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## **A Simulation Approach to Understanding the Processes That Structure Food Webs**

H. I. Jager  
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D. L. DeAngelis  
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ENVIRONMENTAL SCIENCES DIVISION  
Publication No. 2227

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ENVIRONMENTAL SCIENCES DIVISION

A SIMULATION APPROACH TO UNDERSTANDING  
THE PROCESSES THAT STRUCTURE FOOD WEBS<sup>1,2</sup>

H. I. Jager, R. H. Gardner, D. L. DeAngelis, and W. M. Post

Environmental Sciences Division  
Publication No. 2227

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<sup>2</sup>Submitted as a thesis by Henriette I. Jager to the Graduate Council of the University of Tennessee in partial fulfillment of the requirements for the degree of Master of Science.

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**ABSTRACT**

JAGER, H. I., R. H. GARDNER, D. L. DeANGELIS, and W. M. POST. 1984. A simulation approach to understanding the processes that structure food webs. ORNL/TM-8904. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 182 pp.

A simulation model of food web dynamics, WEB, was constructed and used in Monte Carlo experiments to study the relationship between structure and function in food webs.

Four main experiments were designed using WEB. The first tested the robustness of food web structures at equilibrium to variations in the functional response of predators in the food web to the densities of their prey. It was discovered that a sigmoid functional response did not necessarily facilitate persistence for all species in model food webs as it does in models having only two trophic levels.

The second experiment clarified the roles of predation and resource-limitation in the process of structuring food webs. In particular, a distinction was uncovered between predation and resource control of species selection and the regulation of species densities by predation and resources.

A third experiment studied the influence of productivity on food web structure and function using simulated food webs. The number of supportable trophic levels increased with increased productivity. There were some indications that increasing productivity without allowing higher trophic levels to invade can lead to intense predation pressure on species in the food web.

The final experiment was designed to study the differential successes of generalists and specialists. Experimental results indicated that: (1) the efficiency of predation gained by specializing, (2) trophic position in the food web, and (3) the numbers of prey in the diets of most competitors and

predators, could influence the success of a particular species with a given number of prey.

The main advantage gained by using a simulation approach in each of these experiments was the ability to assess the roles played by processes of predation and competition in structuring model food webs. This was accomplished by interpreting the order of extinction events that occurred in the simulations and relating these to the species configurations at equilibrium.

## CHAPTER I

### INTRODUCTION

#### 1.1 The Equilibrium Approach

Food web ecology is one area in which the modeling approach is important. The difficulties involved in experimentation and measurement of entire natural food webs are great, especially if measurements over time are required, since the measurements are generally destructive. On the other hand, realistic models of food webs are difficult to build without a great deal of experimentally-derived information.

Perhaps for this reason most theoreticians have engaged the assumption that food webs can be treated as though they are close to equilibrium. Yodzis (1981) states that "most current theoretical work on whole ecological communities is based on a conception of community dynamics...in which the community resides in a neighborhood of equilibrium." For the most part, the the greatest progress has been in the discovery of properties that distinguish locally stable Lotka-Volterra-type food webs from a universe of possible webs (see, for example, Pimm, 1979a, 1979b, 1980; Tregonning and Roberts, 1978, 1979). In these studies, predator-prey interactions have taken the form of Lotka-Volterra equations in which the predators' per-capita growth rates are linear with respect to prey densities. The use of this approach has been criticized (Abrams, 1981; Austin and Cook, 1974; Harwell et. al., 1977) and justified (Yodzis, 1981; Weigert, 1974), both on theoretical grounds relating to the neighborhood stability criterion, and as a representation of reality. The usefulness of the equilibrium approach, however, remains undisputed.

Whether or not the equilibrium approach has validity, it does constitute what is essentially a “black-box” approach through time in which only the before and after need be considered, without the dynamics or causality in between. This makes it difficult to interpret food web results derived from these studies in terms of old and familiar ecological processes and causes.

## **1.2 The Simulation Approach**

In this study, a simulation approach has been adopted as a means of studying the process of food web organization and structuring over time. In the simulated webs, variables describing structural and dynamic qualities of food web organization are used to relate web dynamics to the final structural properties observed. From the approach used in this study, using the two sorts of information, it is possible to reconstruct the development of model food webs in terms of ecologically-interpretable processes of competition and predation. It becomes possible to determine “why” certain food web and species properties have beneficial or detrimental effects on the preservation of a particular trophic system. For the purpose of prediction, supplementing our knowledge of successful properties of food webs with a process-oriented understanding of the causal mechanisms selecting those properties is a worthwhile goal.

While equilibrium results are appropriate for comparing observed food web properties to those compatible with local stability, actual questions of food web response to perturbation are more appropriately addressed by dynamic models which can be used to study the system’s behavior away from equilibrium. A simulation approach shifts emphasis from local stability to persistence—from understanding behavior in an infinitely-small neighborhood to knowing where a particular environmental or internal change will push the

system, and, more importantly, why. Transitional sequences of web configurations can be observed through time, whether or not an equilibrium endpoint exists, and without recourse to the assumption that local stability is the primary selective agent in ecological systems. Instead, assumptions resting on the validity of the particular simulation model are accepted. As a result this approach is more compatible with the philosophy expressed by Sutherland (1981) in his study of a fouling community.

Evidence for stability and instability can be found in all communities, depending on the reference point, specific perturbations, and time scale. The search for a relationship between diversity and stability is pointless. One must be content to ask more specific questions such as, "How does a local community react to the specific perturbations it experiences."

Austin and Cook (1974) report the occurrence of multiple stable points in their food web simulations, implying that the much-touted increase in probability of finding locally-stable points implies a more dynamic pattern of global behavior.

With increasing species numbers in an ecosystem similar to that described here, there is an increase in stable points due to compensating adjustments with increasing complexity, however stability declines in the sense that the equilibrium points become less aggregated in the vector field.

The authors support this argument with evidence that equilibria showed resilience to perturbations of species densities, but that reintroductions of species that had previously become extinct usually resulted in their inclusion, and in a new equilibrium configuration. It is unlikely that our understanding of ecological communities will ever operate on a fine enough scale as to be concerned with neighborhood, rather than structural stability. Understanding

the comings and goings of species, and their effects on community dynamics would seem to be fairly important in those systems for which spatial heterogeneity and mobile species are important. In this study, however, only the “goings” are considered, and equilibria, rather than cycles, seem to be the rule.

Starting with a relatively large trophic system, the simulations allow species to be eliminated, but not to reinvade. The development (which is not meant to imply growth) of each food web is reconstructed in ecological terms in order to address some ecological theories that have not yet been extrapolated to, let alone tested in, the context of an entire food web complex having many trophic levels and many competitors.

At the moment there is no comprehensive theory relating trophic structure to ecological processes (function). Trophic function is a two-dimensional problem involving both within-trophic-level competition and between-level predation. Although the whole picture is not yet available, pieces of it are well developed and waiting to fall into place. The links between theories of competition/diversity and exploitation—which deal with horizontal and vertical cross-sections of food webs, respectively—need to be made in order to understand food webs in their full complexity (at least to the extent that those theories hold “true”).

### **1.3 Competition Theory**

In its entirety, competition theory can be considered to consist of the competitive exclusion principle and the collection of theories that postulate mechanisms by which such exclusion is prevented. In the restricted context of

trophic ecology, competition theory refers relationships among coexisting species with similar trophic requirements. The competitive-exclusion principle refers only to the trophic niche dimension, and the only intrinsic mechanism that may prevent exclusion is predation. Since these simulated food webs are protected from outside disturbances by omission from the model, predator-mediated coexistence, which is a special case of the intermediate disturbance hypothesis, (see Section 5.2.1) is the only applicable corollary to the exclusion principle.

#### **1.4 Exploitation Theory**

Fretwell (1977) and Arruda (1979) offer an admittedly simplified, but possibly useful scheme to explain the distribution of standing crop among trophic levels. The simplifications are as follows:

1. Trophic levels can be treated as meaningful aggregate units.
2. Ecosystems have exactly an integer number of trophic links or levels.
3. Trophic levels are limited by food supply or by predation, but not both.
4. A trophic level limited by predation does not limit the trophic level upon which it feeds.
5. A trophic level limited by its resources does limit the trophic level upon which it feeds.

For an idealized ecosystem, the consequences of obeying these rules can be determined as follows: The top trophic level is always assumed to be resource limited. Rule 5 above allows us to assert that the level below the top level is predator limited. This, in turn, leads us to claim, using rule 4, that the

next level down is resource-limited. By extension it becomes apparent that trophic levels alternate from top to bottom between resource and predation control. Theoretically then, one could expect to predict the type of control regulating a given trophic level just by knowing whether it is an odd or even number of links from the top of the web.

If one accepts that productivity is directly related to food chain length, then one would expect an alternation between predation and resource-limited primary producers as the length of the food chain exploiting them increases, changing odd levels to even and even to odd.

Arruda (1979) predicts further that standing crops of biomass will vary according to limitation with a given trophic level having a larger standing crop when it is resource-limited than when it is predation-limited. Reporting on an experiment comparing farm ponds of varying productivity, he discovered that as primary productivity increased, the abundance of top predators increased, depressing the trophic biomass of the level below, increasing the next lower level, etc.. He concludes that "the increase in biomass by both primary and tertiary consumers, the food-limited levels, and the decrease by both the secondary consumers and the littoral producers, the predator-limited levels, is consistent with Fretwell's (1977) construct."

By combining the intermediate predation hypothesis, which deals with competitive communities, and exploitation theory which treats food chains, one is able to derive ecological theories and predictions that apply to complex food webs with more than two trophic levels and more than one competitor per level. The following list of predictions or hypotheses will be tested by simulation experiments in this study.

I. As predicted by Fretwell (1977) for food chains, trophic levels in food webs will alternate between resource and predation control starting with the top predators.

1. Resource-limited trophic levels will have less prey overlap in the equilibrium web configurations.

2. Predation-limited trophic levels will have a higher incidence of overexploitation cases in which predation causes a prey population to go to extinction.

3. Equilibrium biomass of each trophic level will reflect this alternating effect: a particular trophic level being larger when it is even than when it is an odd number of levels from the top level.

II. Diversity among prey will increase along a gradient of predation pressure as competitive-exclusion is prevented at intermediate intensities, and then decrease as overexploitation begins to reduce diversity at high intensities.

1. Along a productivity gradient whose range is restricted to that yielding a given food web height, diversity will show a bell-shaped, unimodal response.

2. Along an extended gradient of productivity, the addition of a new trophic level will mediate an increase in the diversity of its prey trophic level, formerly the top level.

III. Along a gradient of increasing productivity, the following predictions are tested:

1. The number of trophic levels (trophic height) will rise.

2. Predictions in II will hold for the diversity of the highest trophic level as it becomes possible for it to sustain a new level of predators.

Predictions I and II(2) will be tested by means of an exclusion experiment (Chapter IV) in which trophic levels are sequentially removed in food web simulations that are identical in all other respects. Predictions III will be tested in an experiment in which identical webs are simulated with different productivities or levels of energy subsidy. This productivity experiment is described in Chapter V.

Two additional sets of experiments; the trophic strategy experiments and the functional response study will be introduced separately.

### **1.5 Trophic Strategy Experiments**

Much of the attention of theoretical food web ecology has been focused on the obscure relationship between local stability and food web complexity (see, for example, Gardner and Ashby, 1970; May, 1972; DeAngelis, 1975). For a particular species belonging to a food web this problem can be stated in terms of the relative success of having many vs. few prey connections. For example, if food web dynamics tend to select specialists over generalists, then food webs with low connectivity will emerge. In this study, local stability is not addressed, but the differential success (persistence) of trophic strategies ranging from extreme specialists to complete generalists is studied. Again, it is possible to interpret this selection process in terms of ecological processes such as competition and predation. In each of the experiments (Chapters IV, V, and VII), the effect of species' trophic strategies on experimental results, and the effect of the experimental factor (i.e. productivity) on trophic strategy success is considered. Since trophic strategy is the only quality with which species in these ensembles are endowed, it becomes useful to describe the structural

response of these food webs to experimental factors in terms of trophic strategy success.

The strength of interaction between a specialist and its few prey is likely to be greater than the more diffuse interactions between a generalist and its many prey. May (1972) observes that "species which interact with many others (large connectance) should do so weakly (small interaction strength) and conversely those which interact strongly should do so with but a few species." Specialists are, in theory, more effective predators of their prey specialties, and are therefore awarded higher growth rates in this model. In one of the trophic strategy experiments, the "bonus" experiment, the effect of this growth rate bonus awarded for specialization is studied, with the expectation that the success of specialists will increase concomitantly. One expects, then, that food web complexity will decrease as this bonus decreases.

An experiment is designed that shows how the trophic strategies of other species in the web community influence the success of a particular strategy. These are referred to as frequency-dependent effects. The experiment tests the effect of the strategies of a set of predators on the success of the strategy employed by a set of prey species on which they collectively feed. The key question asked is will the survival of a particular species having either a specialist or a generalist trophic strategy be more likely if:

1. its predators and its competitors are all specialists,
2. its predators and competitors are all generalists,
3. its predators are generalists and its competitors are specialists, or
4. its predators are specialists and its competitors are generalists? The null hypothesis states that strategy successes are independent of one another.

## 1.6 Functional Response Experiment

Because so much of the progress in theoretical food web ecology is based on models that use Lotka-Volterra equations to describe predator-prey interactions, it is important either to verify that they do in fact describe predator-prey interactions in nature, or to demonstrate that theoretical results are not extremely sensitive to the particular formulation chosen to describe those interactions.

In this experiment, a gradient between a linear functional response and a sigmoid “type 3” functional response is set up. The robustness, or sensitivity of structural and functional variables describing the simulated food webs to functional response curvature is estimated by interpreting changes that occur along this gradient. The main a priori prediction in this experiment is that a strongly sigmoid functional response will decrease the incidence of overexploitation on all trophic levels by protecting prey at low densities. This is the simplest imaginable extension of the 2-species result in which a sigmoid functional response depresses the predator’s feeding rate below that of its linear counterpart when prey density is low, reducing the likelihood of causing its extinction.

## 1.7 Summary

The five experiments described here are carried out by means of a simulation model in which one or more parameters are varied for a collection of food web structures that are drawn from a well-defined universe of possible configurations. The objective of these experiments is to make the connection

between ecological theory and the observed changes in structure invoked by the experiment.

## CHAPTER II

### DESCRIPTION OF THE FOOD WEB MODEL

There are two basic approaches to building viable food web structures without resorting to huge numbers of random trials. One is to construct food webs in a successional manner, adding species to the web and permitting extinctions that result (see, for example, Post and Pimm, 1983). The other alternative is to start with large initial web structures, allowing them to reduce to steady-state configurations of species by means of species extinctions, but without invasions (for example, Tregonning and Roberts, 1978, 1979). The approach taken in this study falls into the second category in which viable configurations are achieved through a series of transitions motivated by species eliminations.

WEB is an interactive simulation food web model written in FORTRAN (see Appendix A). The initial structure of the food webs is meant to be a null model with a high number of trophic levels (5), each having an equal number of species (5). For simplicity it is assumed that feeding relationships are restricted to adjacent trophic levels. The only quality distinguishing species of the same trophic status in this study is the degree of trophic specialization as defined by the number of prey species each predator may consume. This will permit interpretation of configurational changes in terms of the relative successes of trophic strategies in the web. In light of this goal, species on each trophic level are assigned a certain number of prey species according to a uniform distribution. This produces a spectrum of diets ranging from completely specialized (monophagous) to completely generalized (polyphagous) on each trophic level (see Figure 1). At the end of the

TROPIC STATUS	TOP PREDATOR	21	22	23	24	25
	2° CARNIVORE	16	17	18	19	20
	1° CARNIVORE	11	12	13	14	15
	HERBIVORE	6	7	8	9	10
		SPECIALIZED			GENERALIZED	
TROPIC DIVERSITY						

Figure 1. Reference chart relating species identification numbers to trophic characteristics of feeding diversity and trophic level affiliation. Food web simulations start with 25 species, five on each trophic level. On each consumer trophic level the five species range from specialized to generalized predators.

simulation, the null hypothesis that all trophic strategies are equally likely to succeed may be tested by comparing the equilibrium distribution of trophic strategies to the original uniform distribution.

The construction of a typical initial food web used in the simulations will be described in the following sections.

## 2.1 Food Web Structure

Twenty-five species, five per trophic level, are connected so that each level has one species with only a single prey connection, one with two prey, and

so on, up to the completely diversified species with all five prey types included in its diet. The particular choices of connections between predators and their prey are made at random. This results in a uniform distribution for the variable “# prey” on the range [1,5], and a normal distribution of the variable “# predators” among species of the same trophic status over a large sample of pooled webs. Figure 2 shows a typical pattern of trophic connections (designated by ones) for a food web of 25 species. Notice that adherence to strict trophic levels creates a pattern of five subblocks below the main diagonal. McMurtrie (1975) found that,

Systems incorporating a hierarchy where the system components arrange themselves into levels with each level interacting only with levels directly above and below it are more likely to be (locally) stable than purely random systems of the same size and connectance.

Pimm (1979a) suggests that feeding on more than one trophic level should be rare due to a reduced likelihood of stability in his systems as well. Darnell (1961) asserts that, in Lake Pontchartrain, at least, species do not appear to observe any rules for trophic organization into distinct levels:

Evidently the consumers exhibit a broad disregard for narrow trophic lines. In fact, the ability of a given species to utilize alternative foods (often from different “trophic levels”) appears to be one of the main buffering factors which tend to stabilize population levels in complex natural communities.

In Cohen’s (1978) collection of documented food webs, very few of the webs presented have a strict trophic structure devoid of omnivory. However, the tendency for interactions to occur between species on adjacent levels is

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1																									
2																									
3																									
4																									
5																									
6	0	0	0	1	0																				
7	0	1	0	1	0																				
8	1	1	1	0	0																				
9	0	1	1	1	1																				
10	1	1	1	1	1																				
11						1	0	0	0	0															
12						0	1	1	0	0															
13						0	1	1	0	1															
14						1	0	1	1	1															
15						1	1	1	1	1															
16											0	1	0	0	0										
17											0	0	1	1	0										
18											1	1	0	0	1										
19											0	1	1	1	1										
20											1	1	1	1	1										
21																0	0	0	1	0					
22																0	0	0	1	1					
23																1	0	1	0	1					
24																1	1	0	1	1					
25																1	1	1	1	1					

QUALITATIVE INTERACTION MATRIX

Figure 2. Qualitative interaction matrix describing trophic relations in a typical food web simulation. Numbers designating rows and columns refer to species 1-25 in the simulated food web as described in Figure 1. Entries of ones indicate that the row species feeds on the column species.

obvious. If it were not, the concept of a “trophic level” would never have arisen. The extent to which the concept applies differs from system to system for unrevealed reasons. Within a particular food web the strict delineation of trophic levels may lapse for different classes of species or different trophic levels. Lindeman noted in 1941 that lower trophic levels seem more definitive and recognizable than higher levels.

The justification for enforcing strict trophic levels in these simulations is that evolutionary-scale explanations for the restriction of feeding to one trophic level are more plausible, at least for lower trophic level species, than arguments based on local stability. In other words, an evolutionary history of eating vegetation is more likely to constrain giraffes from eating mice, or to predispose them toward herbivory than local stability. The relative proximity of large herbivores in their evolutionary lineages can be expected to produce this observed trend of limited feeding diversity which produces guilds. As such, a strict delineation of trophic levels is better thought of as a pre-determined condition rather than something that the model is expected to produce. The relaxation of this assumption for higher level species may provide a more realistic representation of the majority of food webs in nature.

## **2.2 Initial Densities of Species**

Initial densities for species in the web are derived by assuming that the succession of trophic levels is gradual and that competitors are initially equal. For autotrophs it is possible to find the equilibrium density sustained in the absence of predators for the entire level. This is essentially a carrying capacity. The first trophic level is initialized two orders of magnitude below this carrying

capacity, and each successive level two orders below its prey level. This procedure is intended to be a rough approximation of a successional process of trophic construction, giving each trophic level a head start on its predators. Within each level, biomass is distributed equally among species.

To test the importance of assuming that predators have very small initial densities, a test of WEB's sensitivity to initial densities was performed. A sequence of food webs was replicated with species having closer initial densities to the densities of their prey. See Appendix B for a description of the analysis.

### 2.3 Predator-Prey Equations

Predator-prey equations for species belonging to these food webs simulate biomass or population density. The derivations of the coupled time-derivatives for species in the simulated food webs are described in this section. Parameters involved in the expressions are used in the experiments to manipulate the food web characteristic of interest. There is one set of parameters that serves as a control or default condition to which the treatment groups in the experiments are compared. Table 1 lists all of the parameters used, their ecological interpretation, and the values to which they are set in the control simulations.

Let  $X(t) = (x_1(t), x_2(t), \dots, x_n(t))$  denote the vector-valued function for species densities at time  $t$ .  $E_{i,j}$ ,  $i, j = 1, 2, \dots, n$  represents the  $n$  by  $n$  matrix of qualitative species interactions with  $n$  resource utilization vectors,  $E_i$ . One's are assigned to elements of  $E_{i,j}$  in positions where the column species feeds on the row species, and zeroes are assigned elsewhere (see Figure 2).  $A = (a_1, a_2, \dots, a_n)$

Table 1. Default Parameter Values Used in Control Simulations of WEB.

Parameter	Description	Default Value
NL	In WEB, NL refers to the number of trophic levels in the initial food web. The Exclusion experiment in Chapter V varies this parameter.	5
L(I)	In WEB, L(I) is the number of species initiated on trophic level I, $i = 1, 2, \dots, NL$ .	5
f(t)=Sun	(Constant) energy available to the food web through its primary producers.	5.0
k	Degree of curvature in the functional response of predator feeding rate to prey density.	3
$\alpha$	Factor expressing the efficiency of converting prey biomass into predator biomass. Losses due to incomplete consumption and respiration are involved.	0.1
r	Per-capita loss of population biomass unrelated to predation.	.05
Bonus	Bonus controls the strength of advantage given to more specialized predators. It expresses the magnitude of the negative slope in the linear function determining predation efficiency—A in this model (see Section 2.3).	1.0
Xm	Maximum population density collectively attainable by species on a particular trophic level, for autotrophs, $X_m = M = 100.0$ for other trophic levels, $X_m$ is determined during the simulation.	

denotes the predation coefficient for each of the  $n$ -species.  $f(t)$ -the time-dependent forcing function, has the ecological interpretation of sunlight, or any continually-renewed source of energy that subsidizes the food web through its basal species.  $f(t)$  is sometimes referred to in the text as productivity. The rate of density-dependent population decay attributed to factors unrelated to predation is described by parameter  $r$ . The carrying capacity for autotrophs,  $M$ , is the total plant density attained at equilibrium when no heterotrophs are present. Since autotrophs share a common predation coefficient in this model, ( $a_i = 1$ , for all species  $i$  belonging to the first trophic level),  $M = f(t)/r$ . This result can be derived by considering the equation for an autotroph species' population growth given by (1-5). Setting (1-5) to zero (equilibrium) and discarding the predation term (middle) with the carrying capacity  $M$  set equal to the sum of all autotroph populations at equilibrium,  $\sum_{i=1}^m x_i$ , where  $m$  is the number of autotroph species.

The function chosen to describe the rate of energy intake by autotrophs,  $\Phi$ , increases the density-dependence among plant species as their total density increases, nearing the carrying capacity  $M$ . When autotroph populations are far from carrying capacity, each population obtains energy independently of other plant species in the community, in direct proportion to its absolute density as in equation (1-0).

$$\Phi_{1i}(t) = a_i f(t) x_i(t) \quad (1-0)$$

When total plant density is large, close to the carrying capacity of the area, one expects energy intake to be competitive due to spatial limitations.

Energy is acquired by each population at a rate proportional to its relative density. This is intuitively reasonable since the conversion of sunlight into population biomass occurs at a rate that is proportional to the percent of total area that it covers, the energy input  $f(t)$  being specific to that area. The intake function,  $\Phi$ , becomes

$$\Phi_{2i}(t) = a_i f(t) \frac{\chi_i(t)}{\sum_{i=1}^m \chi_i(t)} \quad (1-1)$$

In the model, WEB, the intake function for autotrophs used is a linear combination of the two approaches such that emphasis shifts from one to the other as total autotroph density increases. This has the effect of allowing plant populations to grow quickly under conditions of sparse vegetational cover, but to gradually decelerate growth as capacity is approached:

$$\Phi_i(t, X) = \left( \frac{\sum_{i=1}^m \chi_i(t)}{M} \right) \Phi_{2i} + \left( \frac{M - \sum_{i=1}^m \chi_i(t)}{M} \right) \Phi_{1i} \quad (1-2)$$

$$= \left( \frac{M - \sum_{i=1}^m \chi_i(t) + 1}{M} \right) a_i f(t) \chi_i(t) \quad (1-3)$$

The intake function for heterotrophs is somewhat different. Function  $g$  describes the feeding rate of a predator on its collective ensemble of prey. The

functional response of this feeding rate to changing prey density can be varied from a linear to a strongly sigmoid "type 3" function by manipulation of parameter  $k$  which is defined below.

$E_i \cdot X$  represents the sum of prey densities for all prey species included in species  $i$ 's diet. Then the heterotroph intake function,  $g$ , is given by equation (1-4).

$$g(E_i \cdot X) = -\frac{2}{3}\beta\chi_m^{-1}(E_i \cdot X)^3 + \beta(E_i \cdot X)^2 + \left\{a_i - \frac{\beta\chi_m}{3}\right\}(E_i \cdot X) \quad (1-4)$$

where  $\beta = k/\chi_m \times \min_i \{a_i\}$ ,

$\chi_m$  is the maximum prey density,

and  $k=0,1,2$ , and 3.

This maximum is initially estimated in the simulations by assuming each successive trophic level to have a carrying capacity one-tenth that of the level below, starting with that of autotrophs which is known. From this point, the maximum is incremented whenever the density exceeds the current estimate in the course of the simulation (see subroutine SOLVE in Appendix A). This formulation differs from other formulations of type 3 functional responses by assigning a finite maximum. In most descriptions the feeding rate approaches a finite asymptote as prey densities become large (for example, see Nunney, 1980). Since it is possible to set a realistic maximum on prey density, it is possible to avoid the implication that prey density is unbounded.

The derivation of this particular formulation (1-4) can be best understood by referring to Figure 3 in which both the linear function and the

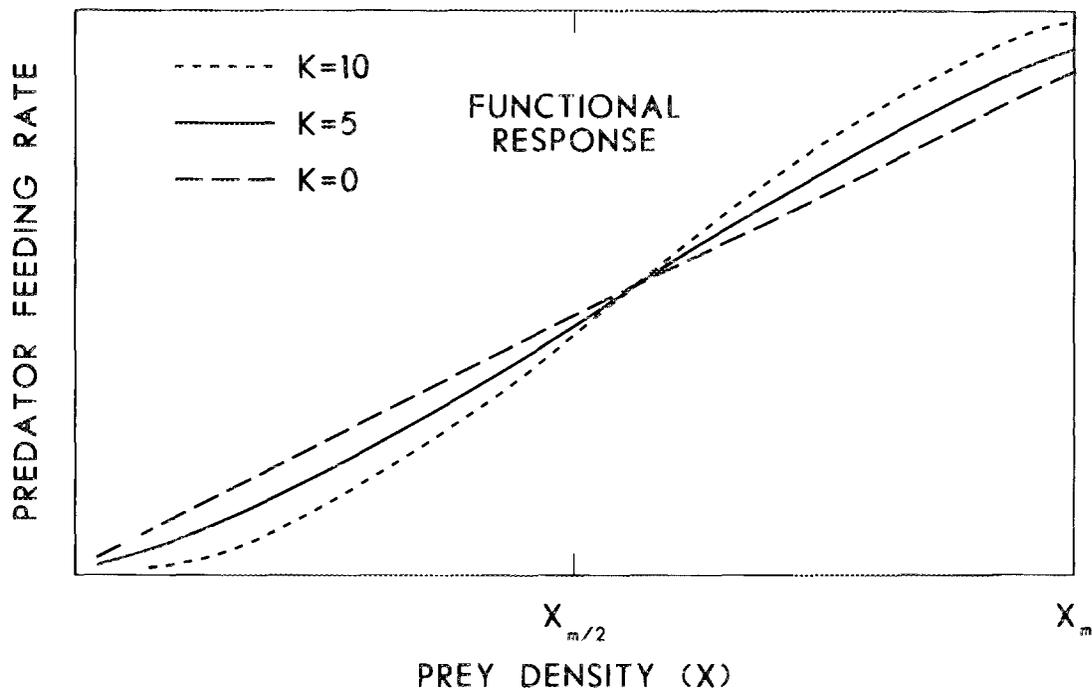


Figure 3. Family of functional response curves ranging from linear to strongly sigmoid. The equation describing the feeding rate of the predator population as function of prey density is referred to as the predator's functional response. As  $k$  increases, the curvature of the functional response increases, becoming more sigmoid.  $X_m$  is the maximum prey density.

family of sigmoid curves are shown. Note that the feeding rate  $g = E_i X$  at three densities: when  $E_i X = 0$ ,  $X_m/2$ , and  $X_m$ —the maximum for prey density. At these points the Lotka-Volterra-type linear response and the type 3 response give the same feeding rates. Using the values at these three points as constraints, simultaneous equations were used to obtain the expression given by (1-4). The expression provides a single parameter— $k$ , which regulates the degree of curvature. When  $k=0$ , the feeding rate is a linear function of prey density. In an attempt to explore the robustness or sensitivity of model food web structure to one's choice of functional response, paired comparisons of simulated webs with four levels of  $k$  are made (see Chapter IV). One goal of

this experiment is to discover in what respects Lotka-Volterra webs ( $k=0$ ) are adequate tools for the study of food webs.

In all experiments with objectives other than the study of robustness, the value used for  $k$  was 3 which lies on the threshold at which feeding rate is prevented from becoming negative at small prey densities (see Table 1 for default parameter values).

The general expression for the time-derivative of a given species' density three forms, depending on trophic status:

$$\text{For Autotrophs} - \dot{\chi}_i = \Phi_i(t, X) - \sum_{j=1}^n E_{ij}g(E_j \cdot X)\chi_j - r\chi_i \quad (1-5)$$

$$\text{For Intermediate Species} - \dot{\chi}_i = \alpha g(E_i \cdot X)\chi_i - \sum_{j=1}^n E_{ij}g(E_j \cdot X)\chi_j - r\chi_i \quad (1-6)$$

$$\text{For Top Predators} - \dot{\chi}_i = \alpha g(E_i \cdot X)\chi_i - r\chi_i \quad (1-7)$$

where  $\alpha$  = represents predation transfer efficiency, which includes waste due to assimilation loss and due to partial consumption,

$f(t)$  = energy input to first trophic level or productivity, and

$r$  = represents the respiration coefficient, or, more generally the density dependent rate of population decay due to factors unrelated to predation.

## 2.4 Predation Efficiency and Feeding Diversification

The predation coefficient is chosen as a function of specialization and diversification of diet in the simulation model.

It is believed that species populations with more specialized diets gain some efficiency in predation. MacArthur (1955) suggested that selection operates to increase individual predation efficiency by specialization, countering the tendency toward highly interconnected food webs with enhanced community stability.

For this reason specialists are given a bonus in the simulation model. In the model, there is a minimum predation coefficient and a bonus factor which describes the slope of the inverse linear relationship hypothesized between the number of prey included in a predator's diet and its predation coefficient:

The predation coefficient ( $a_i$ ) = Minimum predation coefficient

$$+ \text{bonus} \times \left\{ 1 - \frac{\text{number of prey in diet}}{\text{maximum number of prey}} \right\}, \quad (1-8)$$

where the "maximum number of prey" types available is five, the lowest possible predation efficiency gives predation coefficient of 0.2, "number of prey in diet" refers to the actual number of prey types taken by species  $i$ , (its trophic strategy), and "bonus" refers to the increase in predation efficiency awarded for specialization which is set to one in all but the bonus experiment (see Table 1 on page 18).

Since the minimum predation coefficient is set to 0.2, a specialist with only one prey in its diet has a predation coefficient = 1, and a complete generalist has predation coefficient = 0.2.

## **2.5 Definition for Equilibrium and Extinction**

“Equilibrium” and “extinction” are two well-defined concepts that require operational definitions in order to be useful in nature and in these simulations. When changes in population density are sufficiently small, for a given time step, the web is considered to be at equilibrium. Likewise, sufficiently small populations are considered extinct. In a field study, this threshold is defined by the ability to detect low densities using available techniques for sampling. Here a cutoff density is chosen, below which a population is set to zero. This threshold for extinction is very conservative at a density of  $10^{-20}$  th of the initial density of the population. Spatial considerations such as spatially-induced lags in predator tracking and spatial refuges for prey which help to prevent local extinction are essential qualities of natural food webs. In a non-spatial model such as this, the roles of seed populations in surrounding areas and of spatial refuges within an area can be tenuously emulated by permitting populations to become quite small before considering them extinct. Lewis (1980) remarked upon the periodic importance of one zooplankton species in a Venezuelan lake that persisted at virtually undetectable levels for several years before conditions allowed it to become the dominant herbivorous zooplankton in the system. Examples of this sort are common in lake systems such as those studied by Lynch (1979) in which shifts in predation completely altered the apparent composition of zooplankton communities.

The simulations ran for a period of time long enough to allow most webs to reach “equilibrium”, defined as less than .01% change in density for all populations in the web over a fixed time interval. For those webs terminated before equilibration it was usually possible to determine the final configuration by eliminating populations which are obviously approaching the extinction threshold. The final time used was 9000. Time constraints prohibited running all webs until they reached equilibrium. For the purposes at hand no distinction between limit cycles and equilibrium behavior was needed. Figure 4 is an example of a food web’s behavior over time. The simulation in Figure 4

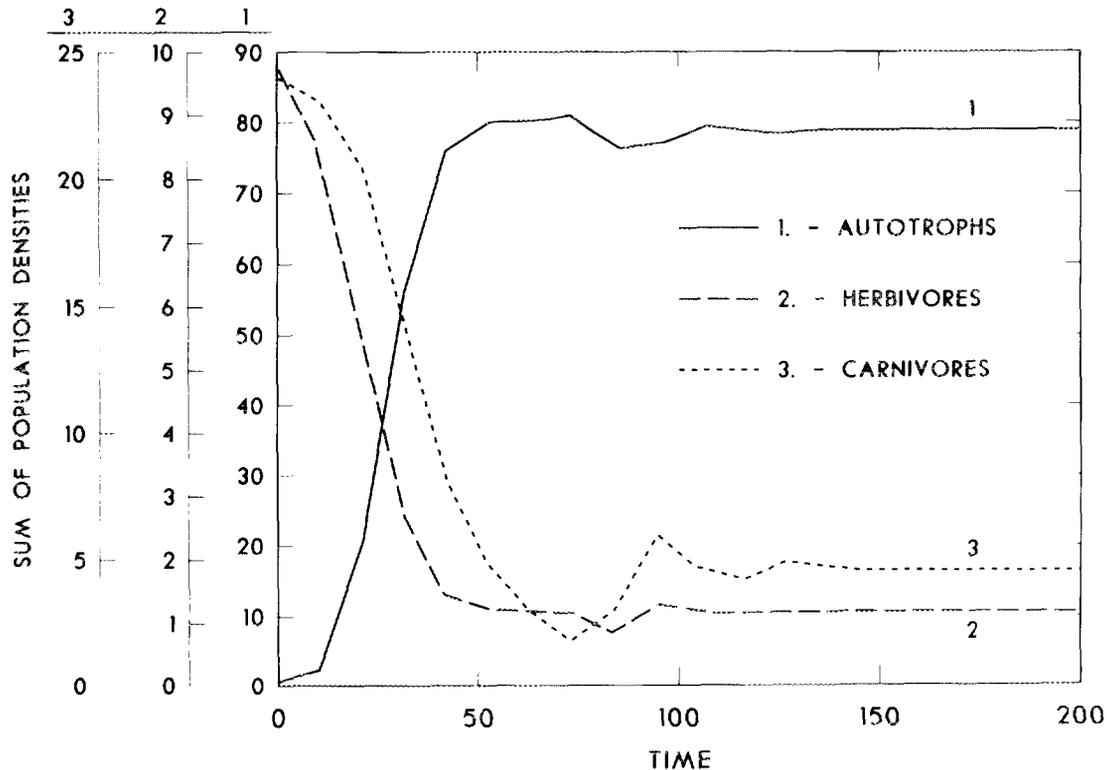


Figure 4. Sample plot of simulation behavior over time. Note that each trophic level has a different scale of density on the left. Populations are initiated close to zero on the scales shown, although the increase of herbivores and carnivores is so rapid as to be vertical along the Y-axis at these scales.

started with default conditions (as described in Table 1 on page 18) with the exception of having only three, and not five, trophic levels.

## **2.6 Reconstruction of Web Dynamics Using Five Extinction Scenarios**

An important advantage of actually simulating the behavior of a food web over time is that one is able to determine what actually causes some species to persist and others to disappear from the web. One can observe the actual reason behind a species' demise in clearly interpretable ecological terms, rather than trying to decipher the meaning of the system's eigenvalues (see Armstrong, 1982). The actual reason for species losses can be observed in clearly interpretable ecological terms.

Species extinctions are divided into two categories. In cases where a population goes extinct because all of its prey species are extinct, the extinction is considered "resource-induced." In other cases, when a species has not overexploited all of its prey but still fails to persist, the extinction of that species is due to predation. In actuality, of course, all extinctions below the top trophic level are caused interactively by both resource and predation effects, but this classification is a useful tool for reconstructing the history of changes in the web and the relative importances of the two effects. In cases when a species is faced with the situation of having no prey species left, a "1" is assigned to its cause of extinction. A "2" is assigned if, for whatever reason (e.g. competition, overexploitation), its density falls below the extinction threshold. This is referred to as predation-induced extinction since the parameters chosen do not permit species to reach the extinction threshold in the absence of predation unless prey density is extremely low, e.g. when the respiration loss rate exceeds the feeding rate.

With this dichotomy of extinction rules it is possible to define five scenarios describing a population and its relationship in the web (see Figure 5).

1. If a species goes to extinction due to predation and at least one of its predators suffers resource-induced extinction as a result, then such a predator is said to have “overexploited” the prey species (predator cause=1). In the analysis, the number of overexploited prey species is used as an indication of predation intensity in the food webs.

2. The prey in this case is said to have been overexploited (prey cause=2). Overexploitations by species which still have alternative prey support are also possible. These predators represent an even greater threat since their alternative prey permit them, not only to grow, but to increase their rates of feeding further along the axis of the sigmoid response function. Since the total prey density is supplemented by alternative prey, the feeding rate of the predator is larger than it would be if no alternatives were available. A prey species is considered overexploited if it goes to extinction having a “viable” predator (one persisting at equilibrium) with alternative prey types or predators that reached extinction because they had no prey alternatives, provided that the prey species under consideration still had prey resources at the time that it reached extinction. Note, however, that this information is based solely on what happens to unsuccessful species and not those remaining in the equilibrium configuration of the webs. As such, this index describes the impact of predation on food web structures that emerge, but not the degree to which predation regulates the equilibrium structures. Comparison of partial derivatives with respect to predators (also resources) at equilibrium could be used to indicate the importance of predation (competition) on those species remaining in the equilibrium configuration of the web.

		PREDATOR'S CAUSE OF EXTINCTION		
		0	1	2
PREY'S CAUSE OF EXTINCTION	0	BOTH PREDATOR AND PREY POPULATIONS PERSIST AT EQUILIBRIUM	NOT POSSIBLE	ONLY THE PREY POPULATION PERSISTS
	1	(NEED TO CONSIDER THE NEXT LOWER TROPHIC LEVEL)	THE PREDATOR POPULATION WAS UNDERMINED BY ITS PREY	(NEED TO CONSIDER THE NEXT LOWER TROPHIC LEVEL)
	2	THE PREY POPULATION HAS BEEN OVEREXPLOITED BY A DIVERSIFIED PREDATOR THAT HAS ALTERNATIVE SPECIES OF PREY	THE PREY POPULATION HAS BEEN OVEREXPLOITED BY A SPECIALIZED PREDATOR, DRIVING BOTH POPULATIONS TO EXTINCTION	RESOURCE LIMITATION CAUSED BY SOME COMBINATION OF COMPETITION, LOW PREY DENSITY, AND INEFFICIENCY LED TO THIS PREY POPULATION'S EXTINCTION

Figure 5. Reference chart for determining the appropriate extinction scenario for a particular population from information provided by the simulation. (a) Cause of extinction of zero implies that no extinction took place and the species under consideration is viable at equilibrium. (b) Cause of extinction of one indicates that every prey species included in the species in question's diet went to extinction, leaving it with no resources. (c) Cause of extinction of two indicates that the species considered went to extinction despite the availability of at least one prey species.

3. When a species reaches the extinction threshold (cause=2) but has no competitors or significant predators at the time of extinction (predator cause=2), then the extinction is due to a combination of insufficient resource availability and inefficient predation.

4. If a species reaches the extinction threshold (prey cause=2) after its predators are gone (predator cause=2) and it has viable competitors, its lack of invasibility is attributed to resource-limitation induced by competition—in other words—the species is outcompeted.

5. If a species goes to extinction because its prey species have overexploited their resources (cause=1 for predator, cause=1 for prey), then it has been undercut by lower level extinctions.

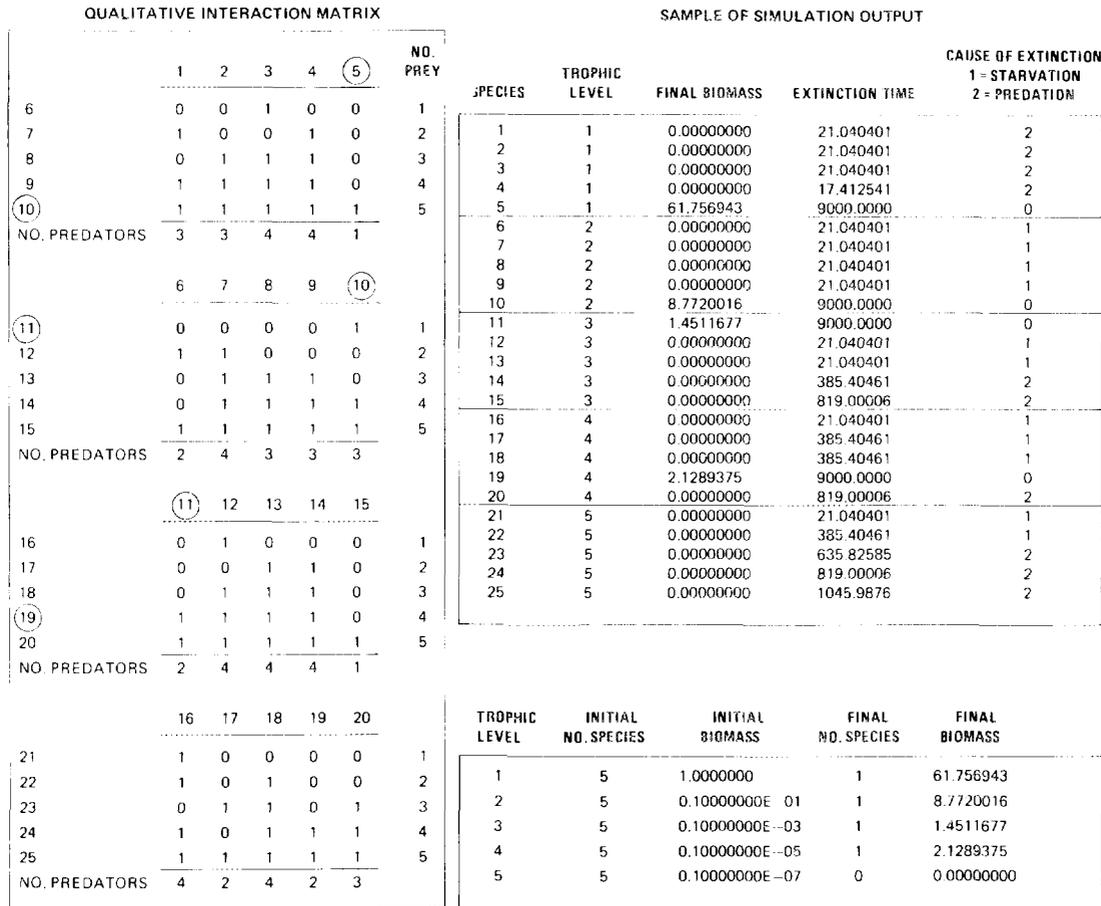
The relative importances of different vectors of species elimination in natural ecosystems has not been explicitly considered, to my knowledge. Reinterpretation of extinction vectors in terms of patch dynamics and local extinctions, rather than absolute elimination, would be prerequisite to such a tabulation. For example, does migration out of a patch due to insufficient prey availability constitute local overexploitation? As a validation technique, the ability to predict of both what is there and what is not, and why, would be quite reassuring since so many empirical results (what is there) in ecology can be derived from many alternative models (for example, lognormal species distributions, wildlife population cycles, species-area relations).

Each of the five extinction scenarios identified in the simulations has an analog in natural food webs. Accounts of species losses falling into the five categories are common in the ecological literature. One method of species elimination that seems to require justification is overexploitation. While the importance of overexploitation in spatially homogeneous model systems may

greatly exaggerate its ubiquity in nature by disregarding the many adaptive mechanisms which prevent its occurrence (e.g. prey refuges, invulnerable size or age classes, emmigration), overexploitation does occur with enough regularity as to play a role in food web structuring. Lynch (1979) reports that *Chaoborus*, an invertebrate zooplankter, is able to become abundant enough to eradicate any single species of herbivore by feeding on alternative species of prey, at least in the absence of vertebrate predators. In the presence of vertebrate predators such as salamanders and fish, *Chaoborus* itself is overexploited. (Actually there is probably a fair distinction between being overexploited or extinct and being undetectable for these zooplankton, since they have no trouble reappearing).

Another extinction scenario that has an air of unfamiliarity is the fifth case listed above. In open systems, one expects that predators unable to find prey will emigrate to more palatable patches. It is conceivable, however, that extinctions due to starvation occur. On a longer time scale, Fowler and McMahon (1982) hypothesize that selective extinction will tend to discourage the occurrence of specialists on higher trophic levels since their probability of extinction is dependent, not only upon their own qualities, but upon the extinction probabilities of their prey, and of their prey's prey, and so on. Paine (1963) demonstrated that predators of filter feeders in shallow-water marine habitats tend to show increased feeding diversity with increased trophic height.

Examples of each extinction scenario can be found in Figure 6, in which a single four-link food chain of species are the only surviving representatives of the original food web. In the figures, species #3 is overexploited by its specialized predator #6. Species #3 falls below the extinction threshold leaving



#6 without any prey. The cause of prey extinction is "2" and predator extinction is "1".

Species #15 was eliminated as a result of competition, even though its cause of extinction is "2", which is generally considered predation induced. This is because its predators are decaying simultaneously, which suggests that insufficient resource support, rather than predation, was the responsible factor. Since there are other third-trophic level species that are still viable competitors of #15's, competition, possibly coupled with inefficiency, is implicated.

Consider species #21 having cause of extinction "1", after losing its prey #16. This is not an example of overexploitation because #16 also has a cause of extinction of "1" due to the elimination of species #12 on the third trophic level. When, as in this case, both predator and prey have a cause of extinction of "1", the predator is said to have been undercut by lower level species extinctions.

With this breakdown of simulation information, it is possible to reconstruct the dynamics of the food web in ecological terms.

## CHAPTER III

### ANALYSIS

Two classes of variables were chosen to describe aspects of the food web simulations: structural and functional. The two aspects of web organization revealed by these classes are very interrelated in the sense that structure determines function, which in turn organizes food web structure in a dynamic loop of circular causality. Structure of the food webs refers to the skeletal configuration of species and their connections. Dynamic or functional variables estimate of the importances of different processes that influence food web organization over time.

#### 3.1 Structural Analysis of Simulated Food Webs

Structural variables describe the final equilibrium configuration of the simulated food webs. Figure 6 lists two structural variables, the final diversity (which is used throughout to mean the number of species), and the final biomass of each trophic level. Other properties, such as the final number of trophic levels (trophic height) and species composition, also fall into this category of structural descriptors. Also, because the final diagram of species interactions is closely related to the successes of species with different trophic strategies (many prey connections or few), the frequency of survival for each trophic strategy, on each trophic level, is tabulated and classified as a structural variable. This variable provides a functionally meaningful summary of final species composition as well. Changes in these structural variables are related, in each of the experiments, to the functional and dynamic attributes of

the web, and vice-versa. The functional-dynamic environment in which the web develops mediates its structural response to variations in the particular factor under consideration. For example, the response of a food web's final configuration (structural response) to productivity (factor) depends on whether species extinctions are caused primarily by lack of resources or by predation (functional environment).

### **3.2 Functional Analysis of Simulated Food Webs**

Functional variables are defined here as those which describe the distributions of intensity of predation and competition. It is assumed that competition and predation are the two primary forces organizing these simulated food webs. While this is not necessarily true in natural trophic communities, non-interactive forces (those not related to species interactions) are excluded from the model, so that any behaviors observed must be caused by these two forces. Presumably there are enough interactively organized ecosystems to make the study of organization by competition and predation worthwhile.

Using the extinction scenarios defined in Chapter II, one can summarize information from a sample of simulated food webs for use as indicators of predation pressure and competition. In the experiments, the total number of overexploitation events on a particular trophic level, summed over all of the sampled webs, is used as an indicator of the predation pressure exerted on that trophic level by its predators. The higher the number, the more accurate it would be to refer to that level as a predation-limited trophic level. Likewise, the frequency of extinctions due to competition can be tabulated from a collection of simulations and used to estimate the importance of competition in

structuring a particular trophic level. In addition, an index of prey overlap is used to infer the importance of competition in the food webs. This index considers all possible pairwise overlaps on each prey species. For example, if three species share a particular prey type, it is counted as three overlaps. However, four species sharing a prey resource have a total of six overlaps when they are considered as possible pairwise combinations. The maximum possible overlap count for a trophic level with five initial species is twenty because of the constraints in food web design.

As noted earlier, structure and function are not independent. In fact, this last index, the overlap index, is a perfect example of how a process such as competition can be measured through its more tangible manifestation in food web structure. Food web structure represents an integration of function (predation and competition) through time.

## CHAPTER IV

### FUNCTIONAL RESPONSE EXPERIMENT

#### 4.1 Introduction

Since Lotka-Volterra type models of food webs are the most practical tool available to the study of trophic ecology, understanding the robustness of structural predictions to deviations from linear Lotka-Volterra interactions is quite important. It would be very nice to discover that theoretical food webs are insensitive to the particular choice of formulation relating predation to prey density.

Lotka-Volterra dynamics describe the predators' per capita growth rate as a linear function of prey density. Weigert (1974) defends this simple model with the claim that "many predator-prey relationships seem to follow essentially this form with no obvious measurable response on the part of the predator to quite wide variations in prey density." The best argument for the choice of Lotka-Volterra representations is, however, one of expedience since this simpler formulation is easily solved. More complex models must either restrict themselves to consideration of simple food chains or rely on expensive simulation techniques.

An alternative formulation of the functional response to prey density is the so-called "type 3" response (Holling, 1959) which is credited with prolonging the global persistence of trophic systems at the very least, and with enhancing probabilities of local stability at best (see Hassell and Comins, 1978; May, 1977; Murdoch, 1969, 1977; Nunney, 1980). This sigmoid-shaped response curve shares with its predecessors (types 1 and 2) the property that

the feeding rate tails off at high prey densities. It is generally agreed that predators become saturated at high prey densities and are unable to increase feeding efforts in response to growing prey densities. This deceleration can have a destabilizing effect on isolated predator-prey interactions by permitting prey populations to “escape” the control of their predators by super-saturation. Prior to saturation, however, the type 3 sigmoid function is above the Lotka-Volterra line (see Figure 7) which helps to prevent an outbreak of prey. One additional feature of the type 3 response is that low prey densities depress the predator’s rate of feeding. This protects prey from overexploitation by its predators.

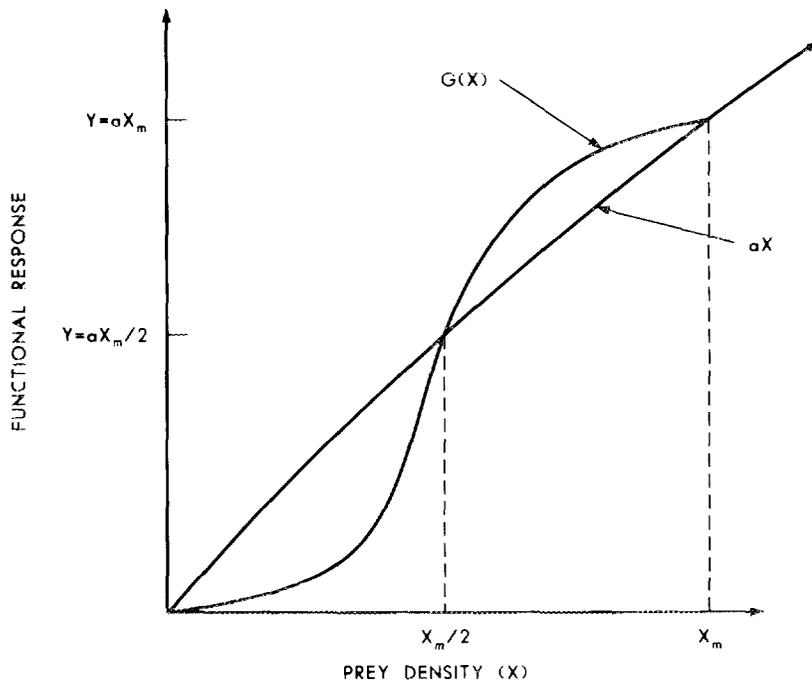


Figure 7. Function describing the relationship between feeding rate and prey density. Increasing the curvature of  $G(x)$  has the effect of depressing the feeding rate  $G$  when prey density is less than half its capacity ( $X_m$ ) and stimulating  $G$  for prey densities greater than this value.

There are several mechanisms in nature which can produce a sigmoid response to increasing prey density:

1. Predators who tend to switch to or concentrate on more abundant species of prey exhibit a sigmoid response, ignoring prey at low densities and feeding at a more than proportional rate at high densities.

2. For all predators there is a trade-off between time spent on foraging and time spent in other activities. At low densities of prey, it makes more sense for the predator to concentrate on non-feeding activities than on predation. Likewise, when foraging increases the predator's risk of predation, low densities of prey may be insufficient motivation for the degree of risk involved (Abrams, 1982).

3. In nature, spatial heterogeneity creates conditions which tend to protect prey at low densities. In many cases some type of prey refuge exists in which the risk of predation is minimal. In addition, predators frequently employ some degree of density-dependent patch selection which provides safety in low numbers for relatively rare prey.

In this model switching is not permitted since feeding on alternative prey is strictly proportional to abundance. The sigmoid response in this model applies to the total ensemble of a particular predator's prey densities and may be attributed to mechanisms 2 or 3 above.

## **4.2 Methods**

This is an experiment testing the effect of functional response curvature on food web dynamics and structure.

The general expression for population change in a species of intermediate trophic status is:

$$\dot{x}_i = \alpha g(\mathbf{E}_i \cdot \mathbf{X}) x_i - \sum_{j=1}^n E_{ij} g(\mathbf{E}_j \cdot \mathbf{X}) x_j - r x_i \quad (1-6)$$

where  $\alpha$  = transfer efficiency

$a_i$  = predation coefficient reflecting efficiency of predation

$r$  = rate of density dependent population loss not due to predation

$\mathbf{E}_i \cdot \mathbf{X}$  = sum of prey densities for species  $i$

$\mathbf{E}_j \cdot \mathbf{X}$  = sum of prey densities for species  $j$

$$g(\mathbf{E}_i \cdot \mathbf{X}) = \frac{-2}{3} \beta X_m^{-1} (\mathbf{E}_i \cdot \mathbf{X})^3 + \beta (\mathbf{E}_i \cdot \mathbf{X})^2 + \left\{ a_i - \frac{\beta X_m}{3} \right\} (\mathbf{E}_i \cdot \mathbf{X}) \quad (1-4)$$

is the general form of the functional response of a predator  $i$ 's feeding rate to its total prey density.  $X_m$  represents the maximum density of the first trophic level, and  $\beta$  represents the curvature of the functional response.

In this experiment, four levels of curvature were compared among simulations of food webs identical in all other respects. Let  $\beta = k \times \min_i(a_i)/X_m$ ,  $k=0,1,2,3$  (see Figure 3 on page 22). At the lowest level of curvature ( $k=0$ ), functional response is linear and the structural characteristics of these food webs are presumably representative of stable Lotka-Volterra webs discussed in literature. The upper end of the scale ( $k=3$ ) is a maximum for this particular formulation of functional response.

### 4.3 Results and Discussion

In general, food webs whose species exhibit a strongly curved functional response show a relaxation in predation intensity acting on the first trophic level. Table 2 shows a decline in the incidence of over-exploitation of autotrophs by their herbivore predators. The sigmoid response has the expected effect of protecting autotroph populations from their overzealous predators. As a result there is an increase in autotroph diversity in 85% of the food webs studied. A signs test indicates a significant increase in autotroph diversity at the  $p=.05$  level. The first two charts in Appendix C show the change in persistence of autotrophs.

Less expected, however, is the net increase in the incidence of over-exploitation on the herbivore level, where the sigmoid response fails to provide adequate protection of herbivores, at least for the same degree of curvature. On higher trophic levels there is no noticeable change in predation intensity as curvature increases. This suggests that the upper half of the sigmoid is encouraging predation on herbivores while the lower half is preventing overexploitation of autotrophs. To explain further, higher rates of predation by herbivores increase the supply of energy available to carnivores. This may have a less-than-desirable effect on herbivore persistence. The increase in throughput caused by the upper half of the sigmoid may also be responsible for the rise in equilibrium density observed for all trophic levels in the strongly sigmoid food webs. Equilibrium levels increased in two-thirds or more of the webs. In some cases the number of supportable trophic levels rose from four to five.

Table 2. Relative Importance of Resource and Predation-Induced Extinction in Food Webs Along a Continuum of Functional Response Curvature.

Trophic Level	Extinction Type	Functional Response Curvature (K)			
		0	1	2	3
1	Predation	63	57	51	31
	Resource	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
	Total	63	57	51	31
2	Predation	19	17	23	42
	Resource	<u>43</u>	<u>41</u>	<u>34</u>	<u>17</u>
	Total	62	58	57	59
3	Predation	29	29	31	30
	Resource	<u>27</u>	<u>26</u>	<u>23</u>	<u>24</u>
	Total	56	63	54	54
4	Predation	12	14	14	18
	Resource	<u>46</u>	<u>41</u>	<u>41</u>	<u>39</u>
	Total	58	55	55	57
5	Predation	0	0	0	0
	Resource	<u>79</u>	<u>77</u>	<u>78</u>	<u>77</u>
	Total	79	77	78	77

With the exception of autotroph persistence and webs on the threshold of adding a new trophic level, trophic structure seems to be quite robust to the type of variation in functional response considered here. Its influence on food web function, including productivity and standing crop density is more dramatic and is not apparent from the structural configuration of the webs.

## CHAPTER V

### EXCLUSION EXPERIMENT

This experiment is designed to study the influence of food web height—the number of trophic levels—on other aspects of food web organization. The food webs compared in this experiment are identical in all respects except that higher trophic levels are removed one by one until only two levels remain. This yields four treatments with five, four, three, and two levels, respectively.

In field ecology this type of manipulation experiment is performed by excluding predators from a particular community and observing changes in structure and species composition that occur (see Dayton, 1971; Thorp and Bergey, 1981). Changes in abundance and diversity are monitored following the removal or exclusion of predators. This provides a useful method for assessing the importance of predation in a particular community. Usually effects on competitive communities are studied, rather than on large, multi-level food web systems.

#### 5.1 The Exploitation Hypothesis

##### 5.1.1 Introduction

In this model analog to an exclusion experiment, Fretwell's theory of alternating predation and resource control of food chains is tested for the model food webs simulated. In essence, the experiment tests the hypothesis that simulation food webs are polarized—having trophic levels that are strongly

resource or predation-limited, but not both. The hypothesis specifies further that odd levels from the top trophic level are predation-limited while even trophic levels are controlled by their resources. The null hypothesis is that resources (predators) are less-than or equal-to predators (resources) in importance for odd (even) trophic levels. There are three implications of Fretwell's exploitation hypothesis that can be tested here:

1. Resource-limited trophic levels, starting with the top predators and alternating down, are organized by competition and should exhibit lower levels of prey overlap.

2. Species on trophic levels predicted by Fretwell to be predation-limited should run a higher risk of overexploitation than species on levels that are, presumably, resource-limited.

3. Standing crop densities of any trophic level should increase or decrease, depending on whether it becomes resource or predation controlled by the removal treatment. By implication, changes in adjacent levels should be negatively correlated, while densities of alternate trophic levels should change in the same direction.

Ample experimental support exists for the contention that removal of a top trophic level can lead to a series of switches in limitation between resource and predation control. By way of example, three cases are described.

Estes et al. (1978) compared islands on which sea otters were present to those on which they were not, in a system based upon macroalgae and their epibenthic invertebrate predators. Of these predators, the sea urchins were the dominant herbivores and constituted an important food source for sea otters. On the island occupied by sea otters, the authors observe that competitive

interactions dominate the macroalgal association because herbivorous species are virtually absent.

When sea otters are removed from this system, the predominant roles of competition and predation are transposed: macroalgae are limited by predation (grazing) and the epibenthic invertebrates (most of which are herbivorous) by competition.

In addition to these observations of controlling processes, Estes and others have observed the response of abundances to predator removals (third corollary) in natural systems. As a result of sea otter removal, sea urchin biomass rose from 374 g/.25m to 3,082 g/.25m and macroalgae were drastically reduced, "essentially absent because of intense overgrazing by the abundant sea urchins" (Estes et al., 1978). In another study, Virnstein (1977) studied the significance of crab and bottom-feeding fishes in controlling the abundance of macrobenthic invertebrates within the sediments (the infauna) of a subtidal sand community. He found that the "densities of all infaunal species increased in exclosures, suggesting that their population densities under natural conditions are not controlled by competitive interactions." A third study by Lynch and Shapiro (1981) on Pleasant Pond revealed an increase of an order of magnitude in phytoplankton biomass following the addition of fish to the system. In addition, they cite numerous examples in which the removal of large herbivorous zooplankton by fish results in a significant increase of phytoplankton abundance. They warn that exceptions to this rule can be found. For instance, in cases where some species are immune to predation, or, in situations in which some species are able to grow to ungrazable levels with the help of a refuge prior to exposure to predation the presence of fish may have less impact.

These examples verify that Fretwell's theory can have application in some trophic systems in nature. Added support comes from the chemostat experiment performed by Chao et al. (1977) in which it was learned that the two stable states of coexistence between bacteria and phage populations were:

- (1) a phage-limited situation where all of the bacteria are sensitive to the coexisting viruses and the sole, and potentially limiting carbon source, glucose, is present in excess; and
- (2) a resource-limited situation where the majority of the bacteria are resistant to these phages and in which there is little free glucose.

From this experiment one might conjecture that mechanisms exist which polarize food webs, tending to accentuate the intensity of one or the other process. The change in polarity as a system moves toward its equilibrium trajectory is not known. This can perhaps best be studied by measuring the difference between sums of partial derivatives with respect to predators and with respect to resources through time for species on each of the trophic levels. In the simulation experiments performed here the functional and structural variables monitored are actually integrations of past fluctuation in the control regime, and may be misleading in inferring the degree of polarization at equilibrium. As a first guess, one might predict that the top predators comprise the driving force, polarizing the web by exerting a strong influence on their prey. As this influence is weakened the polarization should decrease but then increase as the prey level becomes strongly resource-limited, essentially in the absence of its top predators.

### 5.1.2 Methods

Thirty-seven food web structures having five trophic levels each were created according to the description of methods in Chapter II. Four, three, and two level counterparts were then formed by successively removing the highest trophic level from the webs. All four treatments were then simulated for each of the 37 configurations. Figure 8 shows a sample sequence of one five trophic level food web and the successive removals of its trophic levels, starting at the top of the web. The circled species are those that survived the simulation, belonging to the equilibrium configuration of the web. This experimental design differs from most field exclusion experiments in that the top level is removed, in each case, before the system moves toward its five-level equilibrium. The trophic system develops in the absence of the excluded predators. The best way to think of this is to imagine four initially disturbed plots, one having its tertiary carnivores excluded, the next without both secondary and tertiary carnivores, and so on, with only herbivorous predators permitted in the fourth plot.

Three of the implications associated with Fretwell's exploitation theory deal with the classification of trophic levels as predation or resource-controlled. By hypothesis, species belonging to trophic levels an odd number from the top are predation-limited and levels an even number down are resource-limited. In the first corollary, prey overlap in the resource-limited trophic levels is expected to be lower than overlap in the same trophic level when it is predation-limited, supporting an odd number of predator trophic levels. Resource overlap found among predators on each trophic level can be compared every time a top trophic level is removed to see whether the expected

TWO TROPHIC LEVELS						THREE TROPHIC LEVELS						FOUR TROPHIC LEVELS						FIVE TROPHIC LEVELS						
①	②	③	4	⑤		①	②	③	4	⑤		①	②	③	4	⑤		①	②	③	4	⑤		
6	0	0	0	1	0	6	0	0	0	1	0	6	0	0	0	1	0	6	0	0	0	1	0	
⑦	0	0	1	1	0	⑦	0	0	1	1	0	⑦	0	0	1	1	0	⑦	0	0	1	1	0	
8	0	1	0	1	1	8	0	1	0	1	1	8	0	1	0	1	1	8	0	1	0	1	1	
⑨	1	1	0	1	1	⑨	1	1	0	1	1	⑨	1	1	0	1	1	⑨	1	1	0	1	1	
⑩	1	1	1	1	1	⑩	1	1	1	1	1	⑩	1	1	1	1	1	⑩	1	1	1	1	1	
							6	⑦	8	⑨	⑩		6	⑦	8	⑨	⑩		6	⑦	8	⑨	⑩	
						11	0	1	0	0	0	11	0	1	0	0	0	11	0	1	0	0	0	
						12	0	1	1	0	0	12	0	1	1	0	0	12	0	1	1	0	0	
						⑬	1	1	0	1	0	⑬	1	1	0	1	0	⑬	1	1	0	1	0	
						⑭	0	1	1	1	1	⑭	0	1	1	1	1	⑭	0	1	1	1	1	
						15	1	1	1	1	1	⑮	1	1	1	1	1	⑮	1	1	1	1	1	
													11	12	13	14	15							
												⑯	0	0	0	1	0	⑯	0	0	0	1	0	
												17	1	0	1	0	0	17	1	0	1	0	0	
												18	0	1	1	1	0	18	0	1	1	1	0	
												19	1	1	0	1	1	19	1	1	0	1	1	
												⑳	1	1	1	1	1	⑳	1	1	1	1	1	
																			⑯	17	18	19	⑳	
																			21	0	1	0	0	0
																			22	0	0	1	1	0
																			23	1	0	1	1	0
																			⑳	1	0	1	1	1
																			25	1	1	1	1	1

Figure 8. Sample sequence of initial food webs used in the exclusion experiment. From right to left, higher trophic levels are removed from the prior to simulation of the food web. In this example, the only compositional change is the removal of species #15 in the absence of predation by the fourth trophic level.

switches are taking place. The first step taken in analyzing simulation results was to exclude series of webs in which no changes in overlap occurred as trophic levels were removed. For each trophic level in which any change was observed, the overlap was noted. Sample sizes for the respective trophic levels are herbivores (6), primary carnivores (29), and secondary carnivores (16). The difference between this value and the total number of webs simulated for each treatment (37) indicates the number of structures in which no change took place.

The second implication of Fretwell's exploitation theory predicted that predation intensity, as reflected by the incidence of overexploitation, should increase on trophic levels hypothesized to be predation-controlled. On each trophic level, the total number of overexploited species counted in the sample of 37 webs was used as an indication of predation intensity. Both this and the previous corollary were tested using functional indices to estimate the control regime of each trophic level.

The last corollary deals with the manifestation of the two control regimes (predation and resource) on the species in the food webs at equilibrium. At equilibrium, the biomass of each trophic level is expected to increase with each transition from predation to resource control when an odd level above is removed. For each trophic level and web height, the range of equilibrium biomass was found over the collection of simulated webs.

### 5.1.3 Results

Fretwell's exploitation hypothesis of alternating predation and resource control is difficult to test directly, either in the field or in model experiments

such as this. There are implications of the theory, however, that are testable. Three of these were described in the introduction.

The first implication is that trophic levels hypothesized to be resource-limited should have less resource overlap among species on the same trophic level than predation-limited levels. Figure 9 illustrates that this is true for the webs in this exclusion experiment. Along a gradient of increasing trophic height, prey overlap tends to increase or decrease, depending on whether the trophic level is regulated by predation or competition in accordance with Fretwell's hypothesis. A removal that switches control of a given trophic level from predation to resource control results in a decrease in prey overlap, and vice versa. To qualify this result somewhat, it is unusual to find overlap increasing and decreasing nicely as expected for any one food web as levels are peeled off, mainly because of the tendency for species composition to remain constant. Overall, however, the total overlap in a sample of 37 food webs shows support for Fretwell's theory. It is unusual for the "wrong" change to occur, contradicting the theory. A signs test ( $p=.05$ ) was used to test the null hypothesis that trophic levels changing from an odd to an even number of links below the top (even to odd) will show either an increase (decrease) or no change in resource overlap. In a sample of 59 transitions in which overlap changed, a significant number (52) changed in the direction predicted by the first implication of Fretwell's exploitation theory. When transitions from even to odd and from odd to even are considered separately it appears that the first case, presumably a transition from resource to predation control of a trophic level, is more likely to increase resource overlap among predators (42 out of 45 transitions) than the reverse transition is to decrease overlap (10 out of 14).

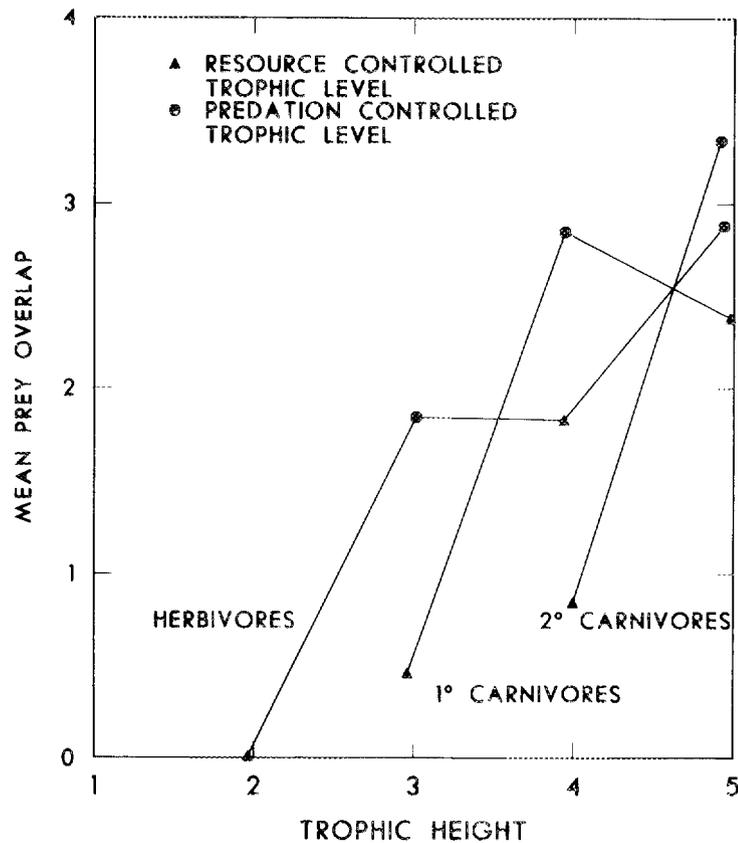


Figure 9. Prey overlap for each guild as higher trophic levels are removed. Triangles identify trophic levels that are resource-controlled by hypothesis and circles denote those hypothesized to be predation-controlled. Prey overlap appears to be better tolerated on predation-controlled levels.

The second implication of Fretwell's theory is that overexploitation should be more frequent between trophic levels hypothesized to be resource-limited and their predation-limited prey. The extinctions experienced by species on a particular trophic level should be mostly predation-induced (i.e. caused by overexploitation) on odd trophic levels from the top and resource-induced otherwise. In the simulations, the incidence of overexploitation was used as an index of predation intensity.

Table 3 lists the number of species driven to extinction by predation and the number of extinctions caused by insufficient resource support for each trophic level of food webs of varying heights.

Table 3. Relative Importance of Predation and Resource-Induced Extinction in Food Webs of Different Heights.

Trophic Level	Extinction Type	Trophic Height			
		Two Levels	Three Levels	Four Levels	Five Levels
1	Predation	106	64	70	65
	Resource	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
	Total	106	64	70	65
2	Predation	0	68	76	76
	Resource	<u>126</u>	<u>44</u>	<u>37</u>	<u>35</u>
	Total	126	112	113	111
3	Predation		0	48	55
	Resource		<u>126</u>	<u>48</u>	<u>40</u>
	Total		126	96	95
4	Predation			0	27
	Resource			<u>114</u>	<u>59</u>
	Total			114	86
5	Predation				0
	Resource				<u>142</u>
	Total				142

Beginning with the top left-hand entry (the autotroph level of food webs having two trophic levels), every other position in the grid is hypothesized to be predation-controlled, with the number of extinctions caused by predation exceeding the number caused by lack of resources. Adjacent column and row entries belong to resource-limited trophic levels according to the theory. The only trophic level that showed the expected pattern was the autotroph level, with predation intensity decreasing for autotrophs in food webs having an even number of trophic levels. All trophic levels that were subject to both resource

and predation induced extinctions failed to support the hypothesis. While the initial addition of a predator trophic level shifted control from resources to predation, adding higher levels seemed only to reinforce the trend toward stronger predation-control.

In general, the addition of higher trophic levels had the effect of increasing the number of predation-induced extinctions. This effect was greatest for the first level added and quickly reached a point beyond which further growth in web height had no effect on the number of extinctions. It was also observed that the percentage of extinctions due to predation decreases almost linearly as higher trophic levels are considered, with a complementary increase in the importance of resource-induced extinction. This is shown in Figure 10. The oddness or evenness of a trophic level had very little influence on these percentages (maximum variance = .004).

To recount, the main effects demonstrated by the extinction data are as follows:

1. Trophic status has the strongest effect, causing a shift from predation to resource-induced extinction for higher trophic levels.
2. Overexploitation of autotrophs does follow the pattern predicted by the exploitation theory, and
3. A shift from resource to predation-induced extinction accompanies the first addition of a trophic level, but the effects of subsequent additions are insignificant for all consumer trophic levels.

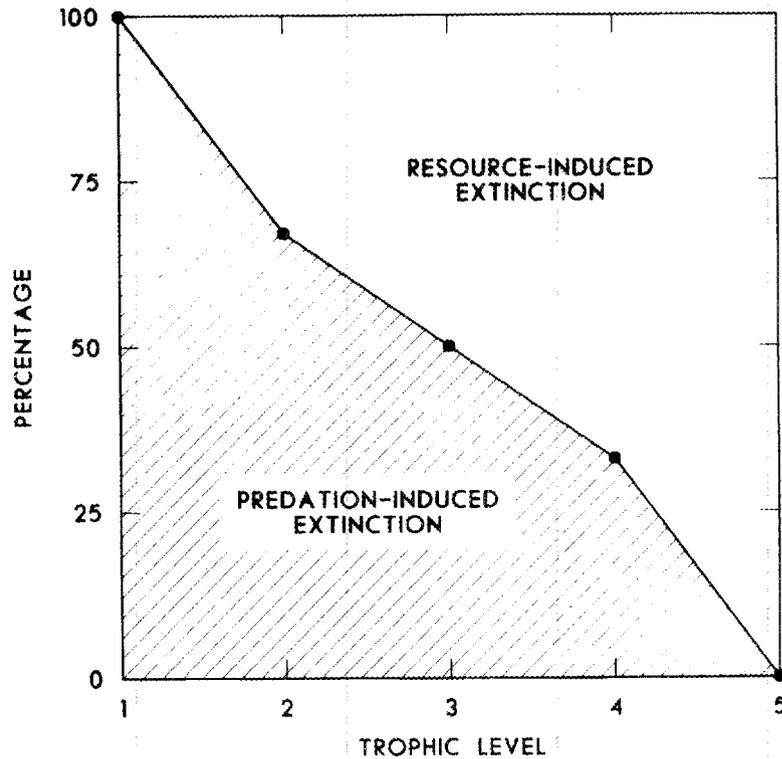


Figure 10. Percentage of extinctions caused by resources and predation as a function of trophic height. Points indicate the percentage of extinctions that are caused by predation (overexploitation). The percentage caused by resource-limitation is 100% minus this value.

#### 5.1.4 Discussion

One paradox in these results is that resource overlap is better tolerated among species of higher trophic status despite the growing predominance of resource-induced extinction higher in the food web. Partial explanation may come from the fact that some of the extinctions experienced by species on higher trophic levels are a consequence of lower trophic level extinctions. Resource support is cut out from under those species. The remaining species are usually generalists with alternative species of prey. Consequently, the remaining species may share a large proportion of their prey.

One might argue that extinctions caused by loss of prey at lower trophic levels misrepresent the degree of resource-control acting on the remaining species on the higher trophic level since competition is not involved. If competition among overburdened prey of high trophic status is resolved to a large extent by species closer to the base of the food web, with species feeding on the dominant food chains persisting, then the effect of being shared by predators is greatly diminished. For example, if a potentially-dominant prey species supporting only one predator depends on resources that go to extinction, then this potential dominant will go to extinction, leaving competitors that support more predators. In other words, success or failure at higher trophic levels may be largely determined by the outcome of competition and predation at lower trophic levels, without regard to the relative merits of the species selected. While the number of species that reached extinction because their resources were undermined is not a large proportion of total resource-induced extinctions, the tendency for resources to mediate the selection of species at higher trophic levels has the same general effect, though less extreme, when higher level species are only partially undermined.

The last implication drawn from Fretwell's theory is the prediction that resource-limited trophic levels will support a larger standing crop. Figure 11 shows that equilibrium densities of alternate levels are positively correlated and that adjacent levels show negative correlations in these simulations. The figure depicts the range of densities at equilibrium for the subset of food webs capable of supporting five trophic levels (35) as successive levels are added. This last implication of the exploitation theory is unequivocally supported by the simulated food web results. Standing crop, at least, seems to show the expected alternating pattern of response to the oddness or evenness of its

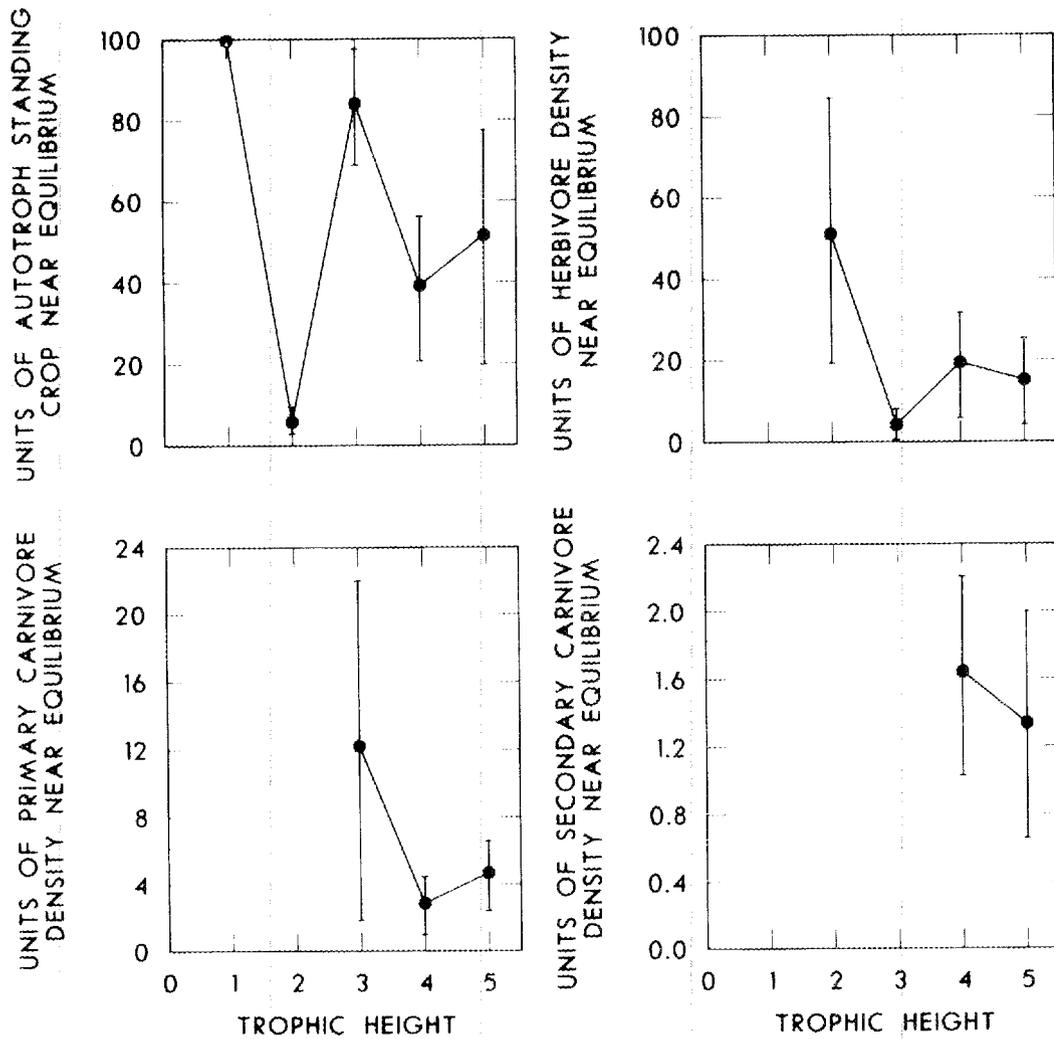


Figure 11. Range of equilibrium densities for food webs with one-to-five trophic levels. Each point designates the midpoint of the range in density (bars) observed in simulated food webs. For example, for all food webs simulated with only one trophic level, autotrophs had a standing crop density of 100 units, with no variation (top-left).

trophic position. The alternation of control seems not to have been diluted beyond detection by the occurrence of different length chains in the final food webs.

In the present study, three implications of the exploitation theory were tested using three different types of information about the relative importance of predation and resources in structuring the webs. Results show that the three types of information: biomass, extinction vectors, and overlap, are not synonymous indicators of predation vs. resource control.

The original purpose of this experiment was to test the theory that trophic levels alternate between resource and predation limitation from the top of the food web down. Since the control or limitation of a trophic level is typically defined as the change in biomass induced by increasing resources (resource-control) or by reducing predator biomass (predation-control), These simulations support the exploitation theory in the test of implication 3 which involves standing crop densities. This definition of limitation depends on the densities attained by species that have successfully established in their respective communities. If densities within a particular trophic level are uneven, then limitation of a trophic level may be defined mainly by its dominant species.

The selection process through which the species composition of a given trophic level is determined seems, however, to emphasize the importance of resource-control or predation-control according to height in the food web, rather than the oddness or evenness of its trophic position. In the investigation of implication 2, a continuous shift in selective importance of predation-related to resource-related species characteristics was observed. This finding is in close accordance with the scheme offered by Menge and Sutherland (1976).

Figure 12 is borrowed from their article as a diagrammatic representation of the theory. The success formula for a species in these model food webs depends upon its general trophic status, and does not vacillate as transient species of top predators enter and leave the web. It is interesting that the regulation of standing crop, which depends on the dominant species, and the regulation of species composition (extinction-persistence), operate so differently in response to trophic position and web height. The autotroph level of a three-level food web contains species (or at least a dominant) that are resource-limited, maintaining densities close to capacity, even though the persistence of autotroph species depends exclusively (in this model) on their susceptibility to predation. Figure 13 illustrates the pattern of resource and predation control over species selection and biomass.

In natural food webs there are at least two problems that restrict extrapolation of these results to real-world systems. First, omnivory—feeding on more than one trophic level—is quite likely to blur the alternating effect, possibly in interesting ways. Theoretically, coexisting food chains (or subwebs) may have opposite control regimes as a result of omnivory. This implies that the resource-limited species should dominate, if not outcompete, their predation-limited competitors on each trophic level. This has been observed in some food webs in which the two dominant autotroph species were those that supported three-link food chains. Their grazers were fed upon by primary carnivores, while autotrophs supporting grazers that were not subject to carnivorous predators had much lower densities.

Secondly, the extent to which the real-world system is interactively regulated is likely to limit the applicability of these theoretical results in which non-biological influences such as disturbance and seasonality are ignored. In

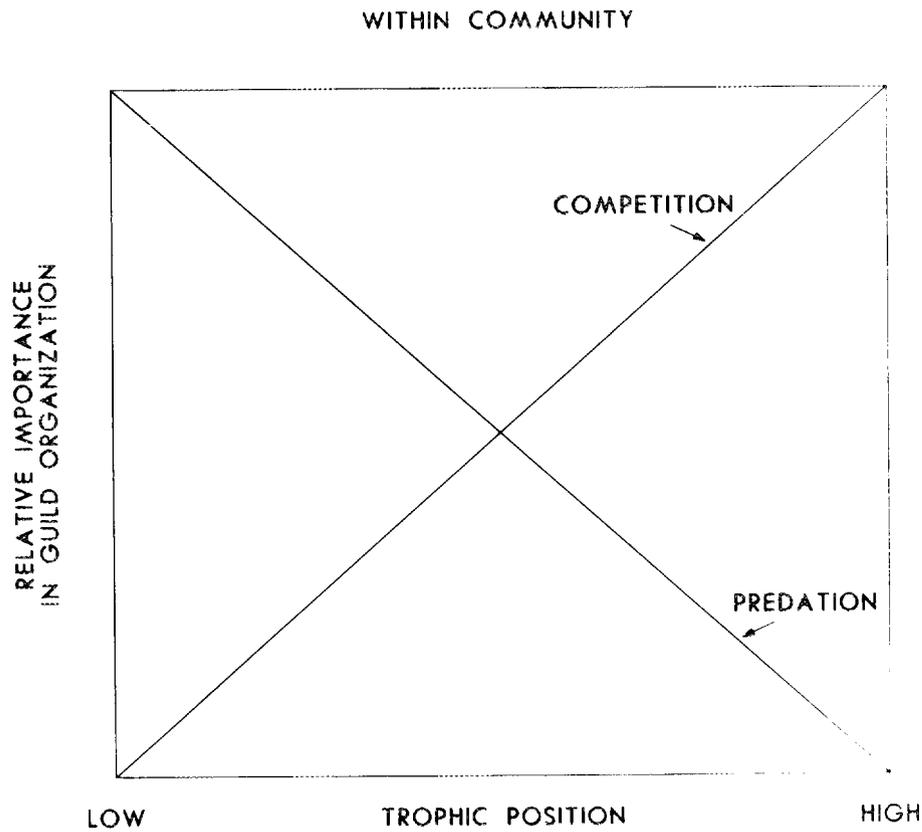
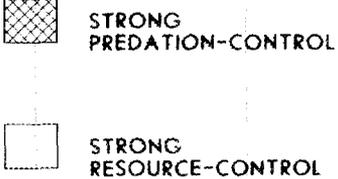


Figure 12. Guild structuring as a function of trophic position. Menge and Sutherland (1976) offer this conceptual diagram as a hypothetical description of the roles predation and competition play in structuring guilds with high and low trophic position.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110:351-369.

SELECTION OF SPECIES	TROPHIC LEVEL	BIOMASS LIMITATION
	1	
	2	
	3	
	4	
	5	



STRONG PREDATION-CONTROL

STRONG RESOURCE-CONTROL

Figure 13. Resource and predation control of species composition and biomass for food webs with five trophic levels.

other words, not only can “non-equilibrium” influences preclude competition, they can mitigate the importance of predation, and of species interactions in general. In fact, Fretwell’s argument suggests that this is true for adjacent trophic levels. If, for instance, top predators are reduced in density to the extent that competition is trivial, they are unlikely to control their prey which would, in any case, be reduced by disturbance. This might have the effect of “depolarizing” food webs. It would be interesting to study the effect of disturbance on food web polarity.

In many systems, the structure of natural food webs is not constant, but instead seems to resonate, as Gallopin (1972) puts it, among alternative

configurations due to seasonal, hydrologic, or other environmental influences. For some systems, this resonance may involve cycling between even and odd numbers of trophic levels. An example of this might be a Canadian marsh food web to the top of which flocks of seasonally migrating herons are added in the warmer months. In cases where some degree of omnivory on adjacent trophic levels and different chains occurs, perhaps at the higher levels, the effect of the resonance may be to prevent exclusion of predation-limited by resource-limited species. This illustrates the suspicion that applications to natural systems can become complicated fairly quickly.

## 5.2 Predator-Mediated Coexistence

### 5.2.1 Introduction

The second hypothesis to be discussed is the hypothesis of predator-mediated coexistence which suggests that prey diversity can be increased by adding predation (See Paine, 1966; Glasser, 1979; Caswell, 1978). This increased diversity results when predation on competitively-dominant species has the effect of preventing the exclusion of less-successful competitors. Predator-mediated coexistence is contained in the intermediate predation (“disturbance”, in its most general form) hypothesis which claims in addition that excessive levels of predation will lower diversity.

Predator-mediated coexistence is typically observed in systems in which two-dimensional space is a primary limitation. Paine (1966) demonstrated the effect in the rocky intertidal zone, where removal of the starfish *Pisaster* resulted in a decrease in the diversity of its prey species, with *Mytilus* and *Mitela* monopolizing the available space. Dayton (1974) found that the sponge,

*Mycale*, was reduced by its asteroid predators to the point of being quite rare in an epifaunal benthic community of Antarctica, despite its outstanding growth rate advantage over other sponges.

More recently, Hay (1981) demonstrated that selective removal by reef-associated grazers prevented algal assemblages found in the adjacent sand plains from competitively-excluding other species residing in the reef slope habitat. In this system, species of algae that are physiologically better-suited to the reef habitat are restricted to the marginal sand plains where they find refuge from grazers. It appears that grazing by reef-dwelling organisms is severe enough to cause local-extinction of competitively-dominant algae.

The intermediate predation hypothesis offers the explanation that predation intensity on the reef is beyond the interval along which diversity is increasing (the mode of the diversity response curve). This study of inter-habitat trophic relations has several interesting theoretical implications. First, such a classification of habitats as refuge and non-refuge areas may be a useful approach to the study of food webs in spatially-heterogeneous systems. It suggests also that it may be possible to predict species compositions of adjacent food webs from trophic structures that emerge with and without top predators. At the scale of presence-absence information, a model similar to WEB, but including the appropriate ecological detail in its trophic parameters, may be able to estimate food web composition emerging in refuge and non-refuge patches from the total pool of available species. The significance of this would be the ability to disregard dispersion rates of species and other parameters involving movement among patches.

### 5.2.2 Methods

In the second part of the experiment the effect of trophic level removals (trophic height) on diversity (numbers of species) was examined. Consideration of the changes in diversity associated with the removal of a trophic level involved calculating the total number of species on a particular trophic level and a given web height for the collection of food webs simulated. The direction of change in diversity for each level removal was tabulated in order to test the operation of predator-mediated coexistence in this model. Changes in success were also traced down to trophic strategy to discover how diversity is augmented by predation and which strategies account for the difference in diversity.

### 5.2.3 Results and Discussion

The purpose of this experiment was to interpret the changes in diversity that accompany the removal of top trophic levels. The theory to be tested was that of predator-mediated coexistence, which claims that addition of a trophic level will increase the diversity of the next level down by preventing competitive exclusion by the dominant prey species. First, the occurrence of competitive-exclusion is considered in the simulated food webs, followed by a test of the theory that predator-mediated coexistence follows trophic level additions in the webs.

In food webs having two trophic levels it was found that there was no resource overlap among predators (see Figure 9 on page 52). In each web, some combination of species was selected among which there is no sharing of prey by predators—no competition. Each prey species wound up with exactly

one predator species. Those prey which initially supported many predators were overexploited. This overexploitation process eliminated a few of the more specialized predators. If too many are overexploited, only the complete generalist would survive, but usually some complementary relationship worked out between the next-to-most generalized predator and one of the specialists such that the prey species lacked by the aforementioned generalist became exploited by the specialist, and any prey which they might have shared at one time were overexploited. Species which coexist on the same trophic level but do not share any prey in the final configuration of the food web, at equilibrium, are referred to as complementary species. For example, in Figure 6 on page 33, species #7 and #9 are complementary.

This is not terribly surprising in light of Levin's (1970) general theorem which was modified later by Kaplan and Yorke (1977) to read: "In an ecological community in which some  $n$ -species are limited by  $k < n$  limiting factors, there is probability zero that the system tends to equilibrium." This is illustrated by an example of two competing species, one which is a very effective predator at low prey densities and another which predominates at high densities of prey. Two zooplankton species, *Ceriodaphnia* and *Daphnia pulex* have this type of competitive relationship (Lynch, 1979). The pair may coexist at some intermediate level of prey density, but the probability that the prey density is exactly that value is zero.

While large numbers of predators on a single prey are a considerable handicap on any trophic level, total competitive-exclusion to the extent that no resource overlap persists occurs only on the herbivore level of these model food webs, and only when two trophic levels are present. Although one might expect to find complementary species on the top trophic level for any web height, this

is not the case, as prey sharing is common among top level species in higher structures. In fact, the degree of overlap increases with increased height in the web. On the herbivore level, no more than two predators share a given species of plant in the final configurations sampled in this study. Among carnivores, however, as many as four predators were observed feeding on a single prey species. In addition to the increase in the absolute numbers of predators able to share a species of prey, the tendency for all prey to have equal numbers of predators decreases with trophic height as well. In other words, the competitive-exclusion principle may not strictly apply to top carnivores in a three level food web, but it is equally unlikely that an herbivore will suffer many more predators than its competitors and survive. Since they are related, it is difficult to separate the relaxation of the rule of minimal overlap with increased trophic height from the decrease in evenness. When the average number of shared predators is small, the variance is also.

Intuitively the reason that competitive-exclusion is not strict for competitors at higher trophic levels in this food web model is that overburdened prey which would have been overexploited as autotrophs have more flexibility in finding support for their predators. On the autotroph level only predation determined competitive rank in this model since no differences in autotroph growth rates or other parameters were involved. Any plant species having more predators than one of its competitors was forced to extinction. The success of species on higher trophic levels depends both on the state of its resources and its burden of predators. Competitors are therefore equipped with new possibilities for equivalence that do not rely solely on supporting the same common denominator of predators. Trade-offs between resources and predators

are found that will permit prey species to coexist in spite of large differences in the number of predators supported.

Addition of a third trophic level to the food webs helps to prevent overexploitation of overburdened autotrophs and tends to permit resource overlap. This tends to raise both herbivore and autotroph diversities. While resource overlap may be permitted, one does not necessarily find increased herbivore diversity in the transition from two to three trophic levels. The added carnivore level also has the ability to overexploit herbivore specialists, the superior competitors. Although there is a net increase in herbivore diversity with the additional level, it is because the generalists added by predator-mediated coexistence outnumber the specialists and moderates lost. In thirty-seven simulations, the number of successful completely-diversified predators rose from seven in the two-level webs to twenty-seven in the three level versions.

Figure 14 shows clearly that the absolute number of successful competitors increases dramatically when a higher level of predators becomes viable. In the transition from two to three levels the number of herbivores rises, in the transition to four trophic levels the primary carnivores increase in diversity, and the addition of the fifth level supplements the diversity of secondary carnivores. A signs test reveals that the tendency for diversity to increase with added predation is significant ( $p=.05$ ) for both primary producers and secondary carnivores.

Figures 15 and 16 give an indication of which competitors are being added with the help of predation. At lower levels of the web, predation acts mainly to bring the generalist with five prey into the food web. Higher in the web predator-mediated coexistence is less selective in its mediation, enhancing

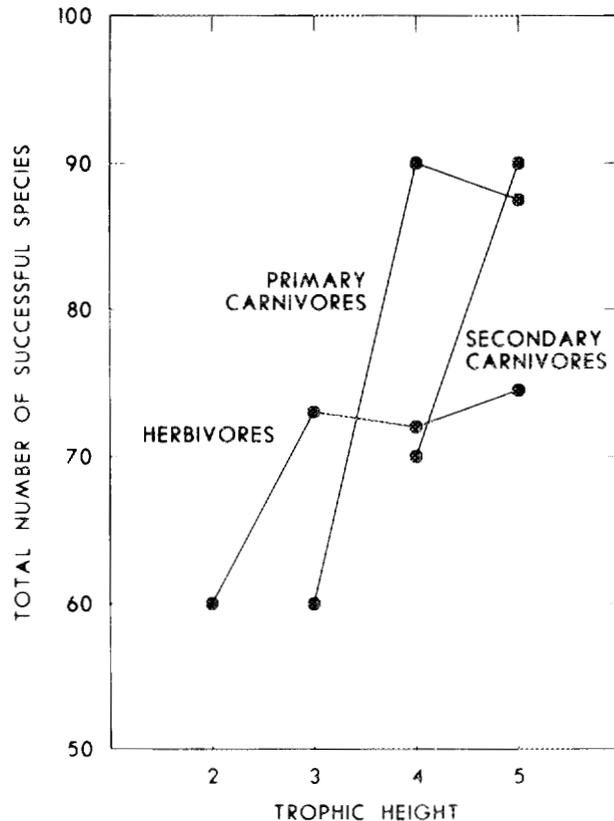


Figure 14. Total species survival for three intermediate trophic levels as top predator levels are removed. In 37 simulations, the total possible number of surviving species is 125.

the probabilities of success for most strategists. The strategists are treated more equally than on the lower levels where mediation showed a distinct bias for complete-generalists. On the herbivore level, adding a third level actually selected against specialists, while on the third and fourth levels the success of specialists was enhanced, although not nearly as much as that of the most diversified predator. Refer to Appendix C for tallies of each species success in 37 simulated webs and with different numbers of trophic levels.

The main results derived from this analysis of trophic height and its effect on diversity are as follows:

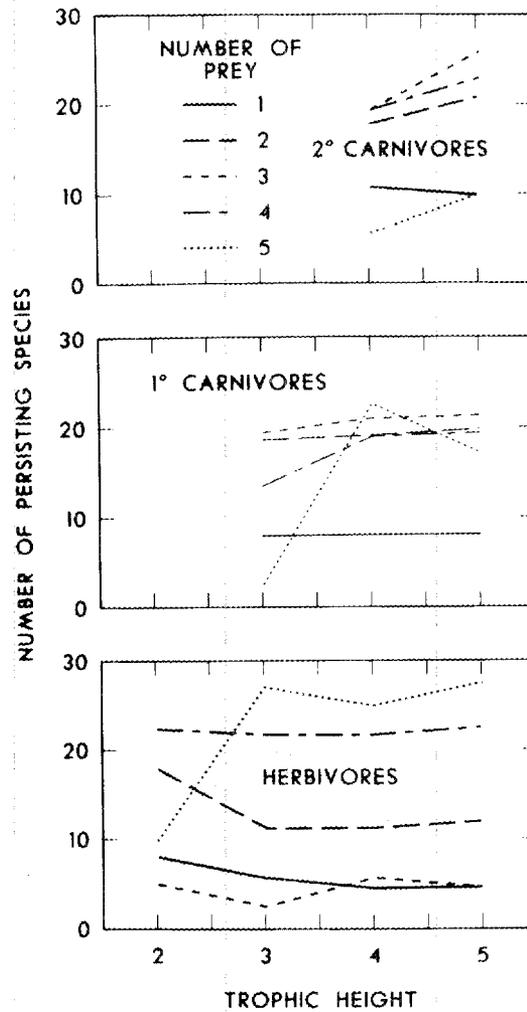


Figure 15. Total number of persistent species for each trophic strategy as trophic height increases. The maximum possible number of surviving species of a given trophic strategy is 37.

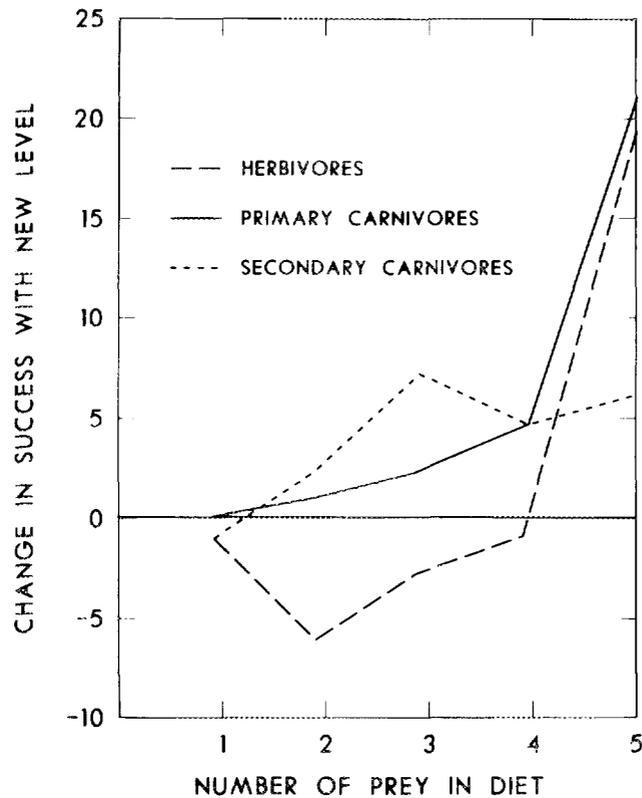


Figure 16. Change in strategy success with the removal of each trophic level. The vertical axis indicates the difference between the number of viable species before and after removal of the next higher trophic level for each trophic strategy.

1. The competitive exclusion principle fails at higher trophic levels in the food webs simulated. In addition, the amount of prey overlap present in the webs shows a strong tendency to increase with increased height in the food web, overlaid with a weaker tendency for increased tolerance for overlap on trophic levels hypothesized by the exploitation hypothesis to be predation-controlled. In distinguishing two types of trophic level control (biomass and species selection), it was observed that predator-controlled species selection of prey is the most important prerequisite for competitive exclusion in these model food webs, and not the degree of resource-limitation of predators.

2. In spite of the potential danger of overexploitation with the addition of a new trophic level, guilds that developed in the presence of their predators generally maintained higher species diversity than those that developed without predators. Less expectedly, carnivores had a greater positive influence on the diversity of autotrophs than on herbivore diversity.

3. In terms of trophic strategy success, the most frequent benefactors of predator-mediated coexistence in these simulations were the extremely generalized species, regardless of trophic status in the web. However this bias toward the generalists diminishes as one considers taller food web structures. Predation is detrimental to specialists on the herbivore trophic level, but aids in their success higher in the web.

This result seems the most applicable to natural systems, but less is known about its robustness to assumptions in this model, and about its occurrence in real food webs. It predicts that colonization will begin with a competitively exclusive community of herbivores feeding on plants that are joined by extremely generalized herbivores in the aftermath of an invasion by primary carnivores. As species of even higher trophic status move into the community, to exploit the primary carnivores, mostly those with diversified feeding habits, but also species with less diverse diets will join the food web on the third trophic level.

The validity of the simulation result that generalized species are the main benefactors of predation, and that species of intermediate and more specialized feeding diversity or specialists are competitively dominant in the absence of predation can be tested in different types of natural food webs.

## CHAPTER VI

### PRODUCTIVITY EXPERIMENT

Two influences of productivity that have been addressed in ecological literature are the relationships between food chain length and productivity and between productivity and species diversity. Both are parts of the larger question of how productivity influences food web structure. An experiment that compares identical webs along a gradient of productivities will lend some insight to this question.

#### 6.1 Productivity and Food Web Height

##### 6.1.1 Introduction

In this exploration of productivity effects, two types of effects were studied, effects of productivity on food web height and on diversity. The two questions required different resolutions in examination along a productivity gradient. The question of trophic height was answered using a large scale gradient which extends from no energy subsidy, at the low extreme, to very high levels of energy input, beyond which no detectable changes in the heights of food webs appeared to be taking place. The second gradient is a more finely-tuned, detailed examination of a section from the larger gradient.

### 6.1.2 Methods

Thirty-seven food web configurations were simulated along the large scale gradient of productivity. In the model there is a forcing function representing energy input available to autotrophs in the food web:  $f(t) = \text{sun}$ , where the constant sun would have units of energy/area/time. Six levels of this productivity parameter “sun” were included in the experiment. After the food webs were simulated under the appropriate energy regime, the analysis of food web heights (number of levels) in the final configurations was carried out. The initial height of the food webs was five trophic levels, which sets a maximum on the number that can possibly remain. Overexploitation events were also recorded to monitor changes in the importance of predation in these systems as production rises. This was used in the test of Oksanen’s hypothesis which predicts a zone of intense predation intensity, and presumably a high incidence of overexploitation along the productivity gradient, prior to the incorporation of a new trophic level. The test of this hypothesis required verification or rejection of the claim that overexploitation shows an increasing trend along either the local or extended gradients among food webs having the same height.

In addition to the information compiled for the study of trophic height and its response to energy enrichment, a few of the variables used in the exploitation experiment to study predator mediated coexistence were also recorded in order to see whether addition of trophic levels would have the same effect when the growth was driven by energy inputs. However, since these variables will be dealt with later in the discussion of productivity’s effect on diversity, the details will be reported there in reference to information derived from the larger scale productivity gradient.

### 6.1.3 Results and Discussion

The number of trophic levels retained in the final equilibrium configuration from the original five showed a definite increase with higher energy inputs. After most of the webs had reached their full height, increasing productivity identified a few webs that were structurally vulnerable to collapse. Figure 17 illustrates the change in food web height along a gradient of productivity. Structural changes in a representative food web as rising energy inputs were made available to its autotrophs are shown in Figure 18.

Overall, the food webs can be seen to move from a resource-limited regime to one in which predation has more importance. At low levels of energy subsidy, the demise of unsuccessful species is a result of competition and

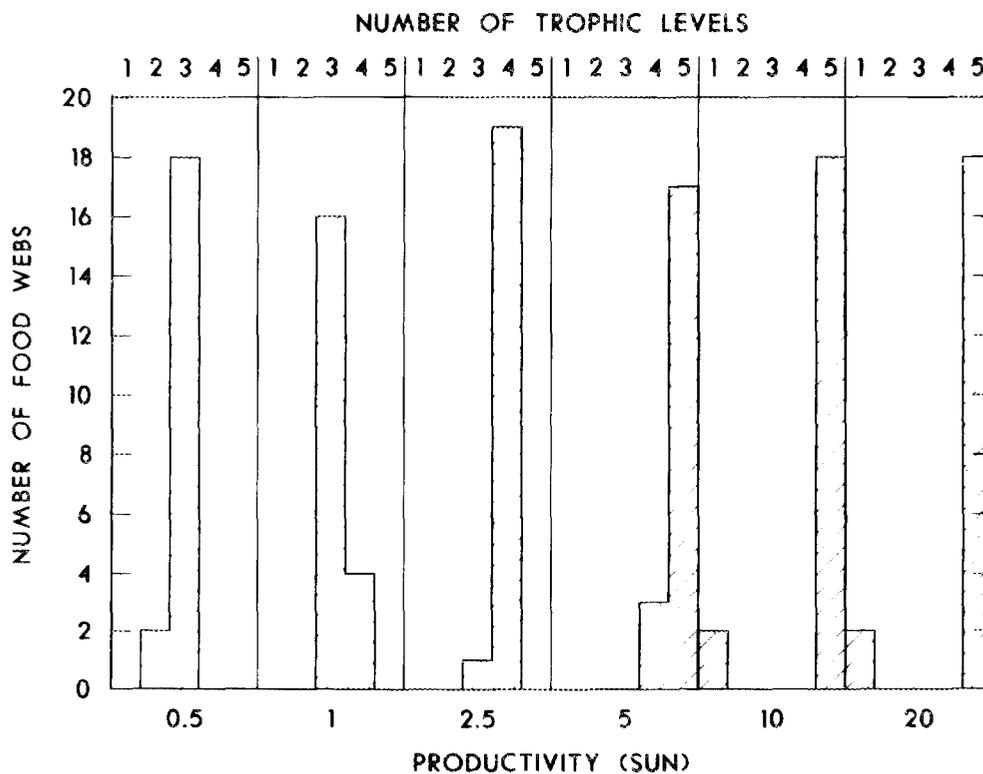


Figure 17. Increasing trophic height along a gradient of productivity. Values of SUN reflect productivity in the sense of energy available to primary producers.

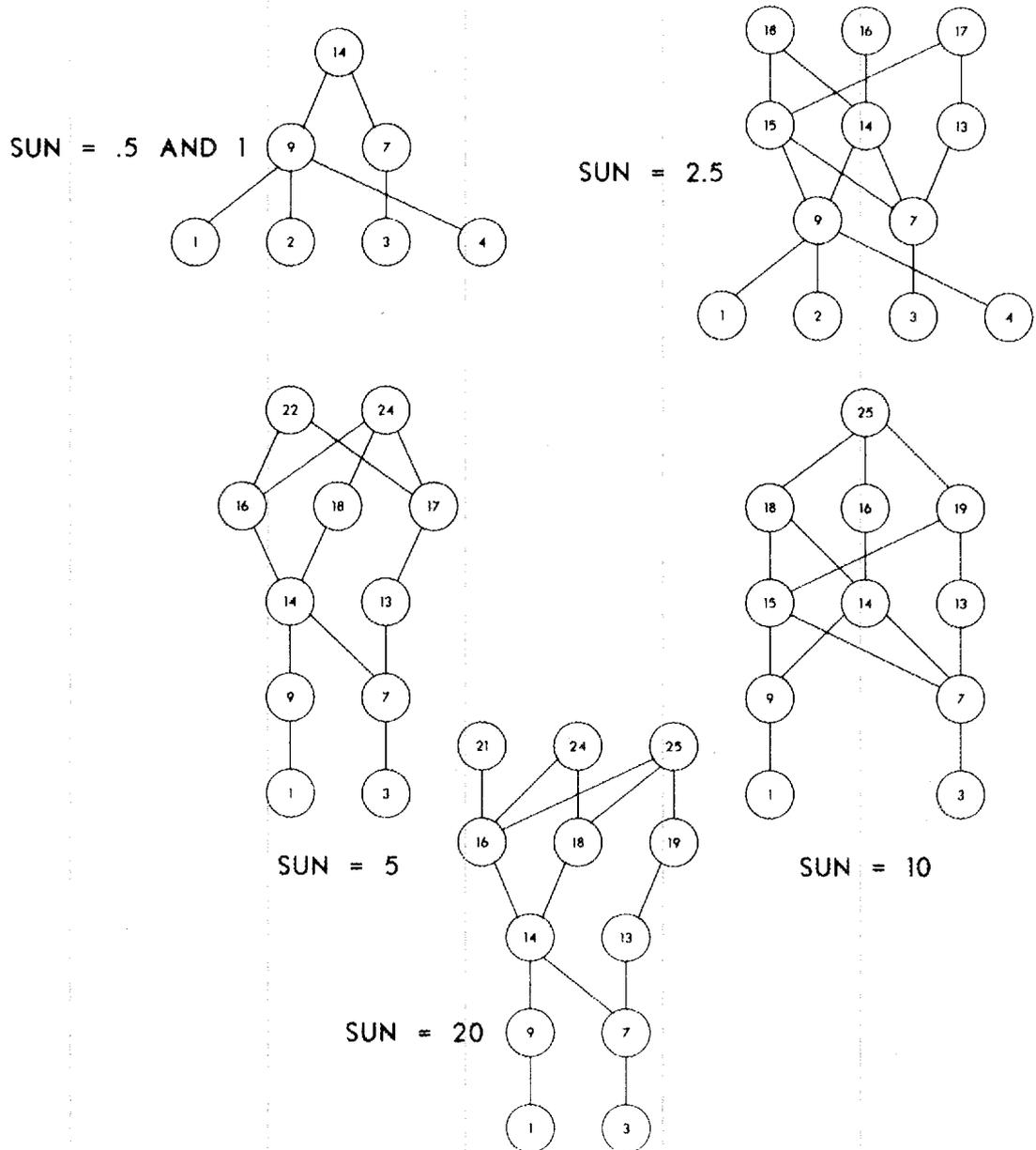


Figure 18. Sample sequence of final food web configurations along a productivity gradient. Values of SUN reflect productivity in the sense of energy available to primary producers. Circled numbers represent species (as in Figure 1 on page 13) connected by lines which represent predator-prey interactions, with predators above their prey.

insufficient prey availability. As higher levels of energy become available, the importance of overexploitation as a cause of extinction rises (see Table 4).

#### 6.1.3.1 Low Productivity and Resource-Limited Food Webs

In low production food webs, higher level species fade away without ever becoming much of a threat to their prey. At first it was suspected that this behavior might be peculiar to webs in which successively higher trophic levels are introduced at very small densities. Recall the assumption that the webs are successional, giving lower trophic levels a head start by initializing their predators two orders of magnitude smaller. Conceivably, if the upper trophic levels were introduced at higher densities, their invasibility might improve for a given level of productivity. To test this, the simulations were replicated with the lowest productivity ( $\text{sun}=0.5$ ), this time with initial densities a single order of magnitude apart. These webs still retained only three trophic levels, indicating that this result is fairly robust to initial conditions.

At  $\text{sun}=0$ , of course, no trophic levels can be sustained. When  $\text{sun}$  was  $0.01$ , only one trophic level was maintained. When  $\text{sun}=0.5$ , most web configurations were capable of sustaining three trophic levels—an autotroph, herbivore, and carnivore trophic level. As before, the tendency was for higher levels to decay due to insufficient resource support. Presumably there is an interval of productivity associated with two-level webs between  $\text{sun}=0.01$  and  $0.5$ . The status quo when  $\text{sun}=1$  was still the three-trophic-level web. Predation pressure (frequency of autotroph overexploitation) on autotrophs had increased from that at  $\text{sun}=0.5$ . The most frequent number of trophic levels shifted from three to four at  $\text{sun}=2.5$ . Carnivores began to make themselves felt on the herbivore level with an increase in the number of overexploited herbivores.

Table 4. Relative Importance of Resource and Predation-Induced Extinction in Food Webs Along a Gradient of Productivity.

Trophic Level	Extinction Type	Productivity (Sun)					
		.5	1	2.5	5	10	20
1	Predation	16	17	24	31	41	42
	Resource	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
	Total	16	17	24	31	41	42
2	Predation	25	31	45	42	43	45
	Resource	<u>26</u>	<u>20</u>	<u>9</u>	<u>17</u>	<u>21</u>	<u>20</u>
	Total	51	51	54	59	64	65
3	Predation	0	1	30	30	36	36
	Resource	<u>59</u>	<u>63</u>	<u>21</u>	<u>24</u>	<u>25</u>	<u>30</u>
	Total	59	64	51	54	61	66
4	Predation		0	0	18	25	32
	Resource		<u>96</u>	<u>64</u>	<u>39</u>	<u>30</u>	<u>34</u>
	Total		96	64	57	55	66
5	Predation				0	0	0
	Resource				<u>77</u>	<u>65</u>	<u>63</u>
	Total				77	65	63

### 6.1.3.2 High Productivity and Predation-Controlled Food Webs

In the transition to  $\text{sun} = 5$ , webs having four trophic levels gained a fifth level. Overexploitation rose sharply on the first two trophic levels, and less sharply on the third. When  $\text{sun}$  was raised to 10 and 20 most five-level webs retained their height, but two collapsed down to only an autotroph level as a result of increased overexploitation on the second level. This fate befell food webs in which one autotroph had the decided advantage of supporting only a single diversified (i.e. inefficient) herbivore which, in turn, happened to be the specialty of a consumer species. The food chain which persisted at low levels of energy subsidy in the configurations that collapsed consisted of the dominant autotroph, its generalized grazer, and the specialized carnivore feeding upon the grazer. Increasing productivity caused the specialized carnivore to overexploit its prey, leaving only the dominant autotroph. (The other species of autotroph were inviable, having too many predators). In nature, it is suggested that in food webs characterized by low autotroph species evenness, with one or more dominants that are relatively immune to predation and subject only to diffuse, non-specialized herbivory, the occurrence of specialized heterotrophs feeding on those grazers will make the system acutely vulnerable to enrichment.

### 6.1.3.3 Applicability of Simulation Results to Natural Systems

In nature, the importance of overexploitation is probably not as great as the predictions of this model suggest since there are a variety of spatial mechanisms which are believed to prevent such extinctions. In the event that the last described collapse occurred, it would be likely that some seed

populations could rebuild a structure. The infrequency of collapsing food webs in these simulations is caused by the tendency for extremely specialized and efficient predators to overexploit early, possibly forestalling large scale extinction of many prey species by generalist predators.

The main conclusion about productivity and food web height is that the simulations seem to support a positive correlation between the two. In an applied sense this suggests that invasibility of higher levels into systems characterized by low productivity is improbable. In natural food webs characterized by more specialized species, i.e., in food webs characterized by low connectivity, this correlation is less likely to hold true. The absence of generalists destroys the averaging of prey availability over a whole trophic level and makes the webs less reticulate. This increases the probability that nonvulnerable prey will succeed in "locking up" the biomass that would otherwise be funnelled to the next trophic level higher. Of course, the results here are also limited in applicability by the fact that web heights in nature are determined not only by trophic dynamics, but also by the availability of suitable higher level consumers that are able to get to and establish in the community, fulfilling all non-trophic life-history requirements. A more appropriate question might be whether top predators previously associated with a given system spend a significantly larger percentage of time in a patch when it is characterized by higher productivity than at times when less energy is available to its basal species.

In predicting the effects of enrichment, it appears that both the ability of the system to add higher trophic levels (seed populations) to the number of levels in the current food web, and the degree of enrichment must be known in order to predict how standing crops of each levels will respond. For example,

phytoplankton blooms are more likely to occur in three-level (odd) aquatic food webs where no predators are available to feed on the third trophic level. The importance of this effect is underscored by Tilman et.al. (1982) who call for a “broadening of the aquatic ecologists’ perspective to include processes at other trophic levels” in studies of eutrophication.

#### 6.1.3.4 Oksanen’s Hypothesis

Recall the hypothesis offered by Oksanen et.al. (1981) stating that along a continuum of increasing productivity there should be a zone characterized by intense grazing pressure preceding the addition of a third trophic level. A generalized version of this hypothesis might predict a zone of intense predation pressure preceding the addition of any new trophic level. Table 4 lends support to this hypothesis with evidence that the incidence of overexploitation increases on the top trophic level along the plateaus in trophic height between  $\text{sun} = .5$  and 1 and  $\text{sun} = 5, 10,$  and 20 where a large majority of webs are characterized by three and five levels, respectively (see Figure 17). Along these plateaus, food web height remains constant as productivity increases. On both plateaus the intensity of predation exerted by the top level seems to increase before a new trophic level is added (in the three level case). However, this is also true for 81% of the transitions, most of which are not on the top level of a plateau. In addition this intensification of predation pressure does not seem to relax with the addition of a higher level. This makes it difficult to separate the influence of trophic height from that of productivity. The influence of trophic height is obscured by productivity effects.

Since the effect of trophic height alone was observed in the exclusion experiment, the two influences can be separated by comparison. Table 3 on

page 53 shows that, in the exclusion experiment, the addition of a new trophic level did in all cases result in a relief of predation pressure by the ex-top trophic level. Again it appears that two factors are involved: productivity, which always has the effect of intensifying predation pressure on all trophic levels which tend to prevent overexploitations of prey by predators on the newly covered level.

In the following section (5.2), attention will narrow in on just one interval along the productivity gradient along which almost all webs normally support three trophic levels (sun=.3) to sun=1). Sun=3 is also tested with three levels despite its ability to support higher structures. Table 5 provides information about predation pressure based on extinction information. This can be used to test Oksanen's hypothesis of intensified predation pressure prior to addition of higher trophic levels. According to the hypothesis, the percentage of extinctions caused by predation should increase on the herbivore trophic level along this local gradient.

Table 5. Relative Importance of Predation and Resource-Induced Extinction for Herbivores Along a Local Productivity Gradient in Food Webs with Three Trophic Levels.

Extinction Type	Productivity (Sun)					
	.3	.4	.5	.6	1.	3.
Predation	17	65	63	58	68	86
Resource	<u>108</u>	<u>32</u>	<u>19</u>	<u>20</u>	<u>20</u>	<u>21</u>
Total	125	97	82	78	88	107

The first value, 17, at  $\text{sun}=.3$  is associated with all cases of webs in which only two levels persisted (11 of 20). The last count, 86, refers to the number of predation-induced extinctions occurring at a production level beyond that normally associated with three-level food webs. If higher levels had been initially present, the webs would have been capable of supporting them. This suggests that predation intensity does not show a strong response to rising productivity, as long as the increase is restricted to a range of energy input that corresponds to a "natural" plateau in food web height (i.e. one that is not imposed by exclusion of higher predators). Given that the large scale experiments have some inherent variability in the numbers of trophic levels supported among webs sampled, my conclusion is that Oksanen's hypothesis has not been supported by these results based on overexploitation.

Although predation intensity does not appear to climax prior to the addition of a higher level, productivity increases that are adequate to support higher levels, when no species of higher trophic status are present, seem to elicit a strong intensification of predation pressure. This was corroborated using three and four level food webs from the exclusion experiments. These food webs were provided with enough energy to support five trophic levels ( $\text{sun}=5$ ), except that the higher trophic level species were excluded. These food webs were compared with food webs driven by considerably lower productivities ( $\text{sun} = 0.5$  to  $2.5$ ) which were unable to support more than three and four trophic levels. The number of species driven to extinction by predation in the "super-charged" systems was greater than the number overexploited in food webs naturally capable of supporting only three and four trophic levels (see Tables 6 and 7). In the comparison of four level food webs, the total number of surviving species decreased when productivity was greater

Table 6. Relative Importance of Resource and Predation-Induced Extinction in Food Webs with Three Trophic Levels and Productivities Commensurate with Three and Five Trophic Levels.

Trophic Level	Extinction Type	Productivity (Sun)		
		.5	1.	5.
		Number of Supportable Trophic Levels*		
		2-3	3-4	4-5+
1	Predation	16	17	31
	Resource	<u>0</u>	<u>0</u>	<u>0</u>
	Total	16	17	31
2	Predation	25	31	37
	Resource	<u>26</u>	<u>20</u>	<u>19</u>
	Total	51	51	56

\*Most food webs with Sun=.5 and 1. support three trophic levels and most food webs with Sun=5 support five (see Figure 17 on page 74 for details).

Table 7. Relative Importance of Resource and Predation-Induced Extinction in Food Webs with Four Trophic Levels and Productivities Commensurate with Four and Five Trophic Levels.

Trophic Level	Extinction Type	Productivity (Sun)	
		2.5	5.
		Number of Supportable Trophic Levels*	
		4-5	5+
1	Predation	24	28
	Resource	<u>0</u>	<u>0</u>
	Total	24	28
2	Predation	42	42
	Resource	<u>8</u>	<u>14</u>
	Total	50	56
3	Predation	29	28
	Resource	<u>18</u>	<u>21</u>
	Total	47	49

\*Figure 17 on page 73 shows the number of four and five trophic level webs for Sun=2.5 and 5.

than required for four level structures, but the new extinctions were equally split in causality among predation, resources and undermined prey. Predation-induced extinction did not show an increase. This can be seen by referring to Table 7.

## **6.2 Productivity and Diversity**

### **6.2.1 Introduction**

#### **6.2.1.1 Definition of Enrichment**

The scale of change in productivity is quite important to define because such a change can refer to situations ranging from isolated enrichment events, for example sewage influx to a lake, to long term geographic gradients running from temperate to tropical ecosystems. Kirchner (1977) describes two scales of enrichment and his theory about the effect of each on community diversity.

Enrichment may have a destabilizing effect on competitive systems (Rosenzweig, 1971). Release from physical limiting factors may increase the biotic interactions of a community. On the other hand, perturbations which have a direct detrimental effect on the majority of species involved, i.e., negative stresses, may affect only the responses of the least tolerant organisms. Likewise, a single, short-term perturbation (acute stress) may only affect those organisms capable of rapid response, while continuous, long-term perturbation (chronic stress) would permit the response of a large segment of the ecosystem. Chronic stress may also allow an ecosystem to reach a new equilibrium of community interactions. Thus, a chronic, positive stress may provide insight into the biotic interactions of an ecosystem during a long-term period of change.

The productivity gradient simulated in this model experiment is analogous to chronic enrichment in which initially identical trophic systems develop alternative trophic configurations in response to different ambient levels of production.

#### 6.2.1.2 Field Studies of Enrichment Effects on Diversity

The relationship between productivity and diversity has been studied mainly in reference to a single isolated trophic level, usually the primary producers. Onuf et. al. (1977) report, concerning addition of nutrients to a body of water, that “the observed results have usually been increased primary productivity, reduction in numbers of species, and dominance by less desirable species. These outcomes of eutrophication have commonly been explained as resulting from differences in the capacity for increase in numbers of various species when released from nutrient limitation, leading to the elimination of some due to interspecific competition.” The outcome of enrichment depends on the tug-of-war between direct effects of high productivity on each species and the negative indirect effect on diversity mediated by competition. In this manuscript diversity is used in the sense of species richness.

There is no comprehensive theoretical treatment of total food web response in diversity to increased production, but a few field experiments have studied enrichment of systems with more than one trophic level.

Kirchner (1977) subjected a shortgrass prairie to nutrient enrichment with a combination of nitrogen fertilization and irrigation. He discovered a decrease in plant species diversity and an increase in arthropod diversity and biomass. Primary production was also higher. The author concluded that “the arthropod community was apparently influenced more by factors related to herbage biomass than by plant species diversity.”

Higher herbivore diversities were also found by Onuf et. al., in their study of enriched mangrove islands, "Larvae of the five lepidopteran species that we observed feeding on buds or leaves were either more abundant or only present in the high nutrient area...."

#### 6.2.1.3 The Intermediate Predation Hypothesis for Polarized Food Webs

The intermediate disturbance hypothesis predicts a unimodal response in species diversity to higher frequencies of disturbance (see Figure 19). In these food webs, it is hypothesized that predation intensity acts as a disturbance that increases with increasing productivity. While resource-limitation may encourage competitive exclusion, predation acts as a disturbance preventing species losses.

A fine example of the intermediate predation hypothesis operating in nature is found in the marine intertidal communities studied by Lubchenco (1978). Predation by the herbivore marine snail *Littorina littorea* controlled the abundances and types of algae in the high intertidal pools studied. It was found that the highest species diversity of algae occurred at intermediate densities of snails. In the absence of *Littorina* the green alga, *Enteromorpha*, is competitively dominant, excluding other species in the tide pool. At high densities of *Littorina*, *Chondrus*, a red alga, became dominant as a species much less desirable to snails than other species of alga, most of which were removed by intense grazing. This yields a unimodal relationship between algal species diversity and herbivore density.

Huston's (1977) theory of species diversity predicts that highly productive or enriched environments will be characterized by low species

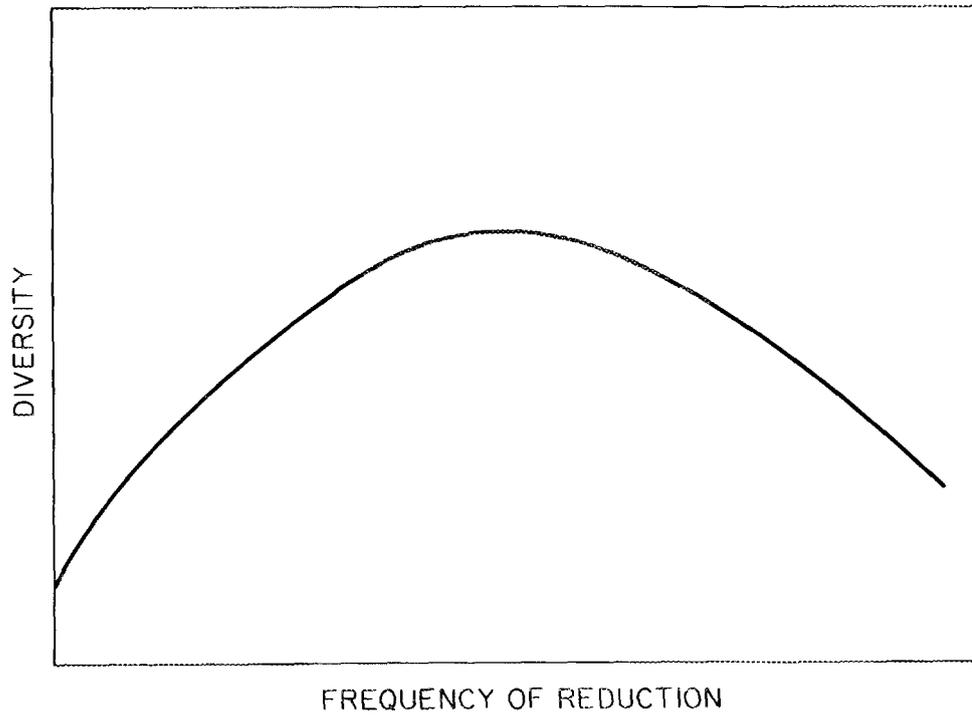


Figure 19. Diversity as a function of the frequency of reduction (Huston, 1979).

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.

diversities as small differences among species predation coefficients are amplified leading to competitive-exclusion of less opportunistic species. On the other hand theory predicts that highly intense predation will reduce diversity.

Combined with the exploitation theory that trophic levels alternate from resource to predation limitation, one might predict that in general, the top trophic level will have low diversity along with alternate resource-limited levels below, while predation-limited trophic levels enjoy relatively high diversities, provided that the predation pressure is not excessive. However, the increased production continually raises the number of trophic levels supported and switches the oddness or evenness of a particular level. Thus trophic levels are cycled between resource and predation control as higher levels are added, according to the version of the hypothesis adapted for polarized food webs.

Two levels of diversity response were predicted along the gradient of increasing productivity. A "local" change in productivity supplied to a trophic system is defined as a change small enough to prevent the addition or loss of a trophic level. When slight changes in productivity occur, species diversity (richness) is expected to follow the unimodal curve which the intermediate predation hypothesis describes. Fretwell (1977) predicts that maximal diversity will occur in food webs that are "between" integer numbers of trophic levels. He predicts cycles of plant and grazer species diversity, with peaks between all of the systems having integer numbers of links.

### 6.2.2 Methods

It has been shown that trophic systems respond to large increases in productivity by supporting species on higher trophic levels than was previously possible. This suggests that one level of response of diversity to increased

productivity may be an increase due to predator mediated coexistence as new trophic levels emerge. This effect was observed for a constant level of productivity in the exclusion where the numbers of trophic levels were changed forcibly by removal rather than driven by energy supply.

In the investigation of predator-mediated effects of large scale changes in productivity, several techniques of analysis were used with the simulations that were replicated along the larger-scale gradient of energy input as described earlier. Paired comparisons of diversity (before and after) were made in all cases where the rise in productivity resulted in the incorporation of a new trophic level. As a control, the same was done for transitions in which the final height of the web did not change.

In addition to studying the large-scale response of diversity to productivity, a smaller-scale, local response was postulated to exist as well. The intermediate predation hypothesis applies to more subtle changes in productivity, changes that influence diversity within an interval of productivity having no impact on trophic height (see Figure 17 on page 74). The section of gradient chosen covers the transition zone in food web height, starting where the third trophic level is added and culminating where a fourth level should be added. Food webs with species on three trophic levels were simulated with the following amounts of energy subsidy:  $sun = .3, .4, .5, .6, 1.0, \text{ and } 3.0$ . (Recall that the majority of webs at  $sun = .5$  and  $1.0$  had three trophic levels in the larger scale experiment with webs initialized with five trophic levels.) Each trophic level began with an assemblage of ten species, twice the usual number, in order to observe more detailed changes in diversity pattern. The objective in this approach was to test the intermediate predation hypothesis by using productivity to manipulate predation intensity.

### 6.2.3 Results and Discussion

#### 6.2.3.1 Predator-Mediated Coexistence

As productivity increases, species from higher trophic levels become adopted into the food webs. Each additional trophic level usually has the effect of permitting generalized species on its prey trophic level to coexist with their more specialized competitors. If Oksanen's hypothesis holds, then increasing productivity has the effect, first of intensifying the predation pressure acting on trophic level  $n-1$ , and then, as level  $n+1$  becomes established, of allowing diversity on level  $n$  to increase by alleviating competition.

Fifteen of thirty-nine paired comparisons in which a new trophic level was added resulted in an increase in diversity of level  $n$ , while diversity decreased in only one. A signs test verifies that this increase is significant at  $p=.05$  allowing us to reject the hypothesis that diversity is less likely to increase than to decrease when a new trophic level is added as a result of higher productivity. Overall, when a new level is added it is more likely that diversity in the sense of species richness will remain unchanged than that it will increase.

From this test, however, it is impossible to separate the effect of increased productivity from that of adding a trophic level. Since only the latter qualifies as predator-mediated coexistence, the matter was investigated further.

First a control test compared the number of increases and decreases in diversity among pairs of webs adjacent along the discrete gradient in productivity but having the same number of trophic levels. Most of these occur along two "plateaus", one where food webs retain three trophic levels in

transition from  $\text{sun} = .5$  to 1, and another as sun rises from 5 to 10 and to 20, with the majority of food webs having five trophic levels. Seventeen of the 56 paired comparisons showed an increase in diversity in contrast to only two instances of decreased diversity. This suggests that productivity alone plays a large role in permitting increased diversity through some mechanism other than predator-mediated coexistence.

One additional method available to separate productivity and height effects on diversity is to recall what happened to diversity in webs simulated at a constant level of productivity but varying in the initial number of trophic levels. If these webs show the same rise in diversity then the addition of a new trophic level is likely to be responsible. In the exclusion experiment approximately 44% of the level additions resulted in an increase in diversity on the  $n$ th level. This is not far from the 38% exhibited by the productivity-driven webs. This swings the pendulum back toward the conclusion that predator-mediated coexistence is implicated in the sequential addition of trophic levels due to enrichment.

In short, predator-mediated coexistence is responsible, to some extent, for the enhanced diversity of intermediate trophic levels. In addition, productivity also has a positive effect on level  $n$  diversity. The degree to which diversity can increase is limited and not additive so that the causality in any one instance is obscured. Once the initial species additions are made, no consistent changes in diversity result from the addition of yet higher trophic levels.

### 6.2.3.2 Intermediate Predation Hypothesis

Along the fine-tuned or local productivity gradient, the expected trend of maximal diversity at intermediate predation intensity (productivity) was observed without exception in twenty food webs. In the simulations, herbivore diversity increased after one or more species on the third trophic level became viable, and continued to increase until, at some higher productivity, the diversity began to decline slowly. The increasing trend is much sharper than the decline as can be seen in Figure 20. This can be compared with the diagram offered by Huston shown in Figure 19 on page 88. Diversity did, in

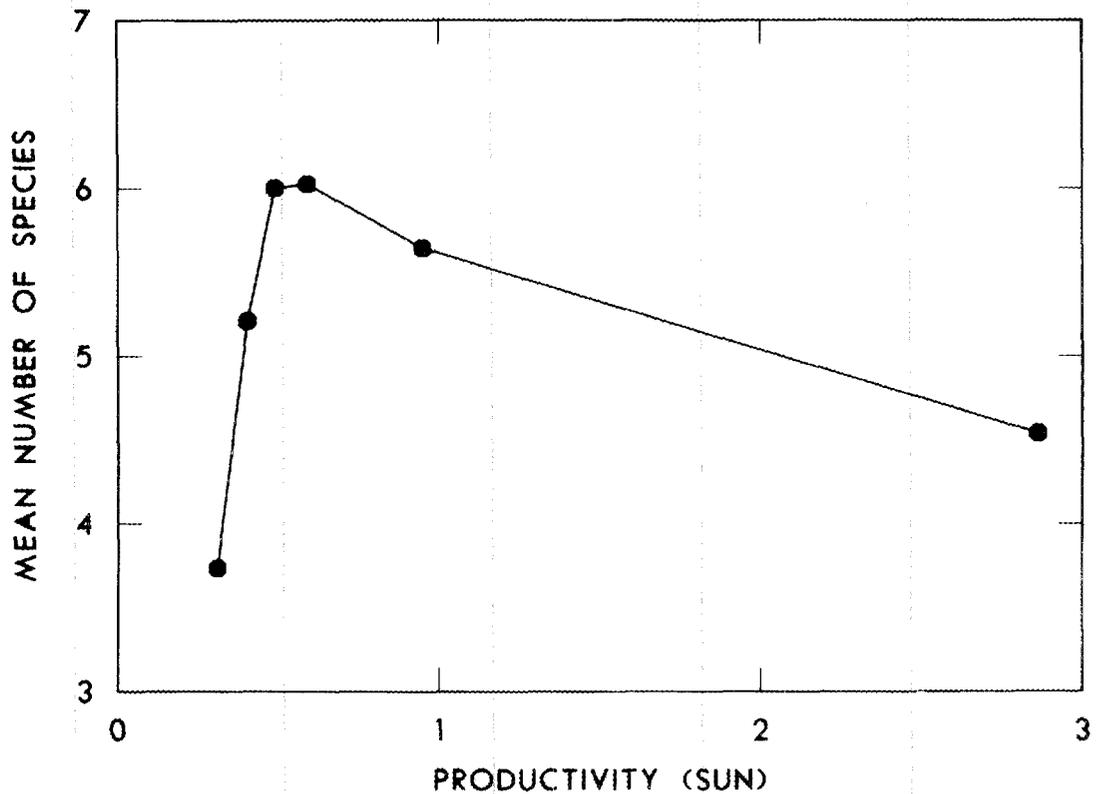


Figure 20. Diversity along a local productivity gradient. The curve illustrates the change in herbivore diversity with rising productivity for food webs with three trophic levels having ten species, initially, on each level.

some webs, remain constant at one end of the productivity scale, as though the length of the scale was not sufficient, truncating one tail of the unimodal response. However, not one of the food webs showed a decrease followed by an increase in diversity. In other words, a “wrong” trend was never encountered.

### **6.3 Productivity and Trophic Strategy Success**

#### **6.3.1 Introduction**

Kirchner's (1977) shortgrass prairie enrichment study showed that autotroph biomass, but not diversity, increased due to enrichment. To explain why this should cause arthropod diversity to increase, he speculates that “the greater density of available prey in  $H_2O + N$  [the enriched treatment site] may support a greater proportion of more efficient predatory specialists.” It is also suggested that the increased standing crop may increase structural diversity, decreasing the risk of predation for predators, and increasing the number of niches available. This mention of predation risk for arthropods suggests that a third trophic level may be part of the answer. Possibly the third level is benefitting from the enrichment and mediating coexistence among its arthropod prey. The author inferred from the correlation between herbage biomass and arthropod densities that arthropods had been food-limited, which increases the likelihood of this explanation.

In the mangrove islands studied by Onuf et al. (1977) herbivore diversity increased, but this time with the addition of generalized species that would not normally feed on mangroves. The authors speculate that enrichment may destabilize the system and cause a reduction in primary producer diversity

if, as in the case of eutrophication and blue-green algae, the joint burden of specialists and generalists selects for the less-palatable species.

In these two studies there was no consensus about the change in selection acting on trophic strategies as a result of increased productivity. One speculates that efficient and specialized herbivores may feed on the increased autotroph biomass due to the abundance of resources (see Glasser, 1982), and the other that generalized species who are opportunistic enough to take advantage of the autotroph biomass increased by enrichment. This was an island study, suggesting that more motile and diversified herbivores would have an advantage in relatively closed systems.

### 6.3.2 Methods

Simulations replicated along the larger scale productivity gradient were analyzed for differences in the number of predators employing each trophic strategy (number of prey in diet) surviving the simulations. Support for trends in trophic strategy success with production was sought in the three trophic level food webs simulated along a local productivity gradient. In these food webs, ten species were initially installed on each trophic level with a uniform distribution of numbers of prey take. This yields a finer-tuned spectrum of trophic strategies, from highly specialized with one prey type to highly diversified with all ten possible prey species taken. Only changes that were fairly large (>20%) are reported for each trophic level.

### 6.3.3 Results and Discussion

As productivity increases, the success rate for specialized herbivores decreases. Rising productivity increases the tendency for specialized species to

either overexploit or be overexploited due to their relatively high predation coefficients. While a high predation coefficient has its advantages in noninteractive (non-equilibrium) systems, in these simulations, efficient specialized predation is rewarded, all too frequently, by overexploitation of one's prey, or by attracting the attention of predators. This model predicts that high productivity can lead to exclusion of the dominant competitor by overexploitation. In other words, predator-mediated coexistence assumes an intermediate intensity of predation. When productivity is too high, the range of predator densities which is sufficiently large to prevent specialized prey from overexploiting, but not large enough to actually overexploit their specialized prey, is very narrow. Theoretically, this can be best explained by visualizing a bell-shaped curve describing diversity as a function of predation intensity (see Figure 19 on page 88). Along this curve extreme specialists are the last to come and the first to go. Extrapolating to real systems, the persistence of a food web community as a "keystone" system may depend on the absence of large fluctuations in productivity, and/or spatial heterogeneity or other environmental factors that discourage overexploitation.

The effect of productivity is greatest for generalists, especially on the highest trophic level. As energy supplied to basal species is increased, and a new trophic level is added, it is usually a lucky specialist that initially invades by selecting a dominant prey type as its specialty. As more energy is supplied, the frequency of successful generalists on the highest trophic level increases. This is also evident along the local productivity gradient which has species with a larger range of trophic strategies, ranging from one to ten prey types. The hypothesis drawn from these simulation results is that specialists will initially have better success as top predators of a system that is barely capable of

supporting a new trophic level, if they happen to specialize on a dominant species of prey. Eventually however, this advantage will be lost as the specialists threaten to obliterate the dominant prey and as more diversified top predators become capable of finding sufficient resource support. Appendix C contains tallies of each trophic strategies success for different levels of productivity for both the large scale and the local gradient. One can see the movement from left to right (specialized to generalized) and bottom to top (increased trophic position) with higher energy input.

## CHAPTER VII

### TROPHIC STRATEGY SUCCESS

#### 7.1 Bonus Experiment

##### 7.1.1 Introduction

One of the assumptions of this model is that specialists are more efficient predators on the few prey that they have. This experiment considers the influence of this increased predation expertise on strategy success and on web structure. One expects that increasing the bonus awarded for specializing will shift the distribution of successful trophic strategies toward the more specialized extreme. However the effect may differ from one trophic level to another and the effect on web structure is unclear.

##### 7.1.2 Methods

Twenty food web configurations were simulated under various levels of the specialization bonus parameter. This bonus is a negative linear coefficient of the number of prey included in a particular predator's diet (see Chapter II).

##### 7.1.3 Results and Discussion

When no bonus was awarded for specialization there was a strong preference for the most general predator on each trophic level. In fact it succeeded in every case. More interesting, however, was the difference in the success of more specialized species from one level to the next. In particular,

herbivores seemed to experience fairly strong competition which prevented more specialized herbivores from coexisting with the extant generalist. On the next level higher, among carnivores, there was a strong increase in tolerance toward more specialized competitors. While success was directly proportional to the number of prey utilized, the most diversified predator did not exclude all of its competitors. Basically, anything that happened to feed on the successful, polyphagic herbivore survived. While the complete generalist on the fourth level always succeeded, more specialized fourth level species feeding on the generalized herbivore also persisted. On the first level, with only the most diffuse general herbivore, all autotrophs persisted (see Appendix C).

As the bonus was increased, there were two main changes. First the success of the complete generalist in competing with more specialized predators declined. Secondly, the diversity of autotrophs decreased, probably as a result of overexploitation which becomes more likely as specialists become more efficient. The success of specialists did not change very much, as the percentage of specialists lost to overexploitation approximately equalled the increased percentage successful as competitors.

## **7.2 Feeding Diversity and Trophic Position**

### **7.2.1 General Observations from Control Simulations**

The food web simulations with default parameter values of WEB provided information about the degree of feeding diversity maintained by species that persisted in the simulated food webs.

### 7.2.1.1 Herbivores

In general it was discovered that species low in the food web, especially herbivores, tended to exhibit lower prey overlap than species of higher trophic status. The persistence or extinction of an herbivore can be predicted by means of an algorithm using the fact that overlap is minimized.

On the herbivore trophic level there tends to be a complementary pair of species with no shared prey and the complete generalist. The most frequent trio is the set of species #7, #9, and #10. The failure of species #8, which has 3 prey species, is a bit of an anomaly since #8 is an average species of herbivore, being neither extremely generalized nor completely specific. This interesting discontinuity has an explanation in the complementarity rule by which herbivores succeed. Species #8 is forced to compete with specialists on the one hand, and with generalists having many alternatives on the other. It is easy for the specialists to find a match with species #9, after sifting out the less viable shared prey, but the likelihood of #8 finding a match with #9 such that neither specialist overlaps on the remaining autotroph is low. The rule for predicting herbivore success from a structural matrix of trophic relationships is as follows:

If either of the two most specialized specialists feed on the autotroph which the next-to-complete generalist (#9) lacks, then that specialist will succeed in addition to #9. If neither does, then the complete generalist is usually the sole winner. Other eventualities are harder to predict.

This complementarity rule was strictly true when only two trophic levels were present. When more were added the rule was still true as a general rule of thumb, probably with the most diversified herbivore present as well.

### 7.2.1.2 Carnivores

Species at higher trophic levels are generally not organized by minimizing the numbers of predators supported (prey overlap among their collective predators). The premium for these species was on obtaining sufficient resources, rather than the avoidance of predation. Success of top predator strategies was more dependent on the productivity available to the system. A shift from specialized to more diverse top predators accompanies increased productivity. The distribution of trophic strategies at the higher trophic levels is unimodal, with a centralizing tendency. The only strategies with significantly lowered success are the extreme strategies; extreme specialists with a single prey species, and extremely diversified predators utilizing all types of prey.

## 7.2.2 Influence of Trophic Position on Trophic Strategy Successes

### 7.2.2.1 Introduction

The advantages of specializing and diversifying can alter from one trophic level to the next. The purpose of this experiment was to find and explain changes in strategy success that relate to trophic status. The null hypothesis that summarizes this experiment is that the probability of success for a species with a given trophic strategy is independent of its trophic status in the web.

#### 7.2.2.2 Methods

Twenty food webs were constructed with three trophic levels as described in chapter one. Four treatment groups were created from the basic webs (see Figure 21):

1. The first version of the webs have all specialists with only two species of prey on the herbivore level and the usual uniform distribution of trophic strategies for the carnivore level.

2. The second treatment is the same as the first except that all herbivores are generalists having four out of the five possible prey (autotroph) species.

3. The third set of webs is comprised of herbivores collectively having a uniform strategy distribution and a carnivore trophic level consisting of all specialists (2-prey).

4. The fourth set has diversified carnivores and a uniform distribution of strategies among herbivores.

The response variable used to indicate strategy success is the final diversity of specialists compared to that of generalists in the alternative treatment. Since webs have the same configurations on the trophic level with uniformly distributed strategies, paired comparisons can be made between each of the twenty pairs of webs. Signs tests were used to indicate the more successful strategy on each level.

#### 7.2.2.3 Results and Discussion

A signs test of the comparison between specialist and generalist success on the herbivore trophic level indicated that generalized herbivores had a

HERBIVORES WITH SPECIALIZED PREDATORS						HERBIVORES WITH GENERALIZED PREDATORS					
	1	2	3	4	5		1	2	3	4	5
6	0	0	0	1	0	6	0	0	0	1	0
7	0	0	1	0	1	7	0	0	1	0	1
8	0	1	1	1	0	8	0	1	1	1	0
9	1	1	0	1	1	9	1	1	0	1	1
10	1	1	1	1	1	10	1	1	1	1	1
	6	7	8	9	10		6	7	8	9	10
11	0	0	1	1	0	11	1	1	1	0	1
12	0	0	0	1	1	12	1	1	1	1	0
13	1	0	0	0	1	13	0	1	1	1	1
14	0	0	1	0	1	14	1	1	0	1	1
15	1	0	1	0	0	15	1	0	1	1	1

CARNIVORES WITH SPECIALIZED PREY						CARNIVORES WITH GENERALIZED PREY					
	1	2	3	4	5		1	2	3	4	5
6	0	1	0	1	0	6	0	1	1	1	1
7	0	0	1	0	1	7	1	1	1	1	0
8	1	0	1	0	0	8	1	1	1	0	1
9	1	1	0	0	0	9	1	0	1	1	1
10	1	0	0	0	1	10	1	1	0	1	1
	6	7	8	9	10		6	7	8	9	10
11	0	0	1	0	0	11	0	0	1	0	0
12	1	0	1	0	0	12	1	0	1	0	0
13	0	1	1	0	1	13	0	1	1	0	1
14	0	1	1	1	1	14	0	1	1	1	1
15	1	1	1	1	1	15	1	1	1	1	1

Figure 21. Sample sequence of food web configurations designed to test the interdependence of trophic strategies.

significantly higher success rate ( $p=.05$ ) than specialized herbivores. The number of surviving generalists exceeded the number of their specialized counterparts who survived in 18 of 20 food webs. In all cases, every generalist survived.

The opposite result was obtained for the carnivore level. In a significant ( $p=.05$ ) number of comparisons the success of specialists exceeded that of generalists. In all but one of the cases where this was true, generalists were inviable, leaving no successful representatives. In cases where any generalist succeeded, they enjoyed better success than their specialized counterparts.

This leaves us in a position to answer the question posed by the null hypothesis. It appears that strategy success does depend on trophic status. The most successful strategy for herbivores is to diversify, while the carnivore level is better suited for specialized predators. In general among food webs simulated for the various experiments, it has been noted that herbivores tend to be somewhat predator-regulated, while carnivores are basically selected for solving the problem of finding enough prey resources.

### **7.3 Interdependence of Trophic Strategy Success**

#### **7.3.1 Introduction**

Food web complexity derives from the number of trophic connections maintained by the assemblage of species in the web. To this point, species on each trophic level began with an even distribution of connectances with their prey, ranging from a completely specialized to a completely generalized predator. The food webs were simulated and the relative success of each trophic strategy was compiled in Appendix C.

An interesting question arises concerning the interactive effects among species' trophic strategies within the assemblage. Does the success of having a given number of prey connections depend on the trophic strategies of other species in the assemblage or not?

Interdependence among species' trophic strategies may have three components, two of which will be considered here. The connectances of species on the adjacent trophic levels above and below may be important, and the strategies assumed by competitors may also influence the success of a particular trophic strategy. These three—predator, prey, and competitor strategies—are the most likely candidates for exerting a direct influence on the success of a given strategy. The null hypothesis is that the relative success of exercising a specialist or generalist trophic strategy is independent of the trophic strategies assumed by other species in the food web assemblage.

### 7.3.2 Methods

Three trophic levels were included in the food webs simulated for this experiment, with five species apiece. The herbivore trophic level is focused upon as the trophic level of interest. In this experiment, specialists were allotted two prey species and generalists were allotted four of the five autotroph species.

In half of the simulations the top predators were all specialists, and in half they were generalists. This yields four treatments with twenty simulations each. The four are:

1. a majority of specialized herbivores with specialized top predators,
2. a majority of diversified herbivores with specialized top predators,

3. a majority of specialized herbivores with diversified top predators,  
and

4. a majority of diversified herbivores with diversified top predators.

For each treatment the fraction of successful species was assessed for both the minority and the majority trophic strategy.

### 7.3.3 Results and Discussion

Table 8 illustrates the fraction of successful herbivore species as a function of: (1) their own trophic strategies, (2) the trophic strategies of competitors (i.e. majority or minority), and (3) the trophic strategies of their predators.

Table 8. Success Ratio for Minority and Majority Trophic Strategies in Four Treatments.

Predator Trophic Strategy	Prey Trophic Strategy	
	Generalist	Specialist
Specialist	.8409* (.9545)	.7841 (.8636)
Generalist	.9479 (.4762)	.8810 (.3684)

\*The fraction of successful species with a given trophic strategy is given first for the treatment with that strategy in the majority and then, in parentheses, for the minority.

In food webs with specialized top predators both a specialist and a generalist trophic strategy on the herbivore level derived a higher probability of success when the majority of herbivores had assumed the opposite strategy. Species with the minority strategy had a higher likelihood of persisting than those choosing the same strategy as most of their competitors. In theory this suggests that trophic strategies on the herbivore level oscillate about an equilibrium in which the set of minority species increases through successful invasions until it is no longer a minority, at which point the probability of success of the opposing strategy exceeds that of the new majority strategy. Again, the same process shifts the advantage back to the original strategy when the new minority grows to become the majority. The actual operation of such a mechanism can, however, only be postulated since invasion is not permitted in these simulations.

The situation changes completely when the trophic strategy of the top predators is to diversify. Both generalist and specialist herbivores exhibited a higher success ratio when in the majority. This suggests a tendency toward one extreme (specialists) or the other (generalists) on the herbivore trophic level, depending on which strategy initially gained a majority of the guild.

## CHAPTER VIII

### CONCLUSIONS

This simulation model and its food web design with a uniform distribution of trophic strategies succeeded in raising some interesting questions and in supporting or qualifying several existing theories about food web behavior.

Some of the main results derived from experiments with the simulation model are:

1. In the study of functional response curvature, it was learned that increased curvature does not necessarily enhance probabilities of persistence for two reasons:

- The greater-than-linear feeding rate associated with high prey densities can attract predation to the predator feeding on its abundant resources, possibly leading to overexploitation.
- Species that are rare relative to their competitors, but that are fed upon by shared predators are vulnerable to overexploitation, since the functional response, and feeding rate, of the shared predators will be greater-than-linear for large enough densities of competitors.

2. Predation and resource-control of species selection follows the trend observed by Menge and Sutherland (1976) with a continual shift from predation to resource-induced selection.

3. Predation and resource limitation in the usual sense of biomass regulation follows the scheme laid out in Fretwell's exploitation theory with alternating control of trophic level densities.

4. Predator-mediated coexistence seems to benefit extremely diversified predators most, especially at lower trophic levels.

5. It is suggested that predator control of selection of prey species, and not resource-limitation of predator biomass, is the main factor leading to competitively exclusive communities with no resource overlap.

6. Productivity has a direct influence on the height of trophic structures capable of being sustained with the exception of food webs in which connections are in a particularly vulnerable arrangement.

7. The intermediate predation hypothesis appears to hold in these model food webs. Specialists feeding on a dominant prey are capable of initiating a new higher trophic level to a food web with minimal energy available to support that level. With increased productivity, however, more generalized species emerge and prevail.

8. A hypothesis is offered that enrichment of food webs, when no species belonging to higher trophic levels are present, can make the system vulnerable because of the increase in predator feedback which leads, in some configurations, to collapse.

9. In regard to the success of trophic strategies ranging from highly specialized to diversified, the bonus in predation efficiency aids specialists to an extent, but reaches a point of diminishing returns quickly. Overall, species with medium to highly diversified feeding strategies are most frequently successful. Completely diversified predators rarely occurred on the top trophic

levels unless the productivity supplied to the webs was capable of adding higher species.

10. In general, generalists tended to persist at lower trophic levels where selection of species was predation-controlled causing specialists to overexploit, while higher levels were more conducive to the persistence of more specialized predators. At higher trophic levels the efficiency and ability to glean adequate resource support is at a premium.

11. In three level food webs with specialized carnivores, herbivores with the trophic strategy in the minority has a higher success ratio, while the strategy assumed by the majority of herbivores has a higher success ratio when the top carnivores are generalists.

These eleven results are probably fairly dependent on the assumptions used in the simulation model, WEB. The generality of these conclusions will need further assessment, possibly through a complete sensitivity analysis using realistic parameter ranges and distributions. The exercise has, however, been useful in clarifying concepts of food web behavior and in providing a few insights into the processes that structure food webs. The methods used to translate the order of extinction events into ecological processes has proven to be very useful in interpreting the dynamics of the simulated webs.

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**APPENDIX A. FORTRAN PROGRAM**



```

C*****
C
C   WEB is a simulation model of a generic food web with any
C   number of trophic levels (NL) and species per level (L)
C
C*****
      IMPLICIT REAL*8 (A-H,O-Z)
      INTEGER*2 ICLOK(6),IC
      DIMENSION A(10),ISEEDS(100)
      REAL*8 I(25)
C*****
C
C   LABEL THE PURPOSE FOR THIS SIMULATION
C
C*****
      WRITE(5,310)
310   FORMAT(T2,'DESCRIBE THE PURPOSE OF THIS RUN:')
      READ(5,1000) A
1000  FORMAT(10A8)
      WRITE(6,380) A
380   FORMAT(T2,10A8)
C*****
C
C   INPUT IS A SUBROUTINE THAT READS IN PARAMETER
C   VALUES, INITIAL VALUES, AND CONTROL INFORMATION
C
C*****
      CALL INPUT
C*****
C
C   THIS CODE ALLOWS MULTIPLE RUNS TO BE SUBMITTED
C   ENTER N - THE # OF REPLICATIONS
C
C*****
      WRITE(5,5)
5     FORMAT(T1,' ENTER N- THE NUMBER OF SIMULATIONS TO BE RUN')
      READ(5,*) N
C*****
C
C   TO REPLICATE SIMULATIONS ENTER ISEED FROM TERMINAL
C
C*****
      WRITE(5,10)
10    FORMAT(T1,' ENTER SEEDS OR ZERO FOR RANDOM CHOICES')
      DO 14 K=1,N
      READ(5,*) ISEEDS(K)
      IF (ISEEDS(K) .NE.0) GO TO 14
C*****
C
C   GENERATE SEED FOR RANDOM NUMBER GENERATOR
C
C*****
      CALL TIMDAT(ICLOK,IC)
      ISEEDS(K)=ICLOK(2)
14    CONTINUE
C*****
C
C   DESIGN IS THE SUBROUTINE THAT CREATES THE PATTERN OF CONNECTIONS
C   AMONG TROPHIC LEVELS IN THE FOOD WEB.
C
C*****
      DO 15 I=1,N
      ISEED=ISEEDS(I)
      WRITE(6,3) ISEED
      WRITE(5,3) ISEED
3     FORMAT('1',/T2,' ISEED = ',I4)
      CALL DESIGN(ISEED)

```

```

C*****
C
C SOLVE IS A USER SUPPLIED SUBROUTINE THAT SIMULATES THE MODEL.
C
C*****
      CALL SOLVE
15      CONTINUE
      STOP
C*****
C-----END OF MAIN CALLING PROGRAM-----
C
C*****
      END
      SUBROUTINE INPUT
      IMPLICIT REAL*8 (A-H,O-Z)
      COMMON/LSODP/T0,TF,TSTEP,RELERR,TZAP(25),ABSERR,NEQN
      COMMON/PARM/X0(5),EFF,AUTMAX,BONUS,B,C,R,RV,SUN,NSPP(5),NL
      COMMON/WEB/A(25),IPREY(25),IPRED(25),LEVEL(25),M(25,25)
C*****
C
C NL --- NUMBER OF TROPHIC LEVELS
C NEQN --- NUMBER OF EQUATIONS TO BE SOLVED
C TO ---TIME ZERO
C TF --- FINAL TIME
C TSTEP --- STEPSIZE
C RELERR --- RELATIVE ERROR
C ABSERR --- ABSOLUTE ERROR
C NSPP(I) --- DIVERSITY OF TROPHIC LEVEL I
C X0(I) --- INITIAL BIOMASS FOR EACH SP ON LEVEL I
C AUTMAX --- CARRYING CAPACITY FOR PRIMARY PRODUCERS
C EFF --- FEEDING EFFICIENCY OF PREDATORS
C SUN --- ENERGY INPUT TO THE SYSTEM
C*****
C
CC READ IN PARAMETER INFORMATION:
C
C*****
      TO=0.0D0
      WRITE(5,27)
27      FORMAT(T2,'ENTER TF-FINAL TIME OF SIMULATION:')
      READ(5,*) TF
      WRITE(5,22)
22      FORMAT(T2,'TYPE IN PARAMETER C -- MIN-GROWTH-RATE--:')
      READ(5,*) C
      WRITE(5,96)
96      FORMAT(T2,'ENTER CURVATURE OF FUNCTIONAL RESPONSE, 0<B<3:')
      READ(5,*) B
      WRITE(5,16)
16      FORMAT(T2,'SET SUN-THE ENERGY AVAILABLE TO PRODUCERS:')
      READ(5,*) SUN
      WRITE(5,31)
31      FORMAT(T2,'ENTER THE NUMBER OF TROPHIC LEVELS:')
      READ(5,*) NL
      WRITE(5,32)
32      FORMAT(T2,'TYPE SPECIALIZING BONUS, 0< BONUS< X:')
      READ(5,*) BONUS
C*****
C
C SET VALUES FOR FIXED PARAMETERS
C
C*****
      TSTEP=1.0D0
      DO 201 I=1,NL
201      NSPP(I)=5
      RELERR=0.00001D0
      ABSERR=.00001D0
      EFF=0.1D0
      R=.05D0
      RV=0.0D0

```

```

C*****
C
C DETERMINE THE NUMBER OF EQUATIONS, NEQN
C
C*****
      NEQN=0
      DO 21 I=1,NL
21      NEQN=NEQN+NSPP(I)
C*****
C
C LEVEL (I) INDICATES THE TROPHIC LEVEL OF EACH SPECIES
C
C*****
      DO 8 J=1,NEQN
8        LEVEL(J)=1
          LCUM=0
          DO 9 I=1,NL
          LCUM=LCUM+NSPP(I)
          DO 9 J=1,NEQN
          IF (J.GT.LCUM) LEVEL(J)=I+1
9        CONTINUE
C*****
C
C SET THE AUTOTROPH CARRYING CAPACITY TO THE EQUILIBRIUM
C DENSITY OF PRODUCERS IN THE ABSENCE OF HIGHER TROPHIC LEVELS
C
C*****
      AUTMAX=SUN/R + RV*SUN/R
C*****
C
C PRINT INFORMATION
C
C*****
      WRITE(6,19) NSPP(1),NSPP(2),NSPP(3),NSPP(4),NSPP(5),BONUS,B,
      . C,R,SUN,RV
      WRITE(5,19) NSPP(1),NSPP(2),NSPP(3),NSPP(4),NSPP(5),BONUS,B,
      . C,R,SUN,RV
19      FORMAT(T1,' THE NO. OF PRIMARY PRODUCER SPECIES IS',I3,
      . /T1,' THE SECOND TROPHIC LEVEL HAS ',I3,' SPECIES',5X,
      . /T1,' THE THIRD TROPHIC LEVEL HAS ',I3,' SPECIES',5X,
      . /T1,' THE FOURTH TROPHIC LEVEL HAS ',I4,' SPECIES',5X,
      . /T1,' THE TOP TROPHIC LEVEL HAS ',I4,' SPECIES',5X,
      . /T1,' THE BONUS FOR SPECIALIZING IS ',G10.5,
      . /T1,' B- THE CURVATURE IN FUNCTIONAL RESPONSE TO PREY ',
      . ' DENSITY IS ',G10.5,/T1,' C -- MIN GROWTH RATE IS ',
      . G10.5,/T1,
      . ' R-- THE MORTALITY RATE UNRELATED TO PREDATION IS ',G10.5,
      . /T1,' SUN -- MEAN ENERGY IMPORTED TO THE WEB IS ',G10.5,
      . /T1,' RV -- RESOURCE VARIABILITY OR AMPLITUDE OF SUN IS ',G10.5)
      RETURN
      END
C*****
C
C-----END OF SUBROUTINE INPUT-----
C
C*****
      SUBROUTINE DESIGN (ISEED)
      IMPLICIT REAL*8 (A-H,O-Z)
      REAL*8 X(25)
      DIMENSION IDIET(25)
      COMMON/LSODP/TO,TF,TSTEP,RELERR,TZAP(25),ABSERK,NEQN
      COMMON/PARM/X0(5),EFF,AUTMAX,BONUS,B,C,R,RV,SUN,NSPP(5),NL
      COMMON/WEE/A(25),IPREY(25),IPRED(25),LEVEL(25),M(25,25)
C*****
C
C          CREATE TROPHIC STRUCTURE, M(I,J)
C
C*****

```

```

      L=NSPP(1)
      LP1=L+1
      LM1=L-1
C*****
C
C   LEVEL (I) - TROPHIC LEVEL OF RECIPIENT SPECIES X(I)
C   LEVEL (J) - TROPHIC LEVEL OF DONOR SPECIES X(J)
C
C
C   SPECIES ARE ALLOCATED A CERTAIN NUMBER OF PREY ITEMS
C   FROM A UNIFORM DISTRIBUTION -- 1 THRU NSPP PREY TYPES
C   ACTUAL CONNECTIONS ARE CHOSEN AT RANDOM.
C
C*****
      DO 14 I=1,NEQN
      IDIET(I)=MOD(I,L)
      IF (IDIET(I).EQ.0) IDIET(I)=L
      IPREY(I)=0
      DO 4 J=1,NEQN
      IPRED(I)=0
      M(I,J)=0
4      CONTINUE
      IF (LEVEL(I).EQ.1) GO TO 6
71     IPICK= 1 + L*URAND(ISEED)
      J=(LEVEL(I)-2)*L+IPICK
      IF (M(I,J).EQ.0) IPREY(I)=IPREY(I)+1
      M(I,J)=1
      IF (IPREY(I).LT.IDIET(I)) GO TO 71
C*****
C
C   ASSIGN SPECIES POTENTIAL GROWTH RATES BASED ON DIET BREADTH
C   RATES VARY BETWEEN 1/5 AND 1, GENERALISTS HAVING LOWER RATES
C
C*****
      A(I)=C+BONUS*(L-IDIET(I))/L
      GO TO 14
6      A(I)=1.0D0
14     CONTINUE
C*****
C
C   MAKE SURE NO DUPLICATE SPECIES EXIST
C
C*****
5      DO 15 I=LP1,NEQN
      IM1=I-1
      DO 15 J=1,NEQN
      IF (J.EQ.I) GO TO 15
      DO 10 K=1,IM1
      IF (M(I,K).NE.M(J,K)) GO TO 15
10     CONTINUE
C*****
C
C   IF TWO TOPOLOGICALLY EQUIVALENT PREDATORS EXIST, RECONNECT ONE.
C
C*****
17     DO 11 K=1,IM1
11     M(I,K)=0
      IPREY(I)=0
72     IPICK=URAND(ISEED)*L + 1.0D0
      K=(LEVEL(I)-2)*L + IPICK
      IF (M(I,K).EQ.0) IPREY(I)=IPREY(I)+1
      M(I,K)=1
      IF (IPREY(I).LT.IDIET(I)) GO TO 72
      GO TO 5
15     CONTINUE
C*****
C
C   COUNT THE NUMBER OF PREDATORS SUSTAINED PER SPECIES
C
C*****

```

```

DO 61 I=1,NEQN
DO 61 K=I,NEQN
IPRED(I)=IPRED(I) + M(K,I)
61 CONTINUE
RETURN
C*****
C
C-----END OF SUBROUTINE DESIGN-----
C
C*****
END
SUBROUTINE SOLVE
C*****
C
C SUBROUTINE SOLVE SETS UP CALL TO THE DIFFERENTIAL
C EQUATION SOLVER LSODA.
C
C*****
IMPLICIT REAL*8 (A-H,O-Z)
DIMENSION RWORK (872),XLAG(25),EVEN(5)
DIMENSION XF(25),LF(5),IWORK(45),IM(25)
REAL*8 X(25)
EXTERNAL MODEL,PEDERV
COMMON/LSODP/TO,TF,TSTEP,RELERR,TZAP(25),ABSERR,NEQN
COMMON/PARM/X0(5),EFF,AUTMAX,BONUS,B,C,R,RV,SUN,NSPP(5),NL
COMMON/WEB/A(25),IPREY(25),IPRED(25),LEVEL(25),M(25,25)
COMMON/PLUX/BF,XM(5),CREDIT(25),MORT(25)
C*****
C
C INITIALIZE POPULATION DENSITIES -- ASSUME THAT LOWER TROPHIC
C LEVELS HAVE A HEAD START DUE TO SUCCESSION
C
C*****
X0(1)=AUTMAX/100.000
DO 10 J=2,NL
10 X0(J)=X0(J-1)/100.000
DO 60 I=1,NEQN
60 X(I)=X0(LEVEL(I))/NSPP(LEVEL(I))
C*****
C
C CALCULATE MAXIMUM DENSITIES FOR EACH TROPHIC LEVEL
C BY ASSUMING L-V DYNAMICS AND NO EXPLOITERS
C
C*****
AMAX=C + BONUS*(1.000-1.000/NSPP(1))
XM(1)=AUTMAX
XM(2)=10.000
XM(3)=1.000
IF(NL.GT.3)
. XM(4)=0.100
IF(NL.GT.4)
. XM(5)=.0100
C*****
C
C SET INITIAL CONDITIONS FOR INTEGRATOR LSODA
C
C*****
DO 8 I=1,NEQN
MORT(I)=0
8 TZAP(I)=TF
JT=2
ITASK=1
IOPT=1
TSTEP=1.000
DO 1799 I=5,10
1799 IWORK(I)=0
RWORK(I)=0.000
IWORK(6)=5000
ITOL=1
LRW=22 + 9*NEQN + NEQN**2
LIW=NEQN + 20

```



```

C*****
C
C   IF SYSTEM HAS EQUILIBRATED, TERMINATE THE SIMULATION
C
C*****
      XNORM=0.0D0
      DO 191 I=1,NEQN
      XDIFF=DABS(XLAG(I)-X(I))/(XLAG(I)+X(I))
      IF (XDIFF.GT.XNORM) XNORM=XDIFF
191    CONTINUE
      IF (XNORM.LT.1.0D-04) TOUT=TF
      IF (T.GE.20) TSTEP=TF/25.0D0
C*****
C
C   PRINT POPULATION BIOMASS
C
C*****
      IF (RV.GT.0.0D0) WRITE(6,105) BF
105    FORMAT(/T5,'BF=',G16.8)
C      WRITE(6,121) T, {X(I),I=1,NEQN}
      WRITE(5,121) T, {X(I),I=1,NEQN}
121    FORMAT(/T2,'T=',G12.4,5(/T2,5G12.4))
C*****
C
C   IF THIS IS NOT THE END OF THE SIMULATION GO TO 100
C
C*****
      IF (TOUT.NE.TF) GO TO 100
C*****
C
C   DESCRIBE TROPHIC STRUCTURE AT TIME TF
C
C*****
      DO 160 J=1,NL
      LF(J)=0
      XF(J)=0.0D0
160    CONTINUE
      FCON=0.0D0
      DO 140 I=1,NEQN
      DO 150 J=1,I
      IF (MORT(I).EQ.0.AND.MORT(J).EQ.0.AND.N(I,J).EQ.1) FCON=FCON+1
150    CONTINUE
      IF (MORT(I).EQ.0) LF(LEVEL(I))=LF(LEVEL(I))+1
      XF(LEVEL(I))=XF(LEVEL(I))+X(I)
140    CONTINUE
C*****
C
C   TYPE XMAX VECTOR
C
C*****
      WRITE(6,800) (XM(I),I=1,NL)
800    FORMAT(/T5,'XMAX VECTOR:',5(2X,G10.5))
      IF (TF.EQ.TOUT) WRITE(6,444) T
444    FORMAT(T5,'THE WEB REACHED EQUILIBRIUM AT T=',G10.5)
C*****
C
C   PRINT QUALITATIVE INTERACTION MATRIX
C
C*****
      DO 244 I=1,NEQN
      IM(I)=I
      WRITE(6,24)
24    FORMAT(/T5,'QUALITATIVE INTERACTION MATRIX')
      IFIRST=0
      ILAST=0
      NLM=NL-1
      DO 32 JJ=1,NLM
      IFIRST=ILAST+1
      ILAST=ILAST+NSPP(JJ)
      WRITE(6,400) (IM(I),I=IFIRST,ILAST)

```

```

400  FORMAT(/T7,10I3,' IPREY')
      WRITE(6,39)
39    FORMAT(T9,5('____'))
      DO 33 I=1,NEQN
      IF (LEVEL(I)-JJ.EQ.1) WRITE(6,23) I,(M(I,J),J=IFIRST,ILAST),
      . IPREY(I)
23    FORMAT(/T3,I2,2X,5I3,2X,I3)
33    CONTINUE
      WRITE(6,34) (IPRED(J),J=IFIRST,ILAST)
34    FORMAT(T10,5('____'),/T7,10I3)
32    CONTINUE
      NLF=0
      DO 51 I=1,NL
      IF (LF(I).GT.0) NLF=NLF+1
51    CONTINUE
      IT=T
C*****
C
C  REPORT POPULATION BIOMASSES
C
C*****
      WRITE(6,113)
113  FORMAT(1X, /T5,'SPECIES',2X,'LEVEL',4X,'FINAL BIOMASS',4X,
      . 'EXTINCTION TIME',4X,'CAUSE OF DEATH',/T60,'1=STARVATION',
      . /T60,'2=PREDATION')
      DO 114 I=1,NEQN
      WRITE(6,111) I,LEVEL(I),X(I),TZAP(I),MORT(I)
111  FORMAT(T7,I2,5X,I2,4X,G16.8,4X,G16.8,6X,I4)
114  CONTINUE
C*****
C
C  CALCULATE FINAL WEB CONNECTIVITY
C
C*****
      MAXCON=0
     >NNL=NL-1
      DO 401 I=1,NNL
401  MAXCON=LF(I)*LF(I+1)+MAXCON
      IF (MAXCON.GT.0) CON=FCON/MAXCON
C*****
C
C  PRINT INFORMATION
C
C*****
      WRITE(6,312) CON
312  FORMAT(/T5,'FINAL WEB CONNECTIVITY: ',G10.5)
      WRITE(6,31)
31    FORMAT(/T6,12X,2(6X,'INITIAL'),19X,2('FINAL',10X))
      WRITE(6,311)
311  FORMAT(/T2,'TROPHIC LEVEL',7X,'# SPECIES',7X,'BIOMASS',
      . 17X,'# SPECIES',8X,'BIOMASS')
      DO 40 I=1,NL
      WRITE(6,35) I,NSPP(I),X0(I),LF(I),XF(I)
35    FORMAT(/T6,I2,2(15X,I2,10X,G16.8))
40    CONTINUE
      RETURN
      END
C*****
C
C-----END OF SUBROUTINE SOLVE-----
C
C*****
      SUBROUTINE PEDERV(N,T,X,PD,NO)
      RETURN
C*****
C
C-----END OF SUBROUTINE PEDERV-----
C
C*****
      END
      SUBROUTINE MODEL(NQ,T,X,DX)

```

```

C*****
C
C   SUBROUTINE MODEL IS RESPONSIBLE FOR FOOD WEB DYNAMICS OVER TIME
C
C*****
      IMPLICIT REAL*8 (A-H,O-Z)
      DIMENSION DEBIT (25), BV (5)
      REAL*8 X (25), DX (25)
      COMMON/ PARM/ X0 (5), EFF, AUTMAX, BONUS, B, C, R, RV, SUN, NSPP (5), NL
      COMMON/ WEB/ A (25), IPREY (25), IPRED (25), LEVEL (25), M (25, 25)
      COMMON/ LSODP/ T0, TF, TSTEP, RELERR, TZAP (25), ABSERR, NEQN
      COMMON/ FLUX/ BF, XM (5), CREDIT (25), MORT (25)
C*****
C
C                               FOOD WEB MODEL
C
C*****
C   NSPP'S = # SPECIES ON THE TROPHIC LEVEL INDICATED
C   M (I, J) = A QUALITATIVE MATRIX OF FOOD WEB INTERACTIONS
C   CREDIT (I) = TOTAL BIOMASS ACQUIRED BY SPECIES I THRU PREDATION
C   DEBIT (I) = TOTAL BIOMASS LOST TO PREDATORS ON SPECIES I
C   BV = CURVATURE OF THE FUNCTIONAL RESPONSE
C
C*****
C
C   REDEFINE FORCING FUNCTION SEASONALLY
C
C*****
      BF = SUN + RV * SUN * DSIN (.0172024200 * T)
C*****
C
C                               COMPUTE SPECIES GAINS & LOSSES (CREDIT AND DEBIT)
C
C*****
C
C   INITIALIZE VARIABLES
C
C*****
      DO 91 I=1, NEQN
      IF (X (I) .LT. X0 (LEVEL (I)) * 1.0D-20 .AND. MORT (I) .EQ. 0) TZAP (I) = T
      IF (X (I) .LT. X0 (LEVEL (I)) * 1.0D-20 .AND. MORT (I) .EQ. 0) MORT (I) = 2
      CREDIT (I) = 0.0D0
91      DEBIT (I) = 0.0D0
      DO 92 I=2, NL
92      BV (I) = B * C / XM (I-1)
C*****
C
C   AUTOTROPHS RECEIVE ENERGY FLUX BF --
C   ALLOCATE CREDIT ACCORDING TO REL. DENSITY (SPATIAL LIMITATION)
C
C*****
      ASUM = 0.0D0
      LI = NSPP (1)
      DO 170 I=1, LI
170      IF (MORT (I) .EQ. 0) ASUM = ASUM + X (I)
      DO 180 I=1, LI
      IF (MORT (I) .EQ. 0) CREDIT (I) = A (I) * X (I) * BF * (1.0D0 + AUTMAX -
      ASUM) / AUTMAX
180      CONTINUE
      LI = LI + 1
      DO 25 I=LI, NEQN
      IF (MORT (I) .GT. 0) GO TO 25
      ALL = 0.0D0
      L = ILEVEL (I)

```

```

C*****
C
C   CALCULATE TOTAL PREY AVAILABLE TO PREDATOR X(I) AND
C   CREDIT-THE TOTAL BIOMASS GAINED BY SPECIES X(I)
C   USING A SIGMOID FUNCTIONAL RESPONSE CENTERED AT
C   XMAX/2 MAX GROWTH RATE = A(I) *XMAX(LEVEL(I)-1)
C*****
C   DO 35 K=1,I
C   IF (MORT(K).EQ.0) ALL=ALL+M(I,K) *X(K)
35  CONTINUE
C   IF (ALL.EQ.0.0D0.AND.MORT(I).EQ.0) TZAP(I)=T
C   IF (ALL.EQ.0.0D0.AND.MORT(I).EQ.0) MORT(I)=1
C*****
C   UPDATE XM--MAXIMUM PREY DENSITY
C*****
C   IF (ALL.GT.XM(L-1)) XM(L-1)=ALL
C   CREDIT(I)=EFF*X(I) * (-BV(L)*2.0D0/(3.0D0*XM(L-1))*ALL**3
C   . +BV(L)*ALL**2 - (1.0D0/3.0D0*BV(L)*XM(L-1) - A(I)) * ALL)
C*****
C   CALCULATE: PC-THE % OF TOTAL PREY (ALL) THAT X(J) REPRESENTS
C   IN PREDATOR I'S DIET
C   FLX-THE BIOMASS TRANSFER FROM PREY ITEM X(J) TO X(I)
C   DEBIT-THE TOTAL BIOMASS LOST FROM SPECIES X(J)
C*****
C   DO 15 J=1,I
C   IF (M(I,J).EQ.0) GO TO 15
C   IF (MORT(J).GT.0) GO TO 15
C   PC=X(J)/ALL
C   FLX=PC*CREDIT(I)/EFF
C   DEBIT(J)=DEBIT(J)+PLX
15  CONTINUE
25  CONTINUE
C*****
C
C   DIFFERENTIAL EQUATIONS
C*****
C   DO 14 J=1,NEQN
C   DX(J)=CREDIT(J)-DEBIT(J)-R*X(J)
14  CONTINUE
C   RETURN
C   END

```

**APPENDIX B. SENSITIVITY OF WEB TO INITIAL DENSITIES**



**APPENDIX B****Sensitivity of WEB to Initial Densities****Introduction**

In a simulation model such as WEB, behavior depends to some extent on the initial densities assigned to species comprising the system. In all of the experiments, species on higher trophic levels were introduced at very small densities relative to their prey. Autotrophs started with one percent of their carrying capacity,  $X_m = M$ . Herbivores initially shared one percent of the initial autotroph density, and so on. It was believed that each trophic level would become organized in response to competitive interactions prior to experiencing predation effects of any significance.

This analysis considers the effect of initiating food webs with species densities of predators distant from and close to the densities of their prey. This should indicate the robustness of simulation results to the initial proximities of predator densities to those of their prey. Differences between food webs that can be attributed to the initial allocation of biomass among trophic levels may suggest differences between structural properties of food webs in closed communities (ie. islands) that developed gradually with small initial densities, on trophic level at a time, and food webs in open communities in which ambient densities in surrounding areas (source populations) are not significantly lower than "equilibrium" levels for each trophic level.

## Methods

Recall that the experiments initiated predators with one percent of their density initially given to their collective prey species. Comparisons were made with 37 identical food webs simulated with predator densities initially ten percent of prey level density. These food webs will be referred to as “proximate” food webs since predator densities begin closer to those of their prey. Food webs in which predators are initiated much smaller than their prey are referred to as “distant” food webs.

Default values for parameters not related to initial species densities are the same as for the other experiments (see Table 1 on page 18).

## Results and Discussion

The number of predation-induced extinctions of autotrophs by herbivores in the proximate food web simulations was lower than the number in their distant counterparts (see Figure 22). This results in higher autotroph diversity and evenness. A signs test indicated the significance ( $p=.05$ ) of the tendency for autotroph diversity to increase rather than decrease, although diversity was no more likely to increase than to stay the same. In this subset of paired food webs in which autotroph species diversity (numbers) stayed constant, there was a significant tendency for species evenness to increase. ( $p=.05$ ,  $n=12$ ).

This result seems counterintuitive as the purpose of the successional scheme with distant initial densities was to protect lower trophic levels from predation. In this respect it failed miserably. It appears that herbivores are quite capable of breaking out in such a rich supply of resources, but that the

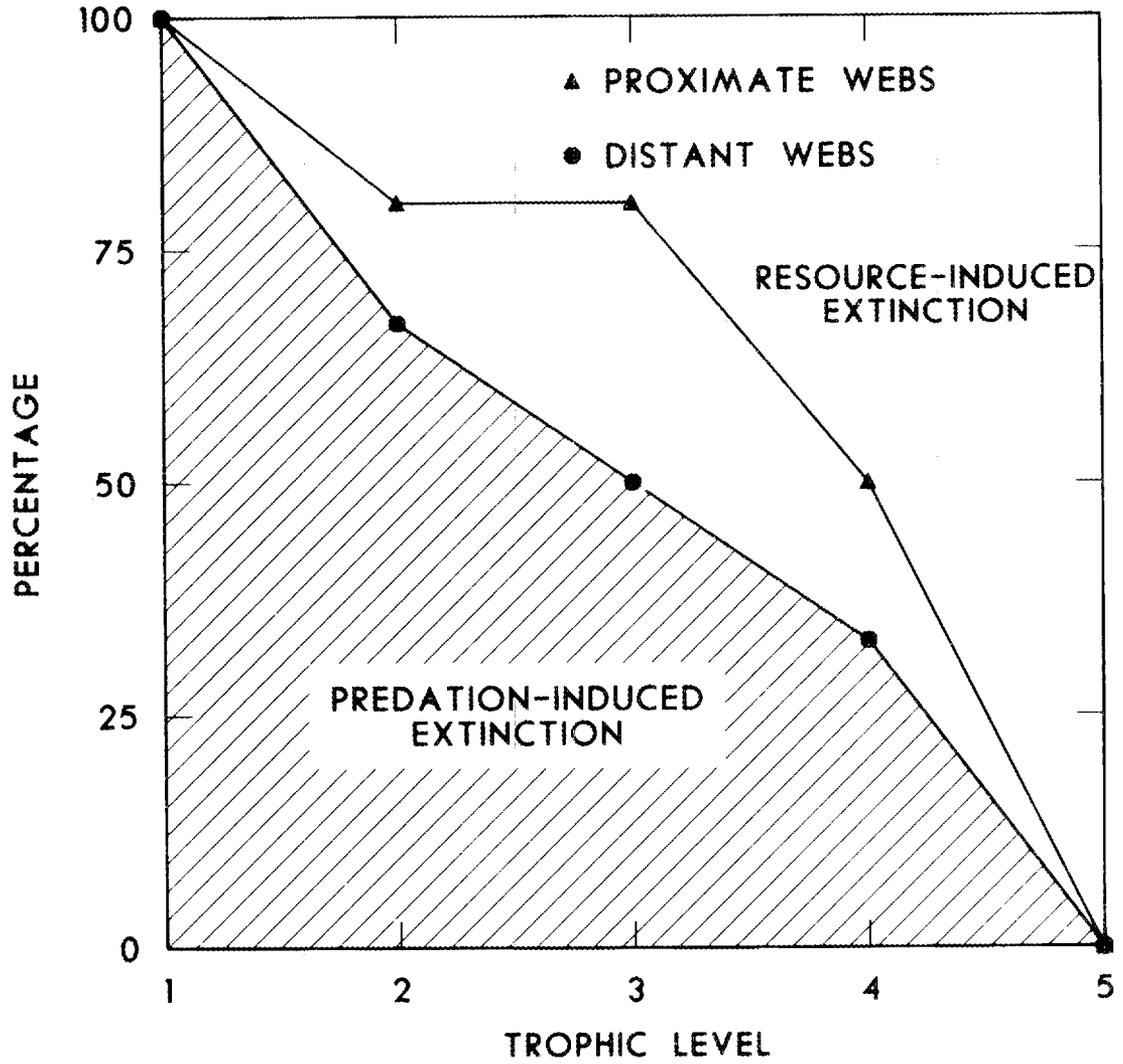


Figure 22. Percentage of extinctions caused by predation and resources for food webs with proximate and distant initial densities.

Table 9. Relative Importance of Resource and Predation-Induced Extinction in Food Webs with Proximate vs. Distant Initial Densities.

Trophic Level	Extinction Type	Proximate Initial Densities	Distant Initial Densities
1	Predation	38	67
	Resource	<u>0</u>	<u>0</u>
	Total	38	67
2	Predation	70	76
	Resource	<u>16</u>	<u>35</u>
	Total	86	111
3	Predation	68	55
	Resource	<u>19</u>	<u>40</u>
	Total	87	95
4	Predation	42	27
	Resource	<u>48</u>	<u>59</u>
	Total	90	86
5	Predation	0	0
	Resource	<u>131</u>	<u>142</u>
	Total	131	142

lag preceding the response of carnivores to this outbreak is too long to protect autotrophs from overexploitation by herbivores. Giving autotrophs a head start is not necessarily conducive to high diversity unless immigration of the carnivore trophic level is synchronized with that of the herbivores.

Overall, predation pressure moved higher up in the webs as the initial biomasses of adjacent trophic levels converged. Table 9 illustrates the distribution of predation pressure for food webs with proximate and distant initial densities. The emphasis of predation intensity shifts from the first two trophic levels in proximate food webs, while the influence of the top trophic level becomes much greater.

Figure 22 illustrates the change in slope of the transition from predation to resource-control of species selection with increased trophic position. The relative importance of predation-induced extinction increases at intermediate trophic levels, curving the slope hyperbolically (the endpoints are fixed). Whether this relationship occurs in natural food webs is not clear.

Trophic strategy success was also different in food webs with proximate and distant initial predator-prey densities. The number of specialists and species of intermediate trophic variety increased on all trophic levels except for the fourth in the proximate webs. The success of generalists did not change. This suggests that specialists are frequently endangered in the distant webs by their predisposition to overexploit, which implies that more immediate control exerted by their predators, as would be expected in proximate food webs, may allow them to persist.

Changes in total species diversity as initial densities converge are shown in Figure 23 for each trophic level. The diagram shows that lower trophic levels support more species in food webs with proximate initial densities, while

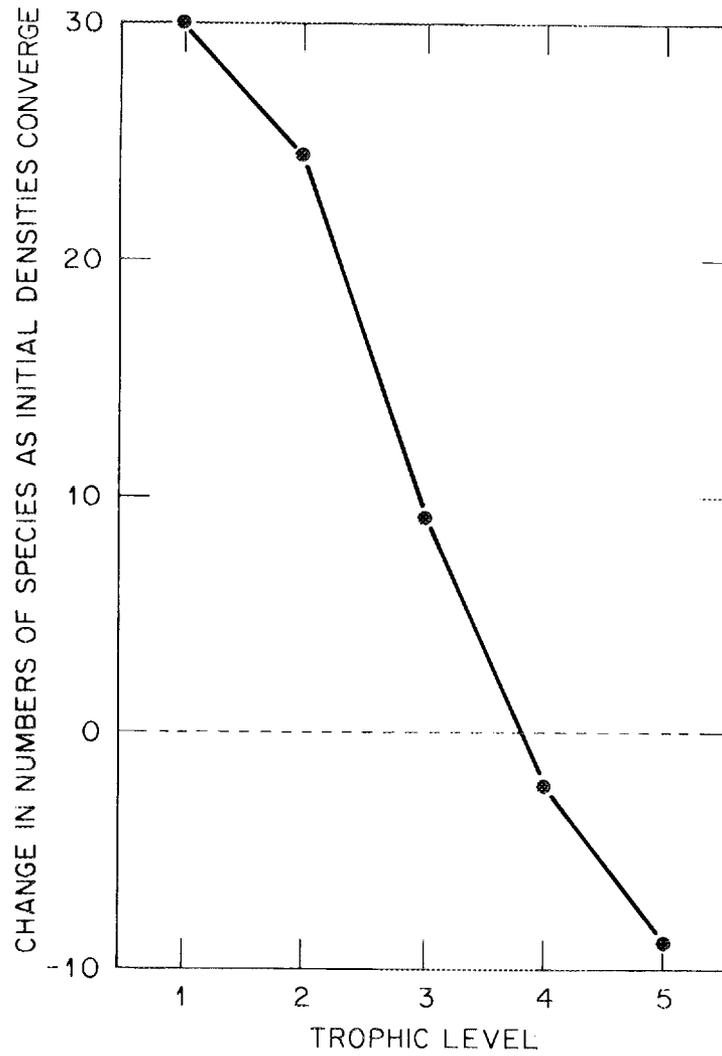


Figure 23. Changes in species diversity for each trophic level in food webs with proximate and distant initial densities.

higher trophic levels become less diverse. The total number of species persisting in proximate food webs is greater than that of food webs with distant initial densities. The diversity gained at lower trophic levels more than compensates for the species lost from the upper reaches of the webs. This result is interesting as an indication that food web connectance can be consistently altered by changing initial conditions.

### **Conclusion**

Results of this analysis suggest that structural properties of a particular food web will be different in communities that develop gradually with small, diffuse initial densities of invading consumers (fine-grained) and communities with more distinct gradients in species density (coarse-grained) where larger, advective infusions of heterotroph species are the rule.

In nature, communities rarely fall neatly into these classifications. Some species or guilds within the community may operate on larger spatial scales than that characteristic of the patch grain while others may be smaller. Qualities of the species themselves may lead to relatively more diffusive movements by some and larger migrational influxes by others. Predator-prey interactions among patches can produce gradients densities due to lags. This, in itself, may give rise to patterns of local extinction and invasion in which initial predator and prey densities are relatively more distant or close. This relates to the ecological problem of identifying minimal patch sizes capable of sustaining a given food web assemblage.



**APPENDIX C. EXTINCTION DATA**



THE SUCCESS OF SPECIES WITH  
DIFFERENT TROPHIC CHARACTERISTICS  
EXCLUSION EXPERIMENT--TWO TROPHIC LEVELS

TROPIC STATUS	3° CARNIVORE					
	2° CARNIVORE					
	1° CARNIVORE					
	HERBIVORE	9	18	7	23	7
	AUTOTROPH•	4	21	8	1	1
		1	2	3	4	5
		NUMBER OF PREY				

•FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1,2,3...etc. SURVIVING AUTOTROPH SPECIES.

THE SUCCESS OF SPECIES WITH  
DIFFERENT TROPHIC CHARACTERISTICS  
EXCLUSION EXPERIMENT--THREE TROPHIC LEVELS

TROPIC STATUS	3° CARNIVORE					
	2° CARNIVORE					
	1° CARNIVORE	8	17	19	13	2
	HERBIVORE	8	12	4	22	27
	AUTOTROPH*	1	11	9	9	7
		1	2	3	4	5
		NUMBER OF PREY				

\*FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1,2,3...etc. SURVIVING AUTOTROPH SPECIES.

THE SUCCESS OF SPECIES WITH  
DIFFERENT TROPHIC CHARACTERISTICS  
EXCLUSION EXPERIMENT--FOUR TROPHIC LEVELS

TROPIC STATUS	3° CARNIVORE					
	2° CARNIVORE	11	18	19	18	5
	1° CARNIVORE	8	18	22	18	23
	HERBIVORE	6	12	7	22	25
	AUTOTROPH•	2	10	9	9	6
		1	2	3	4	5
		NUMBER OF PREY				

•FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1,2,3...etc. SURVIVING AUTOTROPH SPECIES.

THE SUCCESS OF SPECIES WITH  
DIFFERENT TROPHIC CHARACTERISTICS  
EXCLUSION EXPERIMENT--FIVE TROPHIC LEVELS

TROPIC STATUS	3° CARNIVORE	6	10	15	12	0
	2° CARNIVORE	10	21	26	23	10
	1° CARNIVORE	8	20	23	19	17
	HERBIVORE	6	13	6	13	27
	AUTOTROPH*	2	11	8	8	8
		1	2	3	4	5
		NUMBER OF PREY				

\*FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1,2,3...etc. SURVIVING AUTOTROPH SPECIES.

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 0.5

TROPIC STATUS	3° CARNIVORE	0	0	0	0	0
	2° CARNIVORE	0	0	0	0	0
	1° CARNIVORE	5	5	9	12	0
	HERBIVORE	4	11	6	14	14
	AUTOTROPH*	0	0	2	12	6
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPHIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 1.0

TROPIC STATUS	3° CARNIVORE	0	0	0	0	0
	2° CARNIVORE	2	2	0	0	0
	1° CARNIVORE	5	8	11	10	2
	HERBIVORE	5	11	5	13	15
	AUTOTROPH*	0	0	3	11	6
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 2.5

TROPIC STATUS	3° CARNIVORE	0	0	0	0	0
	2° CARNIVORE	5	9	12	9	1
	1° CARNIVORE	4	10	15	10	10
	HERBIVORE	4	11	5	13	14
	AUTOTROPH*	0	3	4	7	6
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPHIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 5.0

TROPIC STATUS	3° CARNIVORE	3	5	7	8	0
	2° CARNIVORE	4	10	12	12	5
	1° CARNIVORE	4	10	13	9	10
	HERBIVORE	3	8	3	11	16
	AUTOTROPH*	1	4	4	7	4
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 10.0

TROPIC STATUS	3° CARNIVORE	6	8	6	11	4
	2° CARNIVORE	4	7	16	12	6
	1° CARNIVORE	2	9	10	11	7
	HERBIVORE	1	8	3	11	13
	AUTOTROPH*	0	6	6	6	1
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

PRODUCTIVITY EXPERIMENT - SUN = 20.0

TROPIC STATUS	3° CARNIVORE	6	7	10	9	5
	2° CARNIVORE	4	6	12	10	7
	1° CARNIVORE	3	7	9	9	6
	HERBIVORE	2	8	3	10	12
	AUTOTROPH*	2	3	8	4	2
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT TROPHIC CHARACTERISTICS

PRODUCTIVITY GRADIENT - SUN = 0.3

TROPIC STATUS	CARNIVORE	0	1	1	4	2	2	0	0	0	0
	HERBIVORE	0	4	7	8	9	11	12	15	7	2
		1	2	3	4	5	6	7	8	9	10
		NUMBER OF PREY									

THE SUCCESS OF SPECIES WITH DIFFERENT TROPHIC CHARACTERISTICS

PRODUCTIVITY GRADIENT - SUN = 0.4

TROPIC STATUS	CARNIVORE	0	3	5	7	9	8	5	5	0	0
	HERBIVORE	1	5	10	10	12	14	12	16	14	9
		1	2	3	4	5	6	7	8	9	10
		NUMBER OF PREY									

THE SUCCESS OF SPECIES WITH DIFFERENT TROPHIC CHARACTERISTICS

PRODUCTIVITY GRADIENT - SUN = 0.5

TROPIC STATUS	CARNIVORE	0	3	5	9	12	12	13	12	3	0
	HERBIVORE	2	7	12	12	12	15	11	18	17	12
		1	2	3	4	5	6	7	8	9	10
		NUMBER OF PREY									

THE SUCCESS OF SPECIES WITH DIFFERENT TROPHIC CHARACTERISTICS

PRODUCTIVITY GRADIENT - SUN = 0.6

TROPIC STATUS	CARNIVORE	0	4	8	9	13	14	16	13	6	0
	HERBIVORE	2	7	11	11	13	14	13	18	18	14
		1	2	3	4	5	6	7	8	9	10
		NUMBER OF PREY									

THE SUCCESS OF SPECIES WITH DIFFERENT TROPHIC CHARACTERISTICS

PRODUCTIVITY GRADIENT - SUN = 1.0

TROPIC STATUS	CARNIVORE	0	3	10	11	13	15	13	13	4	0
	HERBIVORE	0	5	11	10	11	11	12	18	16	15
		1	2	3	4	5	6	7	8	9	10
		NUMBER OF PREY									

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

FUNCTIONAL RESPONSE CURVATURE  $K = 0$

TROPIC STATUS	3° CARNIVORE	3	6	7	5	0
	2° CARNIVORE	4	9	14	15	4
	1° CARNIVORE	7	8	9	11	9
	HERBIVORE	0	7	5	9	17
	AUTOTROPH*	7	10	2	1	0
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPHIC CHARACTERISTICS

FUNCTIONAL RESPONSE CURVATURE  $K = 1$

TROPIC STATUS	3° CARNIVORE	3	6	7	7	0
	2° CARNIVORE	5	8	14	13	5
	1° CARNIVORE	5	10	11	11	10
	HERBIVORE	1	9	5	11	16
	AUTOTROPH*	3	13	2	2	0
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, ... ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

FUNCTIONAL RESPONSE CURVATURE  $K = 2$

TROPIC STATUS	3° CARNIVORE	3	4	7	8	0
	2° CARNIVORE	5	10	15	12	3
	1° CARNIVORE	4	11	12	9	10
	HERBIVORE	2	9	6	11	15
	AUTOTROPH*	2	9	7	2	0
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

FUNCTIONAL RESPONSE CURVATURE  $K = 3$

TROPIC STATUS	3° CARNIVORE	3	5	7	8	0
	2° CARNIVORE	4	10	12	12	5
	1° CARNIVORE	4	10	13	9	10
	HERBIVORE	3	8	3	11	16
	AUTOTROPH*	1	4	4	7	4
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

BONUS EXPERIMENT - NO BONUS

TROPIC STATUS	3° CARNIVORE	0	0	0	0	0
	2° CARNIVORE	1	0	5	4	20
	1° CARNIVORE	3	5	11	14	20
	HERBIVORE	0	0	0	0	20
	AUTOTROPH*					
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

BONUS EXPERIMENT - BONUS = .5

TROPIC STATUS	3° CARNIVORE	1	3	1	8	0
	2° CARNIVORE	6	8	13	13	7
	1° CARNIVORE	6	8	13	12	13
	HERBIVORE	2	9	2	12	17
	AUTOTROPH*	0	0	6	9	5
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

BONUS EXPERIMENT - BONUS = 1.5

TROPIC STATUS	3° CARNIVORE	3	6	4	7	0
	2° CARNIVORE	5	8	13	10	3
	1° CARNIVORE	3	9	10	10	3
	HERBIVORE	0	8	5	12	10
	AUTOTROPH*	2	8	6	2	1
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

BONUS EXPERIMENT - BONUS = 3

TROPIC STATUS	3° CARNIVORE	2	5	4	4	0
	2° CARNIVORE	5	7	7	5	3
	1° CARNIVORE	1	3	6	9	5
	HERBIVORE	0	3	2	11	5
	AUTOTROPH*	9	8	1	0	0
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

SUCCESION EXPERIMENT - DISTANT INITIAL DENSITIES

TROPIC STATUS	3° CARNIVORE	6	11	14	12	0
	2° CARNIVORE	10	20	36	23	10
	1° CARNIVORE	8	19	22	18	23
	HERBIVORE	6	13	6	22	27
	AUTOTROPH*	2	11	9	8	7
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF 1, 2, 3, . . . ETC. SURVIVING AUTOTROPH SPECIES

THE SUCCESS OF SPECIES WITH DIFFERENT  
TROPIC CHARACTERISTICS

SUCCESSION EXPERIMENT - PROXIMATE INITIAL DENSITIES

TROPIC STATUS	3° CARNIVORE	8	16	15	15	0
	2° CARNIVORE	8	22	29	26	10
	1° CARNIVORE	1	22	23	19	23
	HERBIVORE	8	17	14	32	28
	AUTOTROPH*	0	2	9	14	12
		1	2	3	4	5
		NUMBER OF PREY				

\* FOR AUTOTROPHS, THE SCALE 1-5 INDICATES FREQUENCY OF  
1. 2. 3. . . ETC. SURVIVING AUTOTROPH SPECIES



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