

A SIMULATION EXPERIMENT TO INVESTIGATE FOOD WEB POLARIZATION

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ABSTRACT

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The relationship between food web structure and function is complex, with few simplifying theories to aid in isolating patterns. In this paper we consider a hypothesis that relates patterns of trophic-level regulation to opposing forces of resource limitation and predation. A simulation exclusion experiment is used to compare patterns of regulation from lower to higher trophic levels. In these simulated food webs, species presence/absence and subsequent regulation of persisting species densities showed qualitatively different patterns of predation and resource control.

INTRODUCTION

In 1960, Hairston et al. outlined the “Balance of Nature” hypothesis (HSS) to explain why the “world is green”. The perceived abundance of plants was attributed to the regulation of herbivores by their predators. In 1977, Fretwell generalized this hypothesis to explain his observation that while some ecosystems have an abundance of plants, others have very little plant-life. These regions were commonly referred to as the “green” and

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“brown” parts of the world, respectively. Fretwell’s hypothesis proposed that food chains are “polarized”, alternating from top to bottom between resource- and predation-controlled links. Food chains with an odd number of links comprise the “green” regions noted by Hairston et al., while food chains with an even number of links were hypothesized to produce the “brown” regions. Fretwell also formalized the assumptions underlying both HSS and his more general version which is termed the Exploitation hypothesis (Fretwell, 1977). The simulation experiment described here examines the robustness of Fretwell’s Exploitation hypothesis when generalized from food chains to food webs.

Fretwell’s exploitation hypothesis, reviewed

In general, the Exploitation hypothesis contends that adjacent trophic links in a food chain alternate between resource and predation control. Define N as the number of trophic levels in a food chain. The Exploitation hypothesis states that food chains are characterized by a resource-limited top predator (trophic level $M = N$). This resource-limited predator causes its prey ($M = N - 1$) to be limited by predation. The prey population has minimal influence on its own ($M = N - 2$) prey population, as a result of strong predation pressure; therefore the prey population ($M = N - 2$) should be resource-limited. The tendency of trophic levels to be driven to an extreme of resource or predation control can be likened to the polarization resulting from opposing magnetic forces. When this pattern of alternating trophic levels arises the series of events described above will be referred to, here, as “food web polarization”.

Assumptions of the hypothesis are:

- (1) The units involved (species or trophic levels) behave as a single food chain.
- (2) Units can be either predation- or resource-limited.
- (3) Resource-limited units, in turn, limit their resource.
- (4) Predation-limited units do not limit their resource.

The Exploitation hypothesis is an idealization and the types of questions that we consider useful are those that explore the conditions under which this phenomenon occurs, and whether it provides a significant improvement in the prediction of food web behavior. As Slobodkin et al. (1967) state, “the assertion that a population is food-limited does not deny the possibility of simultaneous limitation by predation”. However, there may be some merit to the suggestion that the extremes of resource and predation limitation are attractive states under usual food chain dynamics. Chao et al. (1977) performed a chemostat experiment in which they identified two stable states of coexistence between bacteria and phage populations: “(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". One can envision food chains existing in a polarized state with strongly and alternately limited links, or in a relaxed state in which regulation is equally divided between predation and resources.

While the Exploitation hypothesis is strictly derived from the assumption that the food web in question is, or behaves as, a food chain, evidence from a number of field studies suggests that the hypothesis applies to food webs as well (e.g. Virnstein, 1977; Estes et al., 1978; Lynch and Shapiro, 1981). In addition, a number of studies addressed the prediction of the Exploitation hypothesis that, along productivity gradients, food chain length will increase, creating an alternating of resource- and grazer-limited plant communities. (See, for example, Oksanen et al., 1981; Oksanen, 1982; Oksanen, 1983; Arruda, 1979.)

We present here the results from a simulation experiment designed to investigate the question of whether simulated food webs behave in a manner consistent with the Exploitation hypothesis. The food webs we use in our simulations have multiple species on each trophic level as well as several trophic levels. However, as this is a first step, no omnivory (feeding on more than one trophic level) or decomposition feedback is incorporated. Clearly, the hypothesis will be much more useful if it can be generalized to food webs, and if the conditions under which the hypothesis holds are better understood.

EXPERIMENTAL METHODS

The approach taken in this study resolves around a food web simulation model, WEB. This model has a number of variables of interest that are controlled, while Monte Carlo procedures are used to randomize the remaining variables. Two response variables were used in defining the term 'limitation' for these experiments. In the first definition, we considered a particular trophic level to be predation-limited if the persistence (and conversely, extinction) of its species depends primarily on the pressure exerted by predators. In the second definition, a predator-limited trophic level was defined as one showing a significant increase in total biomass following the removal of predators. The limitation of both persistence and biomass for a given trophic level will be compared using these definitions.

The Exploitation hypothesis offers two testable predictions: (1) a particular trophic level will respond to successive removals of higher trophic levels by alternating between limitation by resources and predation. (2) for food

		TOTAL NUMBER OF TROPHIC LEVELS IN FOOD WEB (N)	
		ODD	EVEN
TROPIC LEVEL OF INTEREST (M)	ODD	M IS RESOURCE-LIMITED	M IS PREDATION-LIMITED
	EVEN	M IS PREDATION-LIMITED	M IS RESOURCE-LIMITED

Fig. 1. Pattern of trophic-level regulation hypothesized by the Exploitation hypothesis. The factor limiting trophic level M in a food web having N trophic levels is shown.

webs of a given height (number of levels), trophic levels will show an alternating pattern of limitation from the top to the bottom of the web. An exclusion experiment is necessary to separate the two effects, that of existing at a particular trophic level from the polarization effect predicted by the Exploitation hypothesis. If the Exploitation hypothesis were completely general, then a sort of stationarity would exist. Limitation of any trophic level would depend solely on the oddness or evenness of its trophic distance from the top predators, and not on its trophic position. A statistical interaction between the two effects would be evident if, for example, the removal of a sixth trophic level had a different effect on the herbivores than it had on the secondary carnivores, despite the fact that both trophic levels were an odd number of trophic levels from the top of the food web. We present here the results of a simulation experiment designed to investigate the question of whether simulated food webs behave in a manner consistent with the Exploitation hypothesis. Clearly, the hypothesis would be much more useful if it could be generalized to food webs, or if the conditions under which the hypothesis held were better understood.

Figure 1 may be helpful in understanding the postulated relationship between trophic height (N) and trophic status (M). Note the effect of removing trophic levels on a given M^* th level, and the effect from the bottom to top of the web ($M = 1, 2, \dots, N^*$) for a constant food web height, N^* . Observe that the evenness or oddness of the quantity ($N - M$) provides an index that incorporates both aspects of the Exploitation hypothesis.

Food web simulation model – WEB

Food web structure. Two factors were incorporated into the experimental design of the food web simulation experiments that were conducted: (1) the initial (maximum) number of trophic levels in the model food webs, and (2) the feeding diversities of the hypothetical species in the model food webs.

	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

Fig. 2. Qualitative interaction matrix describing trophic relations in a typical food web simulation with five species on each trophic level.

Twenty-five species (five per trophic level) were connected so that each level has one species with only a single prey connection, one with two prey, and so on, up to the most diversified predator with all five prey types included in its diet. The particular connections between predators and their prey were selected at random. This resulted in a uniform distribution for the variable 'number of prey' on the range [1, 5] and a normal distribution of the variable 'number of predators' among prey species over a large sample of pooled webs. A sample connectivity matrix with trophic connections designated by ones (1's) is shown in Fig. 2. Note that strict adherence to organization into trophic levels was enforced as there are no connections between non-adjacent trophic levels. Species numbers should be cross-referenced with those in Fig. 3 which assigns a trophic level and a trophic diversity to each species in the web. Figure 3 illustrates the organization of the simulation food webs according to the statistical design used. In the exclusion experiment discussed here the number of trophic levels, and not feeding diversity, will be of interest.

Model equations. The features of the equations used for predator-prey interactions are: (1) a sigmoid functional response, (2) feeding rates based on total prey available to a species, rather than pairwise interactions between predator and each prey, and (3) an efficiency bonus awarded for

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				

Fig. 3. Experimental design of WEB: Assignment of trophic characteristics (1, feeding diversity; 2, trophic status) to species in the webs.

specialization. The parameter values used were chosen as viable values based on experimentation. As such, they do not represent any particular trophic system in nature.

The autotroph equations are designed to mimic spatial density dependence for the primary producers using an intake function that allows plant populations (1) to grow quickly under conditions of sparse vegetation cover (or phytoplankton shading), but (2) to gradually decelerate growth as carrying capacity is approached. The intake function F comprises two terms such that emphasis shifts from one to the other as total autotroph density increases. When densities are low, each population's growth is in proportion solely to its own density. When densities are high, each population's growth is proportional to the fraction of total autotroph density that it represents. Intake for autotroph species i is defined as:

$$F_i(t, X) = \left[1 + M - \sum_{i=1}^m X_i(t) \right] a_i f(t) X_i(t) / M \quad (1)$$

where M represents the maximum density or carrying capacity, m is the total number of autotroph populations, $X(t)$ represents population density as a function of time, $f(t)$ denotes energy input to the producer trophic level (e.g. sunlight) converted to units of biomass, and a_i is the feeding efficiency of species i , which is inversely related to the number of prey species in its diet. For simplicity, in this experiment, the input to producers is held constant (five units), and feeding efficiencies among autotroph populations are set equal (1.0).

The intake function for heterotrophs is somewhat different. Function G describes the feeding rate of a predator on its collective ensemble of prey. This formulation determines the feeding rate of a predator based on the total prey availability and then removes biomass from each prey species according to its proportion of that total. This reflects the intuition that feeding rates are determined not so much by isolated pairwise interactions between each predator and each prey species, as by an integrated assessment of prey availability. The functional response of this feeding rate to changing prey density can be varied from a linear to a strongly sigmoid type III function (Holling, 1959) by manipulating parameter γ which regulates the curvature of the functional response. The effect of varying the function's shape using γ is the subject of another experiment in which these simulations were replicated with various degrees of curvature in the functional response. The heterotroph intake function, G , is given by:

$$G(\mathbf{E}_i \cdot \mathbf{X}) = -\frac{2\beta}{3X_m} (\mathbf{E}_i \cdot \mathbf{X})^3 + \beta (\mathbf{E}_i \cdot \mathbf{X})^2 + [a_i - \beta X_m/3] (\mathbf{E}_i \cdot \mathbf{X}) \quad (2)$$

where

$$\beta = \frac{\gamma}{X_m} \min \{ a_i \}$$

in which X_m is the maximum prey density, and parameter γ ($= 3$) is the slope at the inflection point of this cubic intake function; matrix \mathbf{E} is a qualitative interaction matrix (see Fig. 1), \mathbf{X} denotes the vector of population densities, and the scalar product $\mathbf{E}_i \cdot \mathbf{X}$ represents the sum of prey densities for all prey species included in the diet of species i . The predation efficiency bonus a_i is awarded in inverse proportion to the number of prey included in the predator's diet. It varies on the interval (0, 1) from more generalized to more specialized predators.

Equation (2) was derived by fitting a cubic with endpoints at total prey density $(\mathbf{E}_i \cdot \mathbf{X}) = 0$ and X_m , with the slope of G equal to zero at both. For simplicity, the inflection point was located at $X_m/2$. Figure 4 shows the general form of G as a function of total prey density $(\mathbf{E}_i \cdot \mathbf{X})$.

We define α (set to 0.1) as predation transfer efficiency, including waste resulting from assimilation loss, partial consumption, or, more generally, the percentage of prey biomass obtained by the predator population that fails to contribute to its growth. The number of species on the predator trophic level is n ($= 5$), and r ($= 0.05$) is the respiration coefficient, or more generally, the density-dependent rate of population decay caused by factors unrelated to predation. The general expression for the rate of change in a given species' density over time assumes one of three forms in the model, depending on its trophic status:

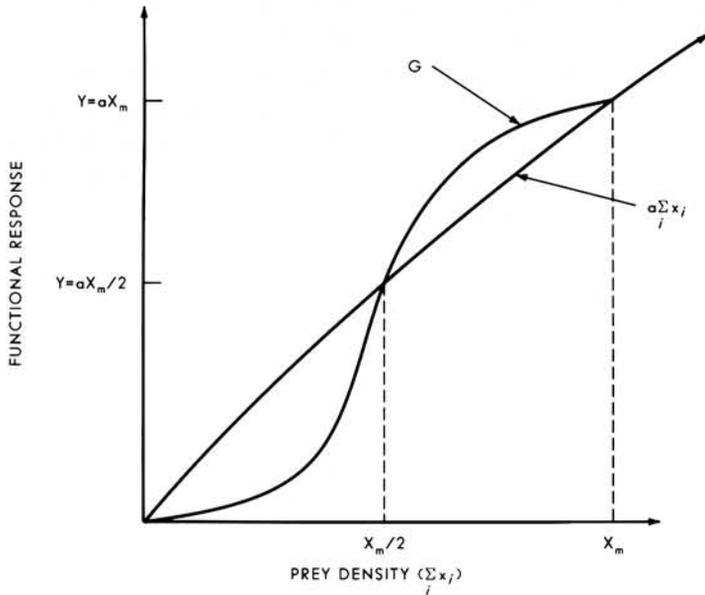


Fig. 4. Function describing the relationship between feeding rate and prey density.

– for autotrophs:

$$\dot{X}_i = F_i(t, \mathbf{X}) - \sum_{j=1}^n \mathbf{E}_{ij} G(\mathbf{E}_j \cdot \mathbf{X}) X_j - rX_i \quad (3)$$

– for intermediate species:

$$\dot{X}_i = \alpha G(\mathbf{E}_i \cdot \mathbf{X}) X_i - \sum_{j=1}^n \mathbf{E}_j G(\mathbf{E}_{ij} \cdot \mathbf{X}) X_j - rX_i \quad (4)$$

– for top predators:

$$\dot{X}_i = \alpha G(\mathbf{E}_i \cdot \mathbf{X}) X_i - rX_i \quad (5)$$

Initial densities, equilibrium and extinction. Initial densities for species in the food web simulations were chosen so that the succession (immigration) of species into successively higher trophic levels is gradual, and that competitors should start with equal densities to eliminate the influence of initial densities. For autotrophs it is possible to find the total equilibrium density or carrying capacity sustained in the absence of predators. The combined density of the first trophic level species is then initialized at 1/100th of this carrying capacity, and each successive level of predators initially comprises 1/100th of the trophic level on which it feeds. This procedure is intended to

simulate the process of invasion and successional trophic web construction, thus giving each trophic level a head start on its predators. Biomass is distributed equally among species within each trophic level. When changes in population density are sufficiently small, the food web is considered to be at equilibrium. Likewise, sufficiently small populations are considered extinct. The extinction threshold used here is a density of 10^{-20} times the initial density. The majority of simulations ran until reaching equilibrium, which was defined for our purposes as less than 0.01% change in density for all species in the food web during a single time step.

Reconstruction of food web dynamics using extinction information. An important advantage of simulating the behavior of a good web over time is that one is able to determine what actually causes some species to persist and others to disappear from the web. Reasons underlying every species extinction were recorded, along with the time of the occurrence, without keeping track of every species' biomass at all times. This extinction bookkeeping system provided a concise summary of useful information. A code was assigned to each species at the time of extinction classifying the extinction as primarily resource-induced if no viable prey remained and predation-induced if the extinction occurred in spite of available prey.

Exclusion experiment design

An exclusion experiment is one in which predation is eliminated in some areas while in other areas (controls) it is left alone (e.g., Dayton, 1971; Thorpe and Bergey, 1981). Exclusion experiments can be simulated with WEB by removing the highest trophic levels one by one in a random sample of otherwise identical food webs. Each food web has a maximum of five trophic levels yielding four treatment groups with five, four, three, and two trophic levels. Figure 5 shows a sample sequence of a five-trophic-level food web and the successive removals of its trophic levels. A '1' in the matrix indicates that the column species is preyed upon by the row species. Circled species are those that survived the simulation and belong to the equilibrium configuration of the food web.

Five was chosen as a maximum number of trophic levels due to limitations in computer resources and because it was felt that at least that many would be needed to distinguish the effect of trophic status from the effect, if any, of polarization.

The Exploitation hypothesis was examined from the standpoint of both the regulation of persistence/extinction and the regulation of biomass. The usual interpretation of 'limitation' measures the effect of some limiting factor on a species' biomass. In this case, as we are focusing on the trophic

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	11	0	1	0	0	0						
						12	0	1	1	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	⑬	1	1	0	1	0						
						⑭	0	1	1	1	1	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	15	1	1	1	1	1						
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												17	1	0	1	0	0	17	1	0	1	0	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	18	0	1	1	1	0	18	0	1	1	1	0
												19	1	1	0	1	1	19	1	1	0	1	1	19	1	1	0	1	1	19	1	1	0	1	1
												⑳	1	1	1	1	1	⑳	1	1	1	1	1	⑳	1	1	1	1	1	⑳	1	1	1	1	1
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																		21	0	1	0	0	0	21	0	1	0	0	0	21	0	1	0	0	0
																		22	0	0	1	1	0	22	0	0	1	1	0	22	0	0	1	1	0
																		23	1	0	1	1	0	23	1	0	1	1	0	23	1	0	1	1	0
																		⑳	1	0	1	1	1	⑳	1	0	1	1	1	⑳	1	0	1	1	1
																		25	1	1	1	1	1	25	1	1	1	1	1	25	1	1	1	1	1

Fig. 5. Sample sequence of initial food webs used in the exclusion experiment.

level as a whole, the combined biomass of species on a trophic level was used to define trophic-level limitation. The direction and magnitude of change in total trophic-level biomass in response to trophic-level removal provides a measure of the limitation regime. Trophic-level limitation can also be defined in terms of the persistence or extinction of species that belong to one trophic level. Frequencies of occurrence of extinctions classified as resource-induced and predation-induced were compared.

RESULTS

Regulation of persistence / extinction

Food web height (N) did not influence the pattern of extinctions, and, in particular, there was no evidence of an alternating pattern such as the Exploitation hypothesis predicts. In general, we found that the percentage of predation-induced extinctions on each trophic level increased as trophic status (M) became lower, with a concomitant decrease in resource-induced

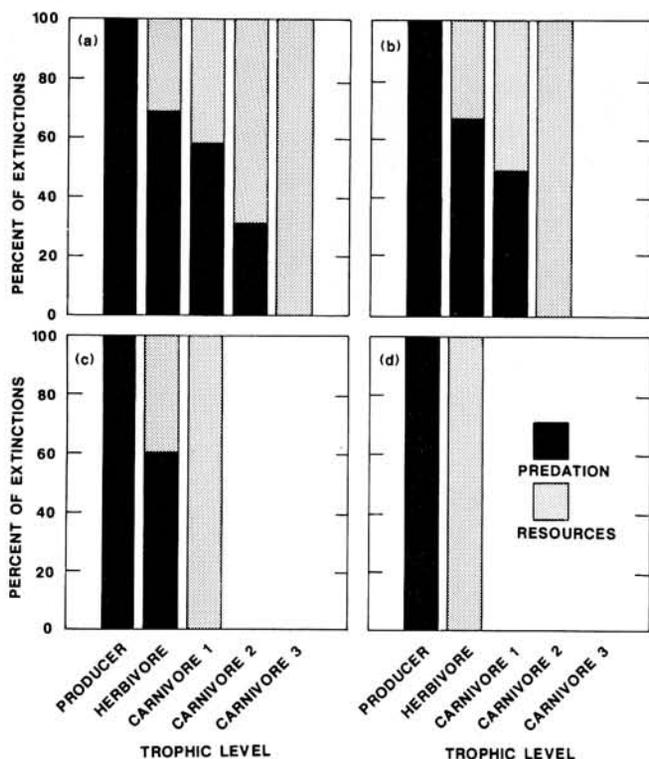


Fig. 6. Percentage of extinctions caused by resources and predation as a function of trophic status for food webs having: (a) five trophic levels; (b) four trophic levels; (c) three trophic levels; and (d) two trophic levels.

extinctions (see Fig. 6). If these model food webs operated according to the Exploitation hypothesis, then one would expect predation-induced extinctions to occur more frequently between trophic levels hypothesized to be resource-limited and their predation-limited prey trophic levels ($N - M$ odd in Fig. 1).

Regulation of biomass

Figure 7 shows that our simulation experiment supports the prediction above, as equilibrium densities of alternate trophic levels correlate in a positive fashion, while those of adjacent trophic levels show a negative correlation. The range of densities at equilibrium is shown for the subset of food webs initially capable of supporting five trophic levels (35) as successive levels are removed. Midpoints of the ranges are joined. It is evident that the removal of each successive trophic level has the predicted effect of changing the quantity of biomass on each trophic level in an alternating

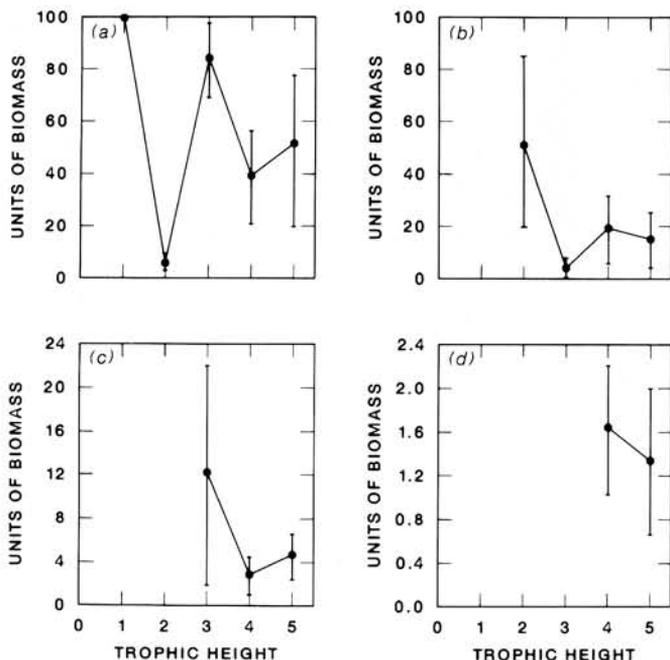


Fig. 7. Range of near-equilibrium densities in simulated food webs as the number of trophic levels changes for: (a) autotrophs; (b) herbivores; (c) primary carnivores; and (d) secondary carnivores.

pattern. This pattern was consistent within each of the food webs simulated under the four treatments and did not appear to depend on the particular connections among species in each model food web's configuration. Furthermore, the direction of change was consistently in the expected direction. Trophic levels hypothesized to be in transition from being predation-limited to being resource-limited showed increases in total biomass and vice-versa.

In addition, a diminishing effect was observed both with higher trophic position and with the removal of more remote trophic levels, suggesting an interaction between trophic position (N) and evenness/oddness of the quantity ($N - M$). The alternating pattern in Fig. 7 appears to be more significant in shorter food webs (in transition from three to two trophic levels) and tapers off in taller webs. Both trophic status (M) and distance from the top level ($N - M$) seem to be involved in damping the polarization. The effect of trophic status is demonstrated by comparing the more dramatic response of lower trophic levels to those of higher trophic levels following any removal in Fig. 7. The first additions of trophic levels cause larger switches in biomass than do subsequent additions, which illustrates that the effect also diminishes with trophic distance ($N - M$).

DISCUSSION

In the present study, implications of the Exploitation hypothesis were tested concerning the importance of predation and resources in structuring food webs. Results of model simulations indicate that the causes of species extinction and the regulation of biomass in persistent species show different patterns of predation vs. resource control along a gradient of trophic position.

Regulation of biomass

The most common definition of 'limitation' in ecology is the change in biomass induced by a change in resource density (resource control) or a change in predator biomass (predation control). Our simulation results show that changes in biomass were greatest when trophic levels were removed from short food webs and tapered off as the number of trophic levels initially present increased. One suggested explanation for this reduction is that the inefficiency of transfer between successive trophic levels results in order-of-magnitude reductions in the impacts of successively higher trophic levels (DeAngelis, personal communication, 1983). Alternatively, taller food webs have higher incidences of mixed-length branches (food chains within the web that do not support a top predator). This may lead to a dilution of the alternating pattern as the number of trophic levels present increases. Ideally one could develop a model to roughly predict the density of a population from its juxtaposition with the different length food chains supported by it: biomass = F (number of odd chains, number of even chains). This would represent an interesting extension of the Exploitation hypothesis from ideal food chains to food webs composed of mixed-length chains.

Regulation of persistence / extinction

It was determined that the species selection process is influenced by trophic position (M) and not by distance from the top trophic level ($N - M$). In contrast to trophic-level biomass, the pattern of species extinctions did not alternate at all, but rather showed a consistent shift from predation- to resource-induced extinction in transition from lower to higher trophic levels. Changes in the number of trophic levels present had little, if any, effect on the percentages of each type of extinction. Figure 8 expresses the contrast in pattern between the limitation of species persistence and that of equilibrium-sustained biomass for trophic levels in a five-level food web.

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



STRONG PREDATION-CONTROL

STRONG RESOURCE-CONTROL

Fig. 8. Contrast between patterns of resource and predation control of species selection and biomass for food webs with five trophic levels.

In this model, autotrophs had a single resource (light) that caused extinction only indirectly when the autotroph's relative abundance declined as a result of herbivory. Because the extinction of light was not permitted, no resource-induced extinctions were recorded for autotrophs, precluding any meaningful interpretation of results for the autotroph level. Nevertheless the trend across trophic levels was quite distinct and persisted in every experimental manipulation of parameters and food web heights.

Comparison of biomass and persistence / extinction

A population reaches extinction as a result of diminishing biomass. At first guess, one would expect factors regulating biomass to be the same as those regulating extinction, at least when biomass is small. However, results here showed clearly different patterns of control for extinction and biomass.

At the scale of the trophic level, regulation of the total biomass is apt to reflect regulation of the dominant species. In contrast, regulation of species extinctions reflects the primary forces acting on species when they are very small. If this is the case, then the differences in regulation patterns observed here correspond to differences in regulation of rare and dominant species. If these results have any bearing on natural systems, managers of endangered species could disregard the Exploitation hypothesis because extinction would

not be expected to show a polarized pattern. Agriculturalists concerned with overall yield of a dominant crop species would, however, be well advised to take the number of predator links above the crop into consideration.

The extent to which these results apply to real food webs depends on the validity of model assumptions chosen. Robustness of the model to the choices of parameter values used has been examined for several parameters in a number of experiments comparing alternative levels of each parameter, one at a time. In particular, the parameter controlling the shape of predators' functional responses, the energy supplied to primary producers, and the size of the bonus in feeding efficiency awarded to more specialized species are three variables that have been studied as the subjects of other experiments involving WEB.

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