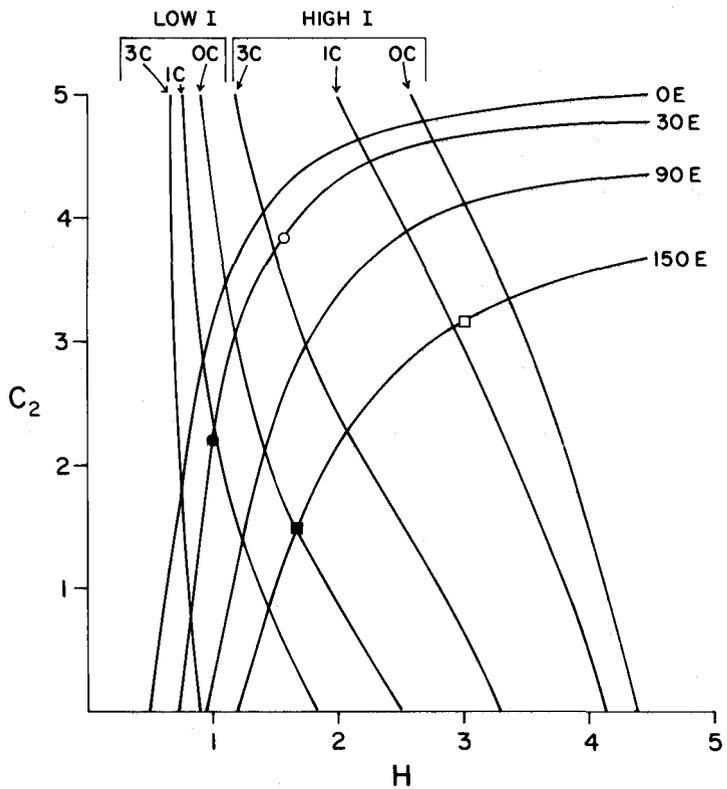
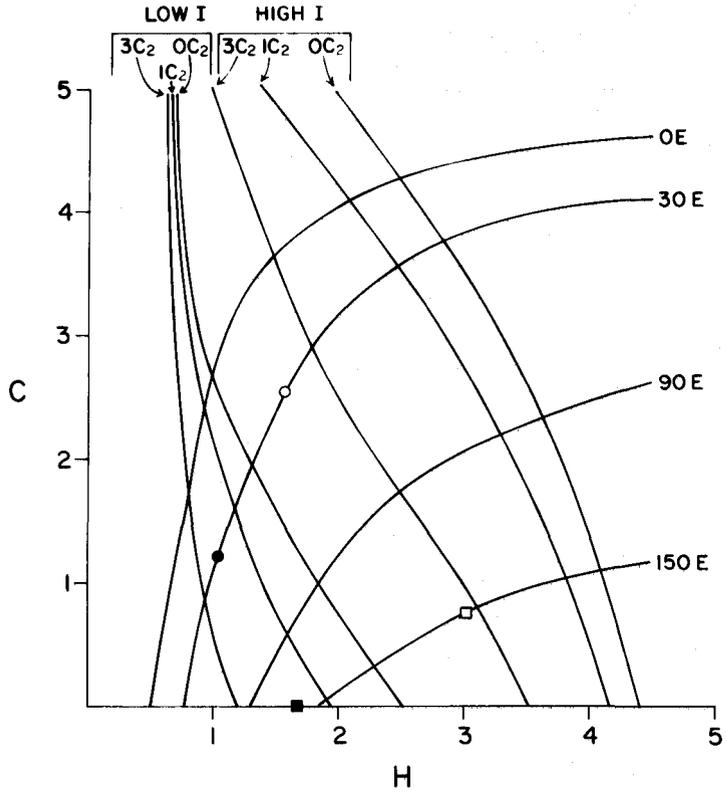


Figure 10

determined by the biological characteristics of the competing carnivore populations, as reflected in their respective gain and loss response functions. The response function curves characterizing C have already been presented (Figures 5 and 6). Here only the differences between these curves and those of carnivore C_2 that lead to differences in the isoclines on the C-H and C_2 -H phase planes will be described.

In general, losses of herbivore H to predation by C_2 are less than losses to C. As a result, the prey isoclines on the C_2 -H phase plane, reflecting the density-dependent relationship between carnivore and herbivore biomass, are steeper than the prey isoclines on the C-H phase plane. But, even though C_2 consumes less H, it utilizes consumed H more efficiently for reproduction and growth than does C. Thus, the recruitment and production response curves of C_2 and its predator isoclines at each level of fishing effort are of greater magnitude than those of C. This is most evident in the predator isoclines generated at OE. It is also true for other levels of fishing effort but here the effect is more complex since C_2 has been designed to be less vulnerable to fishing effort than C. Clearly, then, based on its biological characteristics, C_2 should be at a competitive advantage.

The outcome of the competitive interaction between C and C_2 can now be determined. Examination of each of the

phase planes shown in Figure 10 reveals that a family of possible equilibrium points exists at each rate of light input and level of fishing effort. On each phase plane, an increase in the biomass of the competitor parameterizing the prey isoclines causes the prey isoclines to shift to the left and leads to a reduction in equilibrium biomass of the other competitor and in equilibrium biomass of the prey, herbivore H.

If rate of light input and level of fishing effort were fixed, the trajectory of biomasses on each of the C-H and C_2 -H phase planes would converge upon only one point in the family of possible equilibrium points. Equilibrium biomasses of C and C_2 , for given light input rates I and levels of fishing effort E, can be determined from the isocline systems on the competition phase plane shown in Figure 11. At each rate of light input and level of fishing effort, equilibrium C, C_2 , and H biomasses are defined by single co-relative equilibrium points on the C-H, C_2 -H, and C- C_2 phase planes. The co-relative equilibrium points defining the final equilibrium biomasses of C, C_2 and H at low I and 30E, high I and 30E, low I and 90E, and high I and 90E are indicated on the C-H, C_2 H, and C- C_2 phase planes in Figures 10 and 11. At each rate of light input and level of fishing effort, the three single co-equilibrium points are simply different two-dimensional projections of the same three-dimensional point in phase space

Figure 11. Competition phase plane used to determine equilibrium carnivore biomasses that result from the competitive interaction of carnivore populations C and C₂ at each rate of light input and level of fishing effort. Competition isoclines for C (dashed lines) are derived from the C-H phase plane (Figure 10) and define the set of biomasses of C and C₂ where $dC/dt = 0$. Competition isoclines for C₂ (solid lines) are derived from the C₂-H phase plane and define the set of biomasses of C and C₂ where $dC_2/dt = 0$. For a given light input rate and level of fishing effort on the C-H phase plane, the carnivore C competition isocline is constructed by determining, from the intersections of the prey isoclines parameterized by C₂ biomasses with the predator isocline, the equilibrium C biomasses generated by particular C₂ biomasses. C₂ competition isoclines are derived in the same manner from the C₂-H phase plane. The intersection of C and C₂ competition isoclines for each rate of light input and level of fishing effort define the equilibrium point upon which the trajectory of biomasses of C and C₂ will finally converge. Competition isoclines generated by two light input rates, low I and med I, and two levels of fishing effort, 30E and 150E, are shown on the competition phase plane. These equilibrium points are also shown, with the corresponding symbols, on the C-H and C₂-H phase planes. Competition isoclines generated at low I and 150E do not intersect and a common equilibrium point does not exist. In this case, the trajectory of biomasses approaches the point of intersection of the C₂ competition isocline with the C₂ coordinate axis, and the C population becomes extinct.

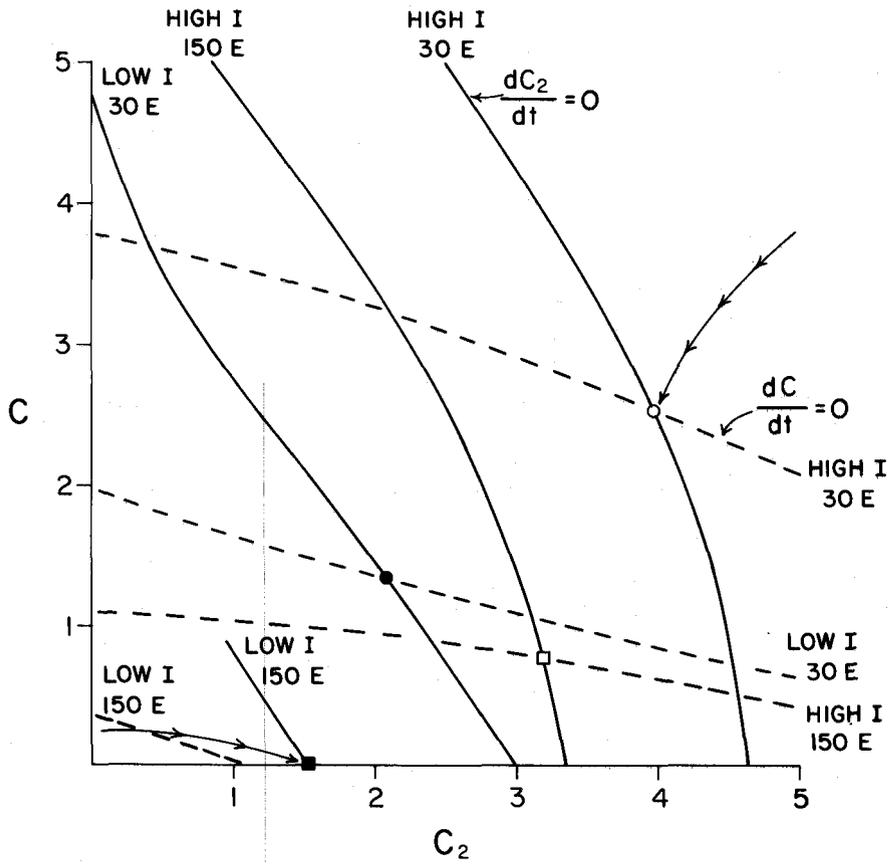


Figure 11

(Booty and Warren, MS). If, as the trajectories approached this equilibrium point, rate of light input or level of fishing effort were to change, the trajectories would progress toward a new equilibrium point defining different equilibrium biomasses of C , C_2 , and H .

At each light input rate and level of fishing effort, the equilibrium biomasses of C , C_2 , and H , determined from the competition phase plane, represent the outcome of the competitive interaction between carnivore populations. Co-existing competitors C and C_2 and their prey, H , maintain equilibrium biomasses that are lower than the biomasses they would maintain in the absence of competition between C and C_2 . For example, at high I and 30E on the C - H phase plane (Figure 10), the equilibrium biomasses maintained by C and H as a result of competition (open circle) are lower than the equilibrium biomasses C and H would maintain in the absence of the competitor C_2 , that is, at OC_2 . Similarly, at high I and 30E on the C - H_2 phase plane, the equilibrium biomasses maintained by C_2 and H as a result of the competitive interaction (open circle) are also lower than the equilibrium biomasses C_2 and H would maintain at OC .

At some rates of light input and levels of fishing effort, the competitors C and C_2 cannot co-exist: one of the populations is driven to extinction. For example carnivore C is capable of persisting at low I and 150E

if it does not compete with carnivore C_2 (Figure 2C, and at OC_2 on the C-H phase plane in Figure 10). Competition with C_2 for the common food resource H, however, leads to the extinction of C at low I and 150E, as shown in Figure 11 where the competition isoclines for these levels of I and E do not intersect to form an equilibrium point. Thus, the introduction of a competitor, carnivore C_2 , has reduced the scope for persistence or stability of the C-H system. That is, by shifting the prey isoclines at each light input rate to the left on the C-H phase plane, competition has reduced the range of values of I and E over which carnivore C can persist. Stated somewhat differently, the C-H system has a greater scope for persistence than the C- C_2 -H system.

Carnivore C_2 , the superior competitor based on its biological characteristics, maintains a greater equilibrium biomass than C at each light input rate and level of fishing effort (Figure 11). It must be emphasized, however, that the outcome of the competitive interaction is dependent upon the biological characteristics of the competing species and upon the rate of light input and level of fishing effort. If the competitor C_2 had some biological characteristics considered inferior to those of C, such as greater nonpredation losses or greater vulnerability to fishing effort, the competitive outcomes would undoubtedly have been different. But, by representing these biological

characteristics as gain and loss response functions, the competitive outcomes can be deduced. The introduction of greater dimensionality, such as plant nutrient concentration or competition on other trophic levels, would further alter the outcomes of competition between the carnivores, but these effects could also be deduced.

In the previous section, environmental factors such as rate of light input were shown to affect the magnitude and form of the system-determined equilibrium recruitment, production, and yield curves of carnivore C. The effect of competition on the magnitude and form of these curves can now be examined. At a given rate of light input, the populations C and H maintain lower equilibrium biomasses at each level of fishing effort in the presence of the competitor C_2 than they would in the absence of competition. In effect, then, competition for a common food resource, herbivore H, alters the density-dependent relationships between the biomasses of C and H. This can be illustrated, on the C-H phase plane (Figure 10) at high I, by comparing the position of the prey isocline parameterized by OC_2 to the position of a prey isocline drawn through the open symbols and, therefore, representing the equilibrium density-dependent relationship between C and H that results from competition.

Recruitment and production curves are derived by coupling the density-dependent relationship generated at

each light input rate with curves relating C relative recruitment and relative growth rates to H biomass (Figures 4 and 6). Competition, by altering the density-dependent relationships, lowers the recruitment and production curves of carnivore C (Figure 12). Brocksen, Davis, and Warren (1968) were empirically able to demonstrate similar effects of competition on the density-dependent interactions between competing species and their prey and on the production curves of these species in laboratory stream communities. Since competition reduces the equilibrium C biomass generated by each level of fishing effort, the yield of C obtained at a given level of fishing effort and the magnitude of the equilibrium yield curves are also reduced (Figure 12).

The effects of carnivore competition are most clearly manifested on the C-H and C_2 -H phase planes, and so it is here that the discussion of competition has centered. But, because of the causal relationships between all populations in the community, the introduction of a competitor at the carnivore level affects not only carnivore and herbivore dynamics but the dynamics of all other populations as well. Competition for a common food resource has been dealt with exclusively here, but by appropriate parameterization of the gain and loss response functions, the effects of competition for nonfood resources such as spawning space could also be deduced (Booty and Warren, MS). Moreover,

Figure 12. The influence of competition on the magnitude and form of the system-determined C equilibrium recruitment, production and yield curves at each rate of light input. System-determined recruitment and production curves are derived from the density-dependent relationship between equilibrium C and H biomass at each rate of light input and from curves relating C relative recruitment and relative growth rates to herbivore biomass. The curves determined in the absence of the competitor C_2 (solid curves) are identical to those derived in Figure 7. At a given rate of light input, the presence of the competitor C_2 alters the density-dependent relationship between the equilibrium biomasses of C and H (Figure 10) and, thus, lowers the equilibrium recruitment, production, and yield curves of C (dashed curves).

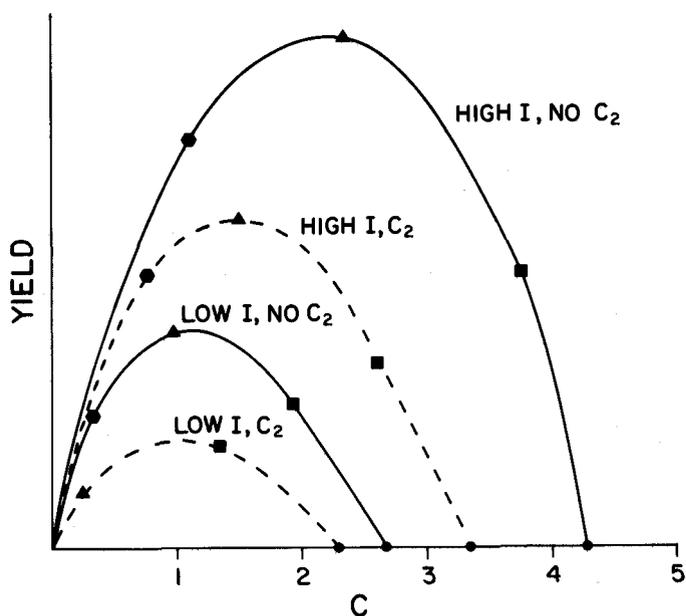
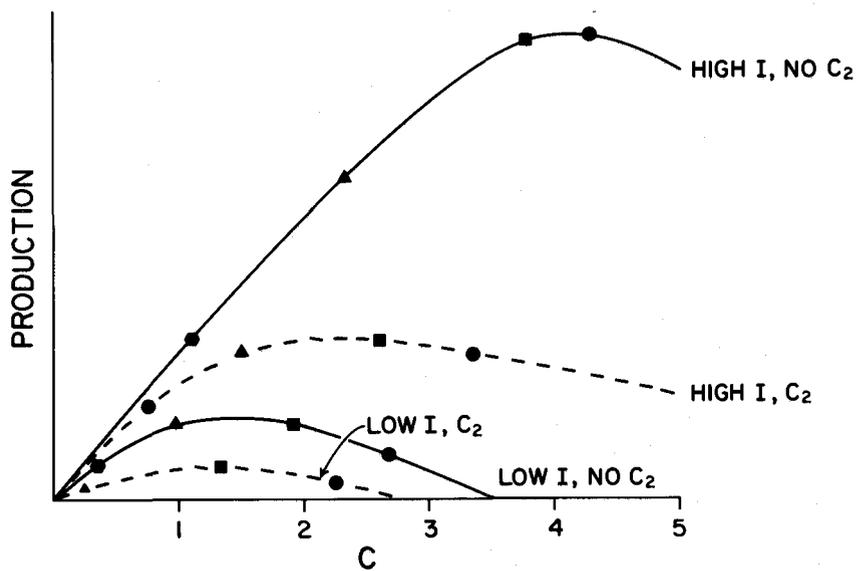
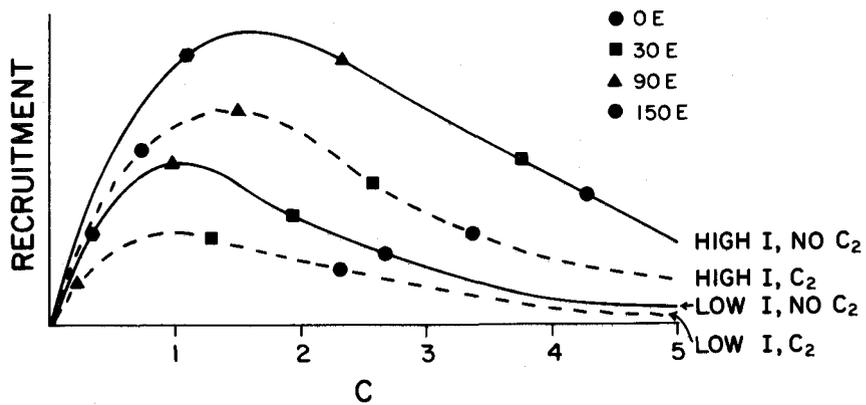


Figure 12

other population interactions such as mutualism or commensalism could have been examined in much the same way as was competition.

Carnivore C and carnivore C_2 are exploited by a common fishery. Although much of the discussion has been concerned with the effects of competition on carnivore C, the interactive performances of both C and C_2 are of interest in understanding multispecies fisheries. The equilibrium yield obtained from each of these populations and the total equilibrium yield ($C + C_2$) to the fishery at two rates of light input are shown in Figure 13. The differences in magnitude and form of the yield curves of these species result from differences in the species' biological characteristics. If C and C_2 were not competitors and were exploited by a common fishery, the equilibrium yield curve of each species and the curve representing total equilibrium yield would be increased in magnitude. At low I, maximum sustained yield to the fishery (a common management objective) is obtained at 150E. But, because C and C_2 are competitors with different biological characteristics, carnivore C, the inferior competitor, will be driven to extinction at this level of fishing effort and rate of light input.

The dynamics of competing (Beverton and Holt, 1957; Larkin, 1963) and non-competing (Paulik, Hourston, and Larkin, 1967; Hilborn, 1976) fish population exposed to exploitation has been examined, primarily with the Lotka-

Figure 13. Equilibrium yield curves of carnivore C and carnivore C₂, and the curve representing total equilibrium yield (the sum of the yields of C and C₂) to the fishery is shown for two rates of light input. The C equilibrium yield curve at each light input rate was derived by solving $dY/dt = qEC$ for each level of fishing effort E and the corresponding equilibrium C biomass generated by that level of fishing effort (Figures 10, 11). The catchability coefficient q, for C, was fixed at 0.2. The C₂ equilibrium yield curve was derived in the same manner. Since C₂ was less vulnerable to fishing effort than C, the catchability coefficient for C₂ was fixed at 0.1.

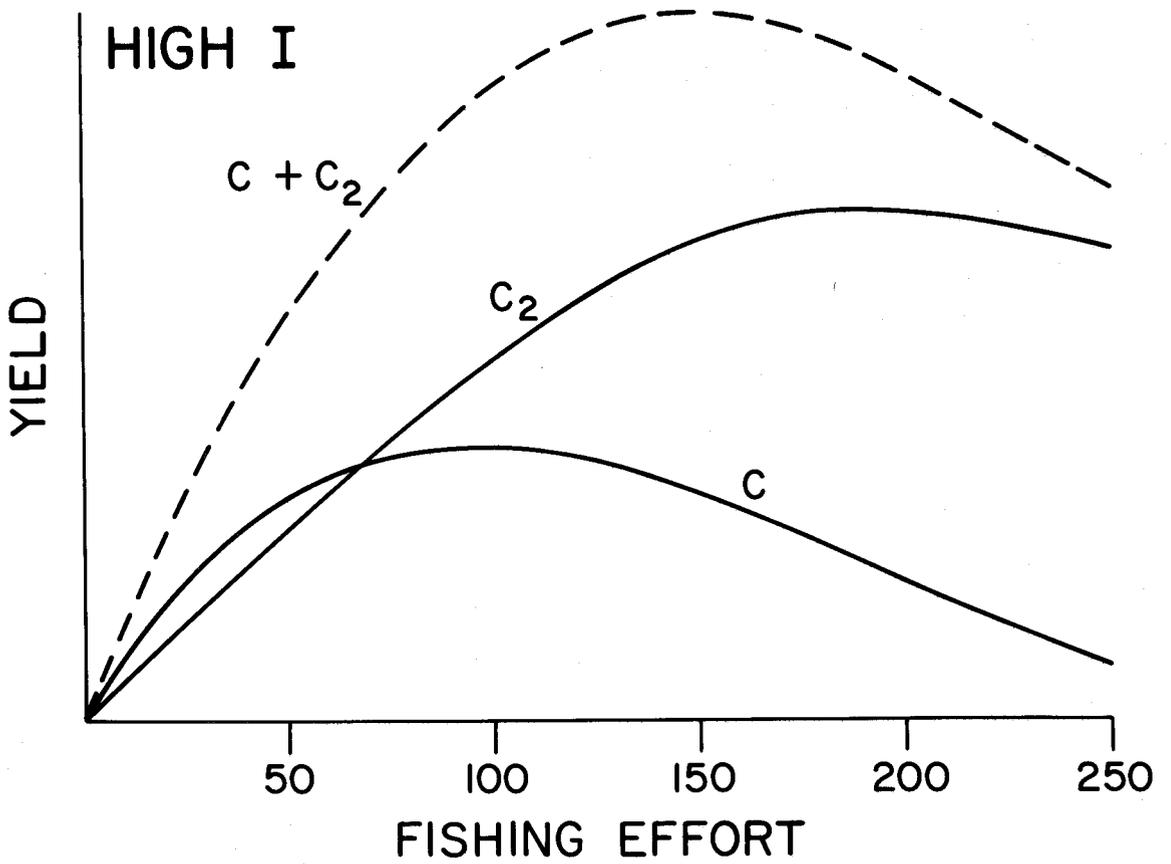
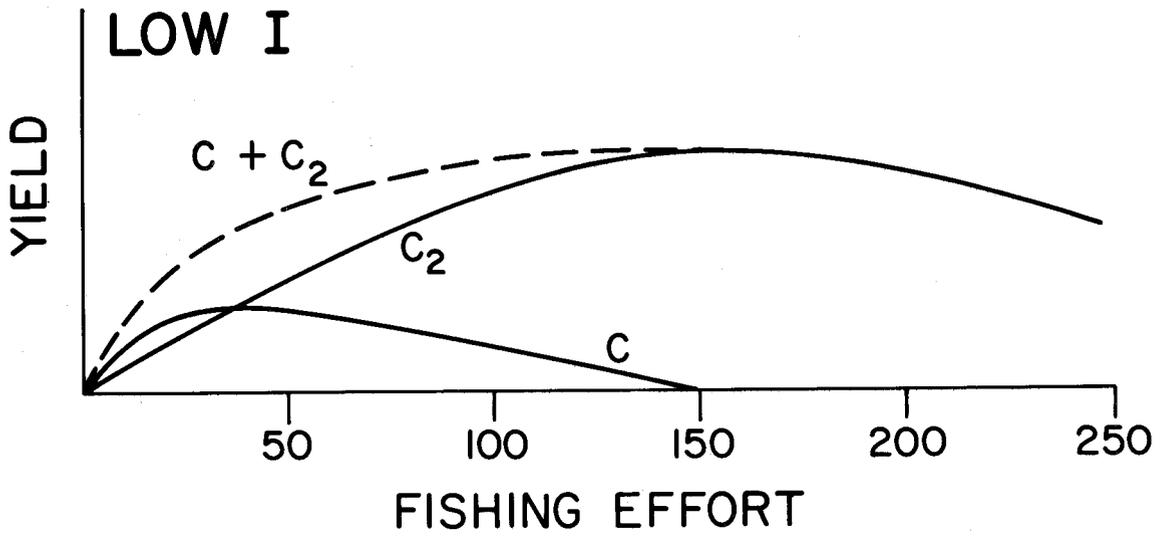


Figure 13

Volterra competition equations, Ricker stock-recruitment equations, and stochastic dynamic programming. These approaches have been useful in developing optimal harvest strategies for multi-species fisheries. But fisheries science still appears to lack a universal theoretical view of exploitation of multispecies fisheries. Such a universal view must couple the dynamics of competing and non-competing fish populations to the dynamics of the biological community and to environmental factors. The theory of exploitation being developed here seems, at least, to have the proper perspective and direction.

REPRESENTATION AND EXPLANATION OF THE DYNAMICS OF
AN EXPLOITED FISH POPULATION FEEDING
ON TWO PREY SPECIES

Ecologists have developed several kinds of models that explicate the optimal feeding strategy of predators foraging on several prey species (Emlen, 1966, 1968; MacArthur and Pianka, 1966; Schoener, 1971; Rapport, 1971; Pulliam, 1974; Katz, 1974; Charnov, 1976). These models employ optimization theory to determine the kinds and quantities of prey a predator should consume to maximize its energy intake per unit of time or minimize its total time spent feeding.

Since these models do not couple particular feeding strategies to the dynamics of predator and prey populations, to the dynamics of other populations in the community, or explicitly to environmental factors, the outcome of these feeding strategies on community dynamics and stability has yet to be determined. Representation and explanation of the consequences of a particular feeding strategy on community dynamics gives context and meaning to that feeding strategy. To the extent that such feeding strategies can be adequately represented by population response functions, this articulation can be accomplished with the theoretical approach presented here. In addition, the recruitment, production, and yield of exploited fish populations feeding on more than one prey species can be examined.

A particular feeding strategy for carnivore C, the fish population, foraging on two prey species, herbivore H and herbivore H_2 , was developed (Interactions 3 and 5 in Figure 1). This feeding strategy is represented by the H and H_2 predation loss curves in Figure 14. Carnivore C has a fixed, stereotyped preference for herbivore H and, thus, the consumption of H by C is dependent only upon the biomass of H and the biomass of C (Figure 14A).

The consumption of herbivore H_2 , the nonpreferred prey, is dependent not only upon its biomass and the biomass of carnivore C, but also upon the biomass of the preferred prey, herbivore H (Figure 14B). When the biomass of herbivore H is increased, the predation loss curve of herbivore H_2 is shifted downward and to the right. Thus, if herbivore H biomass is $2H$, herbivore H_2 will not be consumed by carnivore C unless its biomass is greater than $2H_2$.

The carnivore feeding strategy represented in Figure 14 is similar to experimentally determined and theoretically derived predator feeding strategies. Ivlev (1961) found that increasing the density of a preferred prey type (chironomid larvae) of carp, while holding the density of nonpreferred prey types constant, resulted in increased consumption of the preferred prey and reduced consumption of the nonpreferred prey, with some nonpreferred prey types (mollusks) being eliminated from the carp's diet. Furthermore, when the density of the preferred prey was held

Figure 14. The feeding strategy of carnivore C preying upon herbivore H and herbivore H₂ is represented by the predation loss response functions of herbivore H (A) and herbivore H₂ (B) at carnivore biomass l_C . Herbivore H is the preferred prey. Herbivore H₂ is the non-preferred prey. At a particular biomass of herbivore H₂, the rate of consumption of H₂ by C declines as the biomass of H, the preferred prey, increases. These curves represent the rate of consumption of H and H₂ per unit of carnivore biomass, that is, they represent carnivore relative prey consumption rates. The predation loss curves of H and H₂ at carnivore biomasses greater than l_C are simple multiples of these curves.

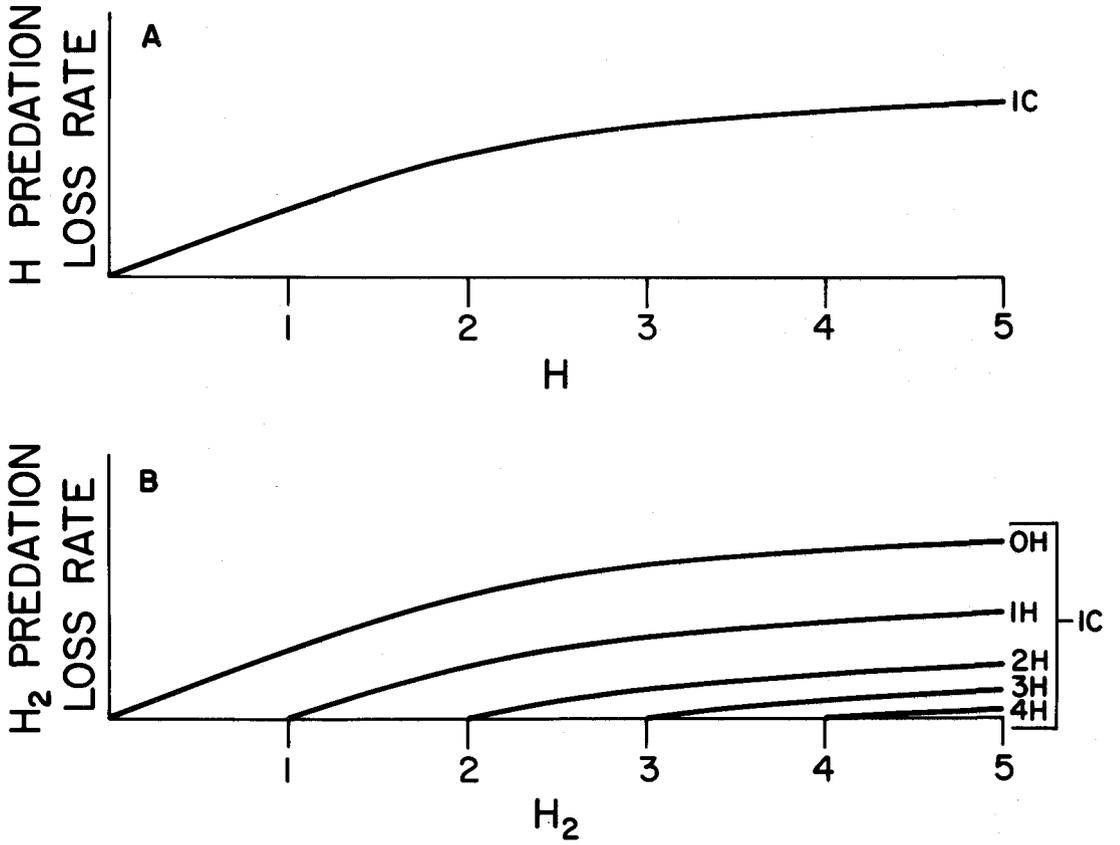


Figure 14

constant and the density of a nonpreferred type was increased, consumption of the nonpreferred prey increased while consumption of the preferred prey remained constant. The optimal foraging model developed by Charnov (1976) also predicts that if the density of a preferred prey increases, the less-preferred prey can be eliminated from the predator's diet.

Other types of feeding strategies can also be represented by the predation loss curves of the prey. An increase or decrease in availability of H or H_2 can be represented by an upward or downward shift in the H predation loss curve or the set of H_2 predation loss curves, as Holling (1959) has shown. Furthermore, changes in predator preference that result from changes in relative abundance or availability of prey types -- "switching" (Murdoch, 1969) -- can also be represented by appropriate parameterization of the predation loss response functions of both H and H_2 .

The phase planes and isocline systems representing the interaction between the carnivore population and its prey, herbivore H and herbivore H_2 , are shown in Figure 15. The position and form of the isoclines on these phase planes are determined by the magnitude and form of the response functions that represent the biological characteristics of the interacting populations, including the feeding strategy represented by the predation loss response functions shown

Figure 15. Phase plane representation of the interaction between carnivore C, an exploited fish population, and its prey species, herbivore H and herbivore H₂. H and H₂ are not competitors. Except for the predation loss response functions, the response functions representing the biological characteristics of H and H₂ are identical to those shown in Figure 3. The predation loss response functions of H and H₂ are given in Figure 14. The predation loss curves used in deducing the prey isoclines on the C-H₂ phase plane include a family of loss curves parameterized by H biomass at each C biomass. Consequently, in addition to light input rate I, H biomasses parameterize prey isoclines on the C-H₂ phase plane. Carnivore recruitment and production response functions are parameterized by biomasses of both herbivore H and herbivore H₂ (Figure 16). Thus, in addition to fishing effort E, H₂ biomasses parameterize predator isoclines on the C-H phase plane and H biomasses parameterize predator isoclines on the C-H₂ phase plane. Carnivore yield and non-predatory loss response functions are identical to those in Figure 5. On each phase plane at a given rate of light input I and level of fishing effort E, an infinite family of possible equilibrium points exists. The smaller symbols at the intersections of the isoclines indicate some of the possible equilibria that exist at low I, OE (solid circles); high I, OE (open circles); low I 90E (solid squares); high I, 90E (open squares). At a given rate of light input and level of fishing effort, trajectories of biomasses on the C-H and C-H₂ phase planes will finally converge upon only one of the possible equilibrium points. This equilibrium point is determined from the foraging phase plane (Figure 17) and its location on the C-H and C-H₂ phase planes at each rate of light input and level of fishing effort is indicated by the larger symbols.

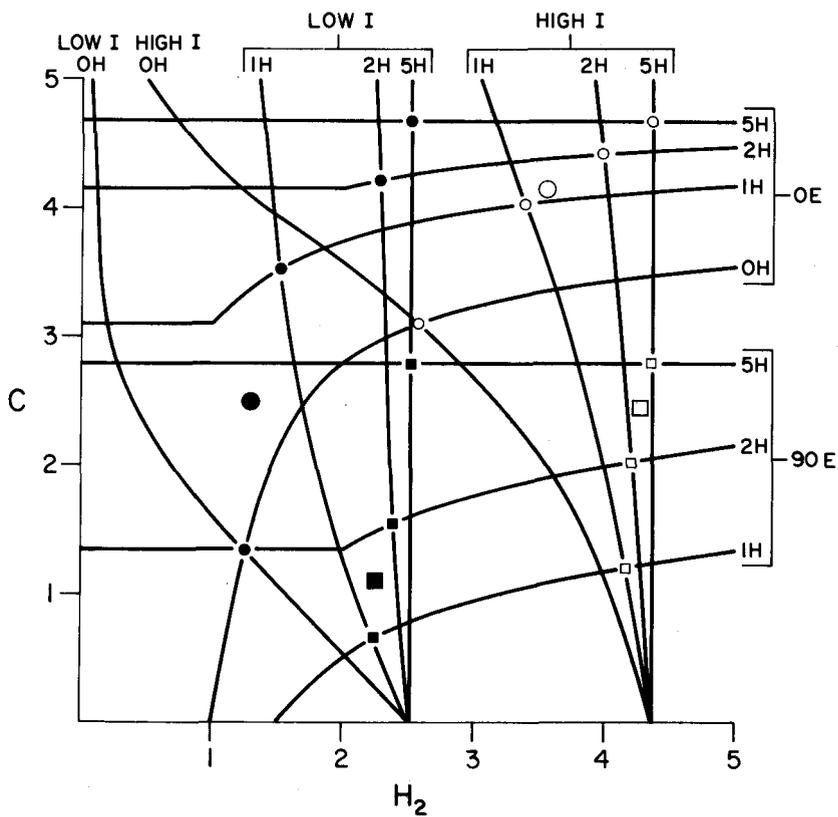
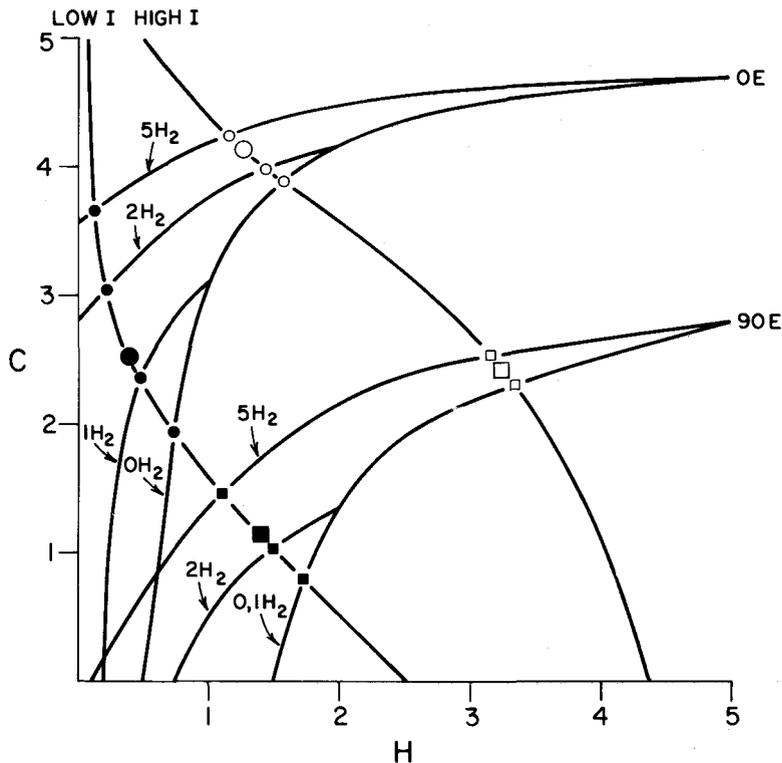


Figure 15

in Figure 14. The biomass of herbivore H was introduced as an additional parameter on the H_2 predation loss curves (Figure 14B). Since these curves are used in deducing the prey isoclines on the C- H_2 phase plane, these prey isoclines become parameterized by H biomass as well as by light input rate. That is, at each light input rate, an infinite family of prey isoclines parameterized by particular H biomasses exists. Only the prey isoclines parameterized by $0H$, $1H$, $2H$, and $5H$ are shown in Figure 15.

Since the carnivore consumes both herbivore H and herbivore H_2 , its relative growth rate and relative recruitment rate are each a function of both the biomass of H and the biomass of H_2 (Figure 16A,B). Carnivore production and recruitment response functions are derived from the C relative growth rate (Figure 6) and C relative recruitment rate functions and are thus also parameterized by particular biomasses of H and H_2 . The carnivore production and recruitment response functions are used in deducing the predator isoclines on the C-H and C- H_2 phase planes. Consequently, in addition to fishing effort, the predator isoclines on the C-H phase plane become parameterized by H_2 biomass and the predator isoclines on the C- H_2 phase plane become parameterized by H biomass. At a particular level of fishing effort, there exists an infinite family of predator isoclines on the C-H phase plane, each parameterized by a particular H_2 biomass, and an infinite

Figure 16. Two sets of curves representing the relationship between the relative growth rate of the carnivore and the biomass of its prey species, herbivore H and herbivore H₂. The carnivore production response function used in deducing predator isoclines on the C-H phase plane are derived from the set of curves in A. The production response function used in deducing predator isoclines on the C-H₂ phase plane are derived from the set of curves in B. Both sets of growth curves yield the same C relative growth rate for each particular combination of biomasses of H and H₂. The sets of growth curves were derived in the following manner. The energy value of herbivore H per unit of herbivore biomass consumed by C was assumed to be twice that of herbivore H₂. For any combination of biomasses of H and H₂, carnivore total relative energy consumption rate is simply the sum of the consumption rate of H (Figure 14A) and the consumption rate of H₂ (Figure 14B), converted to energy units, at 1C. Carnivore relative growth rate at each combination of biomasses of H and H₂ was then determined from a curve relating C relative growth rate to C total relative energy consumption. The relationship between carnivore relative recruitment rate and the biomass of herbivore H and herbivore H₂ was determined in the same manner. The C relative recruitment rate relationships were used to construct the carnivore recruitment response function.

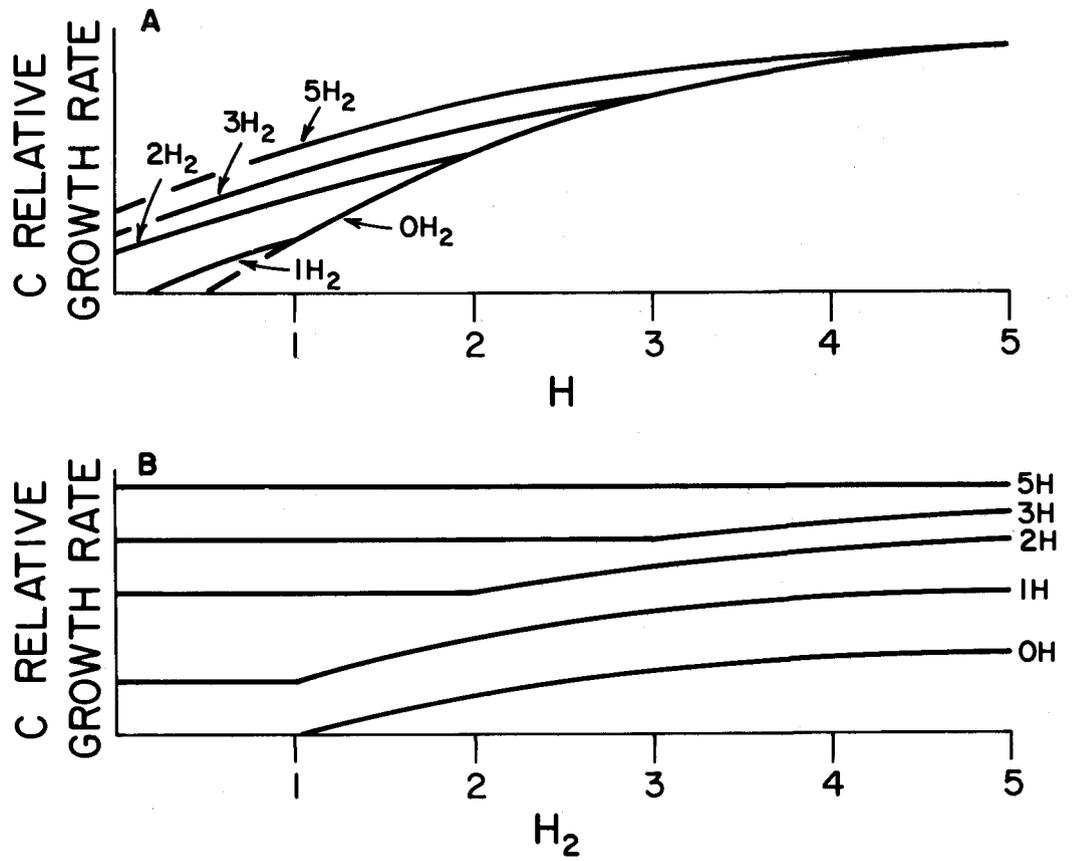


Figure 16

family of predator isoclines on the C- H_2 phase plane, each parameterized by a particular biomass of H.

The relative growth rate (Figure 16) and relative recruitment rate of carnivore C, carnivore production and recruitment response functions, and thus, the position and form of the predator isoclines on the C-H and C- H_2 phase planes (Figure 15) are very much affected by the carnivore's feeding strategy (Figure 14). For example, if H_2 biomass is fixed at $2H_2$, H_2 will drop out of the carnivore's diet when the biomass of H reaches $2H$ (Figure 14B). The carnivore growth curve at $2H_2$ (Figure 16A) intersects the OH_2 growth curve at $2H$. Thus, at biomasses of H greater than $2H$, carnivore growth, production, and also recruitment result only from consumption of H because H_2 was dropped from the diet. For these reasons, the predator isoclines parameterized by $2H_2$ on the C-H phase plane intersect the predator isoclines parameterized by OH_2 at a herbivore H biomass of $2H$. At biomasses of H less than $2H$, the predator isoclines parameterized by $2H_2$ lie above the predator isoclines parameterized by OH_2 . Over these biomasses of H, the carnivore consumes both H and H_2 and carnivore growth, production, and recruitment are greater than carnivore growth, production, and recruitment at OH_2 .

Furthermore, if the biomass of herbivore H is fixed at $2H$, carnivore C does not begin to consume H_2 until its biomass exceeds $2H_2$ (Figure 14B). At $2H$, then, carnivore

growth (Figure 16B), production, and recruitment, and, thus, the predator isoclines parameterized by $2H$ on the C- H_2 phase plane (Figure 15) begin to increase when the biomass of H_2 exceeds $2H_2$. Furthermore, at each rate of light input on the C- H_2 phase plane, the prey isoclines represent the density-dependent relationship between C and H_2 at particular biomasses of herbivore H. As the biomass of herbivore H is increased, the H_2 predation loss curve is lowered (Figure 14B) and the prey isoclines on the C- H_2 phase plane are shifted to the right and become steeper. When the biomass of herbivore H is fixed at $5H$, H_2 will never be consumed by carnivore C. At $5H$, then, the prey isoclines are vertical and the predator isoclines are horizontal.

On each phase plane, a family of possible equilibrium points exists at each rate of light input and level of fishing effort. An increase in the biomass of herbivore H_2 on the C-H phase plane results in an increase in equilibrium biomass of carnivore C and subsequent reduction in equilibrium biomass of herbivore H. Conversely, an increase in the biomass of herbivore H on the C- H_2 phase plane causes an increase in equilibrium biomass of both carnivore C and herbivore H_2 . Equilibrium biomass of H_2 increases as a result of reduction in consumption of H_2 by C, after an increase in biomass of H (Figure 14B).

If rate of light input and level of fishing effort were fixed, the trajectory of biomasses on each of the C-H and C-H₂ phase planes would converge upon only one point in the infinite family of possible equilibrium points. Equilibrium biomasses of H, H₂, and C, at given light input rates I and levels of fishing effort E, can be determined from the isoclines systems on the foraging phase plane shown in Figure 17.

At each rate of light input and level of fishing effort, equilibrium H, H₂, and C biomasses are defined by single co-relative equilibrium points on the C-H, C-H₂, and H-H₂ phase planes. For example, at high I and OE, the co-relative equilibrium points on the C-H, C-H₂, and H-H₂ phase planes are identified by large open circles. These three single co-equilibrium points are merely different projections of the same three-dimensional point in phase space.

For each rate of light input and level of fishing effort, the equilibrium biomasses maintained by C, H, and H₂, when C preys upon both H and H₂ (large symbols in Figure 15), can be compared to the equilibrium biomasses of C, H, and H₂ when C preys only upon H (OH₂ on the C-H phase plane) or only upon H₂ (OH on the C-H₂ phase plane). In general, when carnivore C preys upon both H and H₂, carnivore C maintains a greater equilibrium biomass than it would maintain if it preyed upon only H or H₂. Furthermore, herbivore H maintains a lower equilibrium biomass than it would

Figure 17. Foraging phase plane used to determine, for each rate of light input and level of fishing effort, the equilibrium biomasses of herbivore H and herbivore H₂ that result when both are preyed upon by carnivore C. Foraging isoclines for H (dashed lines) are derived from the C-H phase plane (Figure 15) and define the set of biomasses of H and H₂ where $dH/dt = 0$. Foraging isoclines for H₂ (solid lines) are derived from the C-H₂ phase plane and define the set of biomasses of H and H₂ where $dH_2/dt = 0$. For a given rate of light input and level of fishing effort on the C-H phase plane, the herbivore H foraging isocline is constructed by determining, from the intersections of the predator isoclines parameterized by H₂ biomasses with the prey isocline, the equilibrium H biomasses generated by particular H₂ biomasses. H₂ foraging isoclines are derived in the same manner from the C-H₂ phase plane. The intersection of H and H₂ foraging isoclines for each rate of light input and level of fishing effort define the equilibrium point upon which a trajectory of biomasses will converge. These equilibrium points are also shown, with corresponding large symbols, on the C-H and C-H₂ phase planes.

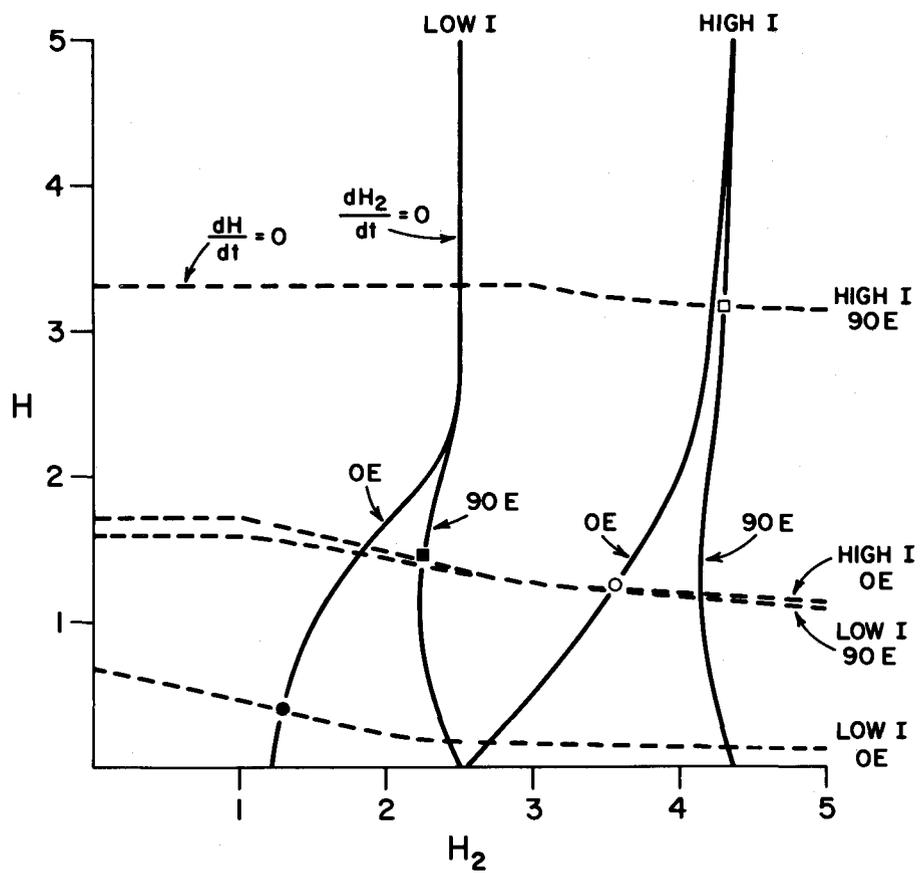


Figure 17

maintain if C preyed only upon H, and herbivore H_2 maintains a greater equilibrium biomass than it would maintain if C preyed upon only H_2 .

At each level of fishing effort, increases in the biomass of herbivore H shift the predator isocline upward on the C- H_2 phase plane, and increases in the biomass of herbivore H_2 shift the predator isocline upward on the C-H phase plane. Thus, the scope for persistence or stability of the C-H- H_2 system is greater than the scope for persistence of either the C-H or C- H_2 system. That is, when carnivore C preys upon both H and H_2 it can persist over a greater range of values of environmental factors I and E.

In previous sections, the effect of light input rate and competition on the system-determined equilibrium recruitment, production, and yield curves of carnivore C were examined. In this section, herbivore H_2 was introduced as an additional prey species of carnivore C. At a particular rate of light input, the addition of H_2 to the diet of carnivore C results in an increase in both equilibrium carnivore biomass and equilibrium carnivore recruitment, production, and yield at each level of fishing effort (Figure 18). Thus, at each rate of light input, when carnivore C preys upon both H and H_2 , the magnitude of its equilibrium recruitment, production and yield curves is greater than the magnitude of these curves when C preys upon only herbivore H.

Figure 18. The effect of the addition of prey species H_2 on the magnitude and form of the system-determined carnivore equilibrium recruitment, production, and yield curves. At each rate of light input and level of fishing effort, the addition of H_2 to the diet of carnivore C results in an increase in equilibrium C biomass (Figure 15). Furthermore, at a particular equilibrium carnivore biomass, C can maintain a greater relative recruitment rate and relative growth rate when it preys upon both H and H_2 . The addition of H_2 to the diet of C therefore results in an increase in the magnitude of the equilibrium recruitment, production and yield curves of C (dashed curves).

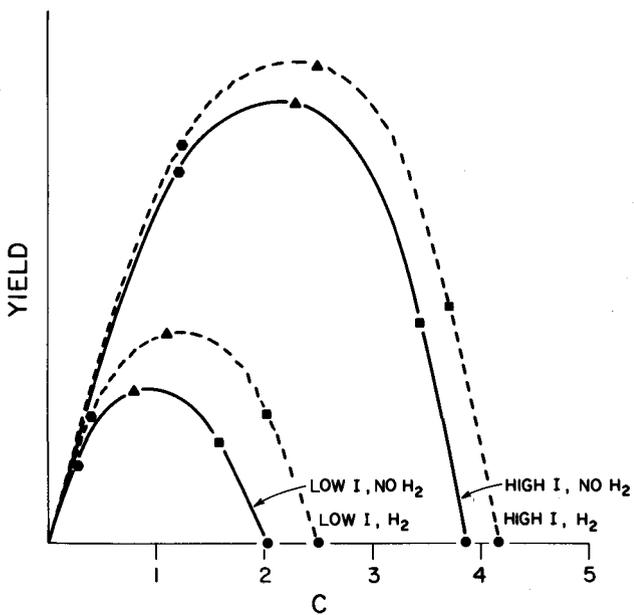
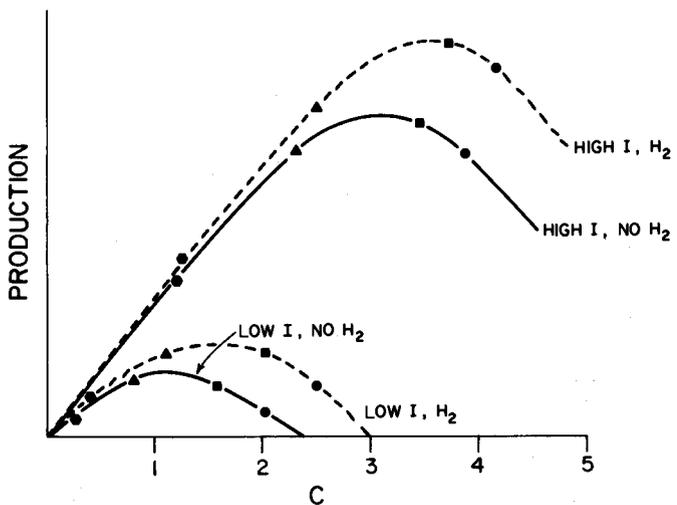
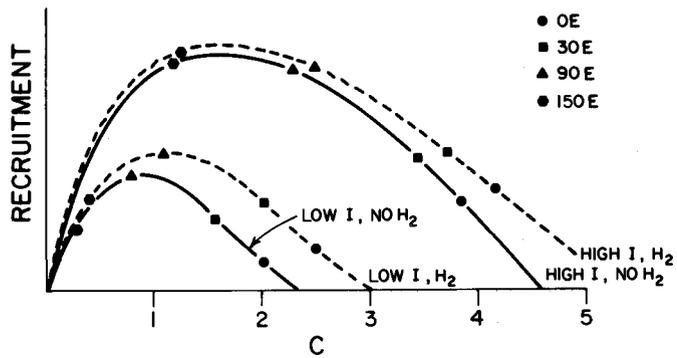


Figure 18

DISCUSSION

The objective of the theory of exploitation developed here is the explanation of the performances of exploited fish populations under different environmental conditions. The recruitment, production, and yield of an exploited fish population are performances of that population; that is, they are an outcome of the interactive performances of its subsystems (Warren, Allen, and Haefner, MS). Individual organisms compose the subsystems of the population, and their interactive performances -- growth, reproduction, and death -- in a particular environmental system determine population recruitment, production, and yield. Recruitment, production, and yield, together with other forms of mortality, within the environmental system, determine and thus explain another population performance, population biomass.

The performances of an exploited fish population are ever varying, their magnitude at any particular time being dependent upon the magnitude of all other biological, chemical, and physical variables composing the environmental system. To explain such time-variant behavior, the effects of changes in environmental factors on the performances of populations must be deduced and represented.

The theoretical approach advanced here attempts to represent, with interrelated systems of isoclines on phase

planes, the impact of environmental factors on the biomass performance of exploited fish populations and all other populations composing a defined biological system. Moreover, the position and form of these isoclines have been deduced, with a graphical calculus, from response functions that represent some of the important biological characteristics of the interacting populations. Thus, with this approach, the effect of any environmental factor on the positions of predator and prey isoclines and the equilibrium points at their intersection on all phase planes can begin to be determined. On a particular phase plane, a trajectory of biomasses, the time-variant performance of the system, is in constant pursuit of an equilibrium point that is continually being shifted by changes in the levels of environmental factors.

In an abstract sense, for a defined system of n populations, the complete set of isoclines on all phase planes, and the response functions from which they are deduced, are the time-invariant and general, and thus universal, explanation of all possible trajectories of biomasses. On any phase plane, an equilibrium point and the trajectory moving toward it are simply a two-dimensional projection of an n -dimensional equilibrium point and trajectory in hyperspace (Booty and Warren, MS).

The complete abstract isocline system defines the domain of all possible performances under all possible

environmental conditions -- that is, it represents the capacity (Warren, Allen, Haefner, MS) of the system to perform. The theoretical concept of capacity was introduced earlier when stability of the C-H system was defined as its capacity for persistence. A particular system has a capacity to perform, its performance at any time being dependent upon its capacity and the immediately effective environmental conditions. As a result, all possible performances of the system under all possible values of environmental variables defines that system's capacity. The capacity of a system cannot be fully evaluated empirically or even theoretically, but the concept of capacity gives context and meaning to empirically or theoretically determined performances under particular sets of environmental conditions.

With the theory of exploitation proposed here, a partial evaluation of the capacities of systems to perform -- their scope for performance -- can be undertaken. Although the scope for performance of individual organisms, such as scope for activity (Fry, 1947) or scope for growth (Warren and Davis, 1967), can be determined in the laboratory, the scope for performance of higher level systems is very difficult to determine empirically.

One of the most important capacities of systems is their capacity for persistence, viewed here as the stability of the system. A partial evaluation of this capacity for the C-H system -- its scope for persistence -- was

undertaken. The scope for persistence of the C-H system was defined as the range of values of environmental factors I and E over which the system could persist, that is, the range of values of these environmental factors over which the performances (such as biomass) of both C and H would always be greater than zero. The scope for persistence of this system is dependent upon the biological characteristics of the interacting carnivore and herbivore populations, as represented by their respective gain and loss response functions. Introduction of a competitor, carnivore C_2 , reduced the scope for persistence of the C-H system, while introduction of an additional prey, herbivore H_2 , increased the scope for persistence. In general, for a given set of environmental factors such as I and E, biological variables that either shift the predator isocline upward (additional prey) or shift the prey isocline to the right (absence of competition) on the C-H phase plane increase the scope for persistence of the C-H system. Furthermore, with this theoretical approach, the effect of other environmental factors such as plant nutrients or other biological interactions such as mutualism, commensalism, or competition at the herbivore level on the scope for persistence of the C-H system or any other system can be deduced and represented.

It is important to further development of fisheries exploitation theory that the presence of a competitor has been shown to reduce both the range of fishing effort over

which an exploited fish population can persist and the yield obtained by a particular level of fishing effort (Figures 10, 11, 12). The presence of the anchovy, a competitor, coupled with poor environmental conditions and high fishing effort (like low I, 150E in Figures 10, 11) appears to have contributed to the irreversible decline of the California sardine population (Marr, 1960; Murphy, 1960; Cushing, 1968).

Recruitment, production, yield and other forms of mortality are performances of exploited fish populations that fisheries scientists have attempted to explain to attain a better understanding of the dynamics of these fish populations. In general, these performances have been represented and explained, for particular fish populations, by single unparameterized curves. Often, however, the variability of these performances is so great (see Parrish, 1973 for example) that little understanding can be gained if they are represented and explained in this way.

With the approach proposed here, families of carnivore equilibrium recruitment, production, and yield curves, each curve generated by particular levels of environmental variables, can be deduced. For a defined system, the complete set of carnivore equilibrium recruitment, production, and yield curves generated by all possible values of all environmental variables represents the carnivore's capacity for recruitment, production and yield.

Over a particular range of values of environmental variables, scope for carnivore recruitment, production, and yield and the carnivore's scope for persistence are identical. This must be so since recruitment, production, and yield are all functions of carnivore biomass, and if carnivore biomass is zero at some values of environmental factors, carnivore recruitment, production, and yield must also be zero.

System-determined carnivore equilibrium recruitment and production curves are derived from both the density-dependent relationships between equilibrium carnivore and herbivore biomass, defined by the prey isoclines, and curves relating carnivore relative recruitment and relative growth rates to herbivore biomass (Figures 4 and 6). Yield curves are derived from the same density-dependent relationships by determining, at each level of fishing effort, the yield obtained from the corresponding equilibrium carnivore biomass.

Some environmental factors, such as light input rate and plant nutrients (Booty and Warren, MS), and biological variables, such as competition and additional prey species, change the magnitude and form of the carnivore equilibrium recruitment, production and yield curves (Figures 7, 12, 18). Other environmental factors, such as fishing effort, affect recruitment, production, and yield by changing carnivore biomass. Changes in the level of factors in this

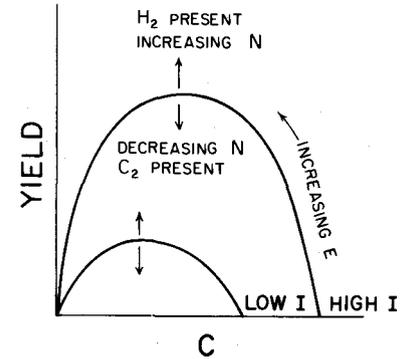
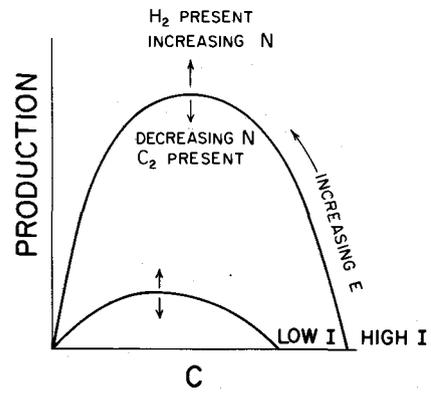
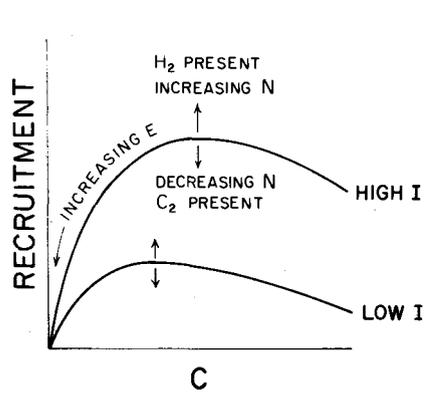
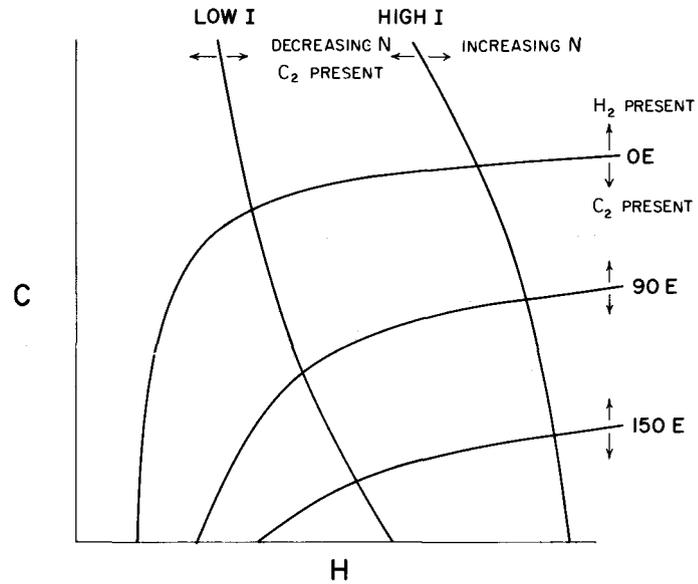
latter class, then, shift recruitment, production, and yield performances along particular curves, rather than changing the magnitude and form of the curves.

Figure 19 represents changes in predator and prey isoclines on the C-H phase plane and in carnivore equilibrium recruitment, production, and yield curves that would result from changes in light input rate I , plant nutrient concentration N , fishing effort E , presence of a competitor C_2 , and presence of additional prey H_2 . In general, any environmental variable that causes either a change in the density-dependent relationship between carnivore and herbivore biomass (light input rate, plant nutrients, competition) or a change in the forms or magnitudes of the carnivore relative recruitment and relative growth rate curves (additional prey) generates a change in the magnitude and form of the carnivore equilibrium recruitment, production, and yield curves. Variables such as fishing effort or other forms of mortality that do not alter the density-dependent relationships or the relative recruitment and relative growth rate curves only shift recruitment, production, and yield performances along a particular curve.

It should be emphasized that environmental factors need not act directly on the carnivore or its prey to affect carnivore recruitment, production, and yield. Rate of light input, plant nutrient concentration, and competition on lower trophic levels indirectly influence the magnitudes

Figure 19. Changes in position of the predator and prey isoclines on the C-H phase plane and changes in magnitude of the carnivore equilibrium recruitment, production, and yield curves that result from changes in plant nutrient concentration N , introduction of a competitor C_2 , and addition of another prey species to the diet of C . If competition between C and C_2 is for a nonfood resource, such as spawning space, as well as for food, C_2 biomasses parameterize the C recruitment response function and thus parameterize predator isoclines as well as prey isoclines on the C-H phase plane.

Figure 19



and forms of the carnivore recruitment, production and yield curves and therefore should be considered in any explanation of these population performances. Furthermore, fishing effort could alter the magnitude and form of the recruitment, production, and yield curves by removing materials from the system that would have been decomposed to plant nutrients.

With a causal-deterministic theory of exploitation that does not uncouple the dynamics of an exploited fish population from the dynamics of its community, the effects of changes in any chemical, physical, or biological factor on the performances of an exploited fish population can be deduced and represented. The theoretical propositions of this theory -- the complex sets of response functions -- are in no way empirically determinable. They can be interpreted, or given whatever forms, as we may choose. In this way, they can take into account whatever theoretical and empirical knowledge we may possess, or they may be purely hypothetical. Thus, this theoretical approach has great heuristic power. Furthermore, the interactions between populations in a community and environmental factors are represented by interrelated systems of isoclines that underlie and so explain the time-variant behavior of the populations. This makes the theory highly visualizable and permits broader understanding of a wide range of population phenomena.

BIBLIOGRAPHY

- Baranov, F. I. 1918. On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiologicheskii Inst. Izv. 1:81-128. (Translation deposited in International Fisheries Commission collection, 1938).
- Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Invest. Lond. Ser. 2, 19:1-533.
- Booty, W. M. and C. E. Warren. A general theory of productivity and resource utilization. Submitted to Ecological Monographs.
- Braithwaite, R. B. 1953. Scientific Explanation: A Study of the Function of Theory, Probability and Law in Science. Cambridge University Press, London. 375 pp.
- Brocksen, R. W., G. E. Davis, and C. E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. J. Wildl. Mgmt. 32:51-75.
- Campbell, N. R. 1920. Physics: The Elements. Cambridge University Press, London.
- Chapman, D. W. 1968. Production. Pages 182-196. In W. E. Ricker (editor), Methods for Assessment of Fish Production in Fresh Waters. Blackwell Scientific Publications, Oxford.
- Charnov, E. L. 1976. Optimal foraging. Attack strategy of a mantid. Am. Nat. 110(971):141-151.
- Cushing, D. H. 1968. Fisheries Biology. The University of Wisconsin Press, Madison. 200 pp.
- Emlen, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100(916):611-617.
- _____. 1968. Optimal choice in animals. Am. Nat. 102(926):385-389.
- Fox, W. W. 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99(1):80-88.

- Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies Biological Series 55. Ontario Fisheries Research Laboratory Publications 68. 62 pp.
- Gilpin, M. E. 1972. Enriched predator-prey systems: Theoretical stability. *Science* 177:902-904.
- Graham, M. 1935. Modern theory of exploiting a fishery and application to North Sea trawling. *J. Cons. Int. Explor. Mer.* 10:264-274.
- Gulland, J. A. 1967. The effects of fishing on the production and catches of fish. Pages 339-358. In S. D. Gerking (editor), *The Biological Basis of Freshwater Fish Production*. Blackwell Scientific Publications, Oxford.
- Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: A new methodology. *J. Fish. Res. Bd. Can.* 33(1):1-5.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of a European pine sawfly. *Can. Ent.* 1:293-320.
- _____. 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4:1-24.
- Holling, C. S. and S. Ewing. 1971. Blind man's buff: Exploring the response space generated by realistic ecological simulation models. *Proc. Int. Symp. Statist. Ecol.* 2:207-229. Yale University Press, New Haven.
- Ivlev, V. S. 1961. *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven. 302 pp.
- Katz, P. 1974. A long-term approach to foraging optimization. *Am. Nat.* 108(964):758-782.
- Larkin, P. A. 1963. Interspecific competition and exploitation. *J. Fish. Res. Bd. Can.* 20:647-678.
- Lewontin, R. C. 1969. The meaning of stability. *Diversity and Stability of Ecological Systems*, Brookhaven Symp. Biol. 22:13-24.
- _____. 1974. *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York. 346 pp.

- MacArthur, R. M. and E. R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100(916):603-609.
- Marr, J. C. 1960. The causes of major variations in the catch of the Pacific sardine Sardinops caerulea (Girard). *Proc. World Sci. Meet. Biol. Sardines and Related Species* 3:667-791.
- May, R. M. 1972. Limit cycles in predator-prey communities. *Science* 177:900-902.
- Murdoch, W. W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335-354.
- Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. *Adv. Ecol. Res.* 9:1-131.
- Murphy, G. I. 1960. Oceanography and variations in the Pacific sardine population. *Cal. Coop. Ocean. Fish. Invest.* 8:55-64.
- Parrish, B. C. (editor). 1973. Fish stocks and recruitment. *Rapp. P-V Reun. Cons. Internat. Explor. Mer*, Vol. 164.
- Paulik, G. J., A. S. Hourston and P. A. Larkin. 1967. Exploitation of multiple stocks by a common fishery. *J. Fish. Res. Bd. Can.* 24:2527-2537.
- Pulliam, H. R. 1974. On the theory of optimal diets. *Am. Nat.* 108 (959):59-74.
- Rapport, D. J. 1971. An optimization model of food selection. *Am. Nat.* 105(946):575-587.
- Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11:559-623.
- Rosenzweig, M. L. 1971a. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.
- _____. 1971b. (Reply to Gilpin). *Science* 177: 904.
- _____. 1973. Exploitation in three trophic levels. *Am. Nat.* 107:275-294.

- Schaeffer, M. B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Bull. Inter-Am. Trop. Tuna Commn.* 1:26-56.
- _____. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Bull. Inter-Am. Trop. Tuna Commn.* 2:245-285.
- Schoener, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.
- Silliman, R. P. 1968. Interaction of food level and exploitation in experimental fish populations. *Fishery Bull. Fish Wildl. Serv. U.S.* 66:425-439.
- Tanner, J. T. 1975. The stability and intrinsic growth rates of prey and predator populations. *Ecol.* 56: 855-867.
- Walters, C. J. and R. Hilborn. 1976. Adaptive control of fishing systems. *J. Fish. Res. Bd. Can.* 33(1):145-159.
- Warren, C. E. 1971. *Biology and Water Pollution Control.* W. B. Saunders Company, Philadelphia. 434 pp.
- Warren, C. E., M. W. Allen, and J. W. Haefner. Conceptual frameworks in biology: A tentative step. Submitted to Science.
- Warren, C. E. and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fishes. Pages 175-214. In S. D. Gerking (editor), *The Biological Basis of Freshwater Fish Production.* Blackwell Scientific Publications, Oxford.
- Warren, C. E. and W. J. Liss. Rationales for the design and evaluation of laboratory ecosystem studies in environmental toxicology. Manuscript to be submitted to CRC Critical Reviews for Environmental Control.