

EFFECT OF INCREASED PRODUCTIVITY ON THE ABUNDANCES OF TROPHIC LEVELS

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Abstract.—Increasing productivity can have a variety of effects on the abundances of higher trophic levels. Previous work, based on models with one type per trophic level, has suggested that increasing nutrient input to the lowest trophic level (1) always increases the abundance of the highest trophic level and (2) increases the abundances of levels that are an even number of levels below the top, while leaving others unchanged. This article investigates how these predictions are altered by the presence of different species or types (i.e., heterogeneity) within trophic levels. The models investigated are Lotka-Volterra-type models of food webs with two or three trophic levels and one or two types per level. Less complete results are derived for models with more levels and more types per level. Several different food web structures may cause the highest level to be independent of nutrient input or actually decrease with nutrient input. However, the majority of possible food web configurations with two species on some or all levels can produce productivity-abundance relationships similar to those obtained when trophic levels are homogeneous. Factors other than heterogeneity within levels can affect the productivity-abundance relationships; these factors and available information on relationships in nature are discussed.

The effects of nutrient addition to ecological systems are of interest to both theoretical and applied ecologists. Agricultural activities add nutrients to both terrestrial and aquatic systems. Nutrient addition is sometimes carried out intentionally to increase the production of organisms on a higher trophic level. For example, salmon production has been increased by fertilizing lakes (Barraclough and Robinson 1972). Such management interventions assume that the inputs to the bottom of a web eventually have a positive effect on the top. However, the theoretical basis for this assumption is very weak (see below), and experiments to answer the question are often difficult to perform because of the large scale of the systems.

Although food web theory has expanded greatly in the past decade (reviewed in Cohen et al. 1990 and Pimm et al. 1991), it has not directly addressed the question of when nutrient addition to the bottom of a food web increases the abundance of the higher levels of the web. This is surprising in light of the fact that other effects of nutrient addition have received extensive attention from theoreticians, for example, the effect of nutrient addition on the stability of predator-prey systems (Rosenzweig 1971) and the effect of nutrient addition on the coexistence of competing species (Tilman 1982; Abrams 1988).

The theory most directly relevant to this question was initiated by Hairston, Smith, and Slobodkin (1960; often abbreviated as HSS) and further developed by Fretwell (1977, 1987) and Oksanen, Fretwell, Arruda, and Niemala (1981; abbreviated OFAN). This approach views whole trophic levels as dynamically equivalent to single species and assumes that there are no direct effects of a trophic level's population density on the per capita growth rate of that level. The basic result of these models is as follows. Increased nutrient input increases the density of the top level and levels that are an even number of levels below the top; the abundances of other levels are unchanged. Hairston et al. (1960) visualized the world as being composed of three trophic levels (plants, herbivores, and carnivores), and suggested that herbivore population densities are regulated by their predators. Oksanen et al.'s explicit model of such a system suggests that increasing resources available to the plants should increase plant and carnivore densities (levels) while leaving herbivore densities unchanged. Regardless of the number of trophic levels, this analysis suggests that increased inputs to the lowest level will increase the abundance of the highest level. However, Oksanen et al. (1981) note that this increase at the top may be extremely small if the middle level has a type 2 functional response. The increase at the top can be thought of as the "trickle-up" effect of nutrient addition, by analogy to an economic theory popular among conservatives in the 1980s.

Oksanen et al.'s (1981) analysis was designed to explain vegetation structure in low-productivity terrestrial environments whose major herbivores are vertebrates. The assumptions of homogeneity of trophic levels may be approached in many of these cases (Oksanen 1983). However, it is desirable to know how trophic levels will respond to nutrients when there is heterogeneity. Several authors have noted that the OFAN predictions can be modified by altering specific assumptions of the analysis. If, for example, there is a direct negative effect of the predator level's population density on its own growth rate, all three trophic levels will increase with an increase in the input to the lowest level (this is discussed for two- and three-level systems in Mittelbach et al. 1988). If different size or age classes of a particular species feed on different trophic levels, it is also possible for increased productivity to have a positive effect on all trophic levels or several levels in a row (Mittelbach et al. 1988). Leibold (1989), extending the work of Phillips (1974), analyzed models of two-level systems with two competing types of different edibility on the lower level. He notes that there will generally be positive effects of inputs to the lower level on the abundance of the higher level. Leibold's (1989) models may be regarded as descriptions of a three-level system in which the dynamics of the bottom level is implicit in the dynamic equations of the middle level.

Another set of exceptions to the Oksanen et al. (1981) conclusions comes from models of three-species food chains in which the middle level adjusts its foraging effort on the basis of the amount of food available and the increased risk of being preyed on while foraging (Abrams 1984, 1991; see also Oksanen 1992). Such models predict that increasing inputs to the bottom species in the chain may increase or decrease the abundance of the top level; these effects occur because the population density of the bottom species has an immediate effect on the top

species via changes in the foraging of the middle species. A decrease in the top species with increased nutrients is especially likely when the middle species decreases its foraging effort in response to greater food availability. Competition between different species within a level is analogous to the process of behavioral adaptation within a species. It therefore seems plausible that such within-level competition could produce effects on abundances similar to those of behavioral adaptation within species in a food chain.

Although the articles by Mittelbach et al. (1988) and Leibold (1989) investigate particular types of heterogeneity within a trophic level, a comprehensive analysis of the implications of heterogeneity within levels for productivity-abundance relationships has not yet been published. Jager and Gardner (1988) examined the abundances of multispecies trophic levels using simulation but did not examine productivity effects. This article seeks to remedy this deficiency by analyzing equilibrium abundances in Lotka-Volterra-type food webs in which there are two or three levels with one or two species (types) per level. The extensions to systems with four or more levels and three or more species per level are treated more briefly. I restrict the main analysis to webs without omnivory. The results of the analysis show that many more patterns of abundance versus input are possible in heterogeneous than in homogeneous systems. In fact, heterogeneity on just one level can produce effects of nutrient input on trophic-level abundances that are opposite to those predicted by homogeneous models.

LOTKA-VOLTERRA-TYPE FOOD WEB MODELS

General Considerations

The models discussed in this section make the following assumptions:

1. All consumers have linear functional responses; therefore, the consumption rate of any prey type by a particular predator individual is directly proportional to the population density of the prey type and is unaffected by any other population density.
2. Different prey types on a particular level are substitutable resources (Leon and Tumpson 1975); that is, the per capita growth rate of a consumer (predator) on two prey types is an increasing function of a weighted sum of the intake rates of each type.
3. Per capita population growth rates are determined entirely by food intake and predation rate per individual. There is no interference competition, direct mutualism, or the like. There are no direct effects of a consumer type's population density on its own per capita growth rate.
4. All trophic species may be assigned unambiguously to a single trophic level, and consumers may not feed on two different trophic levels. This implies that there is no omnivory. Although this assumption is made here to reduce the number of webs that must be considered, Pimm et al. (1991) argue that omnivory is rare (with the exceptions of detritivore webs, insect-parasitoid webs, and aquatic webs with species that shift their food type as they grow).

Food web models with assumptions 1–3 have been investigated by Pimm (1982, 1984), Yodzis (1988, 1989), and others. The first assumption is more restrictive than that of Oksanen et al. (1981) but does not affect their conclusions for models with one type per trophic level. The trophic “types” on each level are characterized by having identical foods and predators. These types could theoretically consist of more than a single biological species, but such a case is unlikely to be dynamically stable. Because there are no nontrophic interactions between different types, I am excluding the possibility that different life stages of a biological species have different diets (as in Mittelbach et al. 1988) and am excluding interference competition within a trophic level.

Homogeneous Systems

First consider models with a single type per level; these are a basis for comparison with models having heterogeneity. I consider a four-level system; the derivation is essentially identical for two- or three-level systems. The population densities of the species on levels 1–4 will be denoted by the letters R , N , P , and S , respectively, and will be referred to respectively as resource, consumer, predator, and top-predator. A four-level homogeneous model has the following form:

$$dS/dt = S[f_s(EP) - T], \quad (1a)$$

$$dP/dt = P[f_p(CN) - D - ES], \quad (1b)$$

$$dN/dt = N[f_n(kR) - d - CP], \quad (1c)$$

and

$$dR/dt = Rg(I, R) - kNR, \quad (1d)$$

where f_n , f_p , and f_s are nondecreasing functions describing the conversion of food eaten into new consumer individuals, the parameters k , C , and E are the consumption rate constants of R , N , and P by their predators, and d , D , and T represent per capita death rates of N , P , and S , respectively. The function g describes the per capita growth rate of the resource population as a function of its own density, R , and nutrient input, I . Increasing I (increasing productivity) increases g , while increasing R decreases g . The effect of increasing I on equilibrium densities may be seen by inspection of equations (1). The unique equilibrium density of P is determined by equation (1a) and is independent of productivity because none of the functions or parameters of equation (1a) is a function of g . The equilibrium value of R must also be independent of productivity because, if it were not, equation (1c) would imply that the consumer population would not be able to reach equilibrium after productivity was increased. If R is unaffected but g increases with I , equation (1d) implies that the equilibrium N must increase. If the equilibrium N increases, equation (1b) implies that the equilibrium S must increase. Thus, only the top and second trophic levels increase as productivity is increased, as predicted by Oksanen et al. (1981).

In some of the subsequent analysis it is necessary to assume specific forms for the functions f ; it will then be assumed that they are linear and that they have

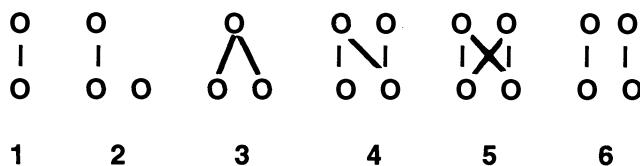


FIG. 1.—The six possible food web configurations with two trophic levels and a maximum of two species per level. In the text, the species on the left-hand side of the web are labeled with a subscript 1, and those on the right with a subscript 2.

the following formulas when there are two prey at each level:

$$f_{si} = Z_{i1}E_{i1}P_1 + Z_{i2}E_{i2}P_2, \quad (2a)$$

$$f_{pi} = B_{i1}C_{i1}N_1 + B_{i2}C_{i2}N_2, \quad (2b)$$

and

$$f_{ni} = b_{i1}k_{i1}R_1 + b_{i2}k_{i2}R_2, \quad (2c)$$

where i is the number (1 or 2) of each species at a particular trophic level. The parameters Z , B , and b all represent efficiencies of converting consumed food into new individuals for S , P , and N , respectively. If it is necessary to assume a specific form for the resource growth equation, it will be assumed to be logistic: $g = r[1 - (R/K)]$, where r and/or K may be functions of I .

Heterogeneous Two-Level Systems

Figure 1 shows all of the possible food web configurations with two levels and at most two trophic species on each level. The case of one species on the first level fed upon by two on the second is omitted because competitive exclusion would occur whenever such a system had a stable equilibrium (Armstrong and McGehee 1980). The effects of nutrient addition may be determined as above. The OFAN prediction for homogeneous levels (web 1 in fig. 1) is that the bottom level remains constant and the top increases as productivity is increased. When there are two species on the bottom level, productivity may be increased by increasing inputs to the growth of either or both resources. The possible changes in abundance with productivity can be determined as in the homogeneous system treated above; details for the nontrivial cases are given in Appendix A.

Four of the six possible configurations (all of those with heterogeneity except for the case of two unlinked homogeneous chains [web 6]) can have outcomes that differ from the OFAN predictions. The additional possibilities are as follows:

1. Both trophic levels increase. This occurs in web 2 whenever the input to the nonconsumed resource is increased, and it can also occur for some parameter values in web 3.
2. The top level increases while the bottom level decreases. This occurs in web 3 when higher productivity causes an increase in the resource that has a greater per capita effect on consumer fitness.

3. The top level decreases while the bottom level is constant. This occurs in web 4 when the productivity of the resource consumed by one consumer species is increased sufficiently more than that of the resource consumed by both consumers. This increases the population density of the generalist consumer but decreases the abundance of the specialist consumer, and can decrease total consumer abundance. The same mechanism can operate with web 5. Here, a reduction in the top level with increased productivity is favored by unequal increases in the productivities of different types of resource and an asymmetry in the degree of specialization of the two consumers.

Thus, of the five possible web structures having some heterogeneity on a level, two can violate the trickle-up prediction and four can result in patterns different from OFAN. There are no web structures for which trickle-up cannot occur: this raises the question for webs 4 and 5 of whether increased inputs are more likely to increase or decrease consumer population size. Appendix A derives an explicit formula for the total consumer density when there is logistic resource growth; in this example an increase in consumer density occurs for a wider range of possible changes in nutrient inputs than does a decrease.

The number of possible input-abundance patterns is increased by allowing more than two species per level. This can be shown by noting that combinations (i.e., a system composed of independent subsystems) of two or more of the five webs in figure 1 can have novel input-abundance relationships. None of the webs discussed above exhibits an increase in the abundance of the bottom level with a decrease in the abundance of the second. If a nonconsumed species is added to the bottom level of web 4 (or 5), then the entire web may clearly exhibit this pattern. If the entire system consists of three species interacting as in web 3 and four others interacting as in web 4, then both levels may decrease with increasing productivity. (This is also possible with weak interactions between the two subsets of this community.) All that is necessary is that the abundance of the four-species subset be sufficiently large relative to the three-species group. This ensures that the decrease in consumer abundance in the four-species subset outweighs the increase of the single consumer species in the three-species subgroup.

The above analysis has assumed that the increase in productivity does not result in any extinctions. However, extinction of one of the resources is a possibility in webs 3, 4, and 5, because of the apparent competition (Holt 1977) between the two resources; in the cases of webs 4 and 5, a resource extinction would result in the further extinction of a consumer species. Extinction of one of the consumers without a resource extinction is possible in webs 4 and 5; in these cases, increased productivity usually changes the competitive relationship between the two consumers. The relationship between productivity and trophic-level abundances may change after an extinction. For example, if one of the consumers in web 5 goes extinct, the system becomes web 3, which has a qualitatively different relationship between productivity and the abundances of the two trophic levels. If further increases in productivity cause one of the resources in

web 3 to be excluded by apparent competition, both levels become homogeneous. The response to still further increases in productivity will then be that of web 1.

Heterogeneous Three-Level Systems

The presence of an additional trophic level results in a significant increase in the number of possible food web structures. Given a maximum of two species per level, no omnivory, and competitive exclusion, all of the qualitatively different types of food webs are illustrated in figure 2.

There are thus 31 possible configurations for a three-level food web, 30 of which have heterogeneity on one or more levels. The effects of increased nutrient inputs for all 31 web structures are summarized in the legend of figure 2. When nutrient inputs are increased, the summed equilibrium population densities of the species on each level may potentially increase (I) in abundance, decrease (D), or remain unchanged (U). Three possible outcomes for each of three levels produces a total of 27 qualitatively distinct outcomes, but not all of these are possible in the model analyzed here. As above, I assume that increased productivity may increase the per capita growth function of either one or both resources. In some cases different relative inputs to the two resources can cause either an increase or a decrease in the abundance of one or more trophic levels, and this is denoted by the (D,I) entries in the legend of figure 2. In such cases there are frequently different results from changes in the r values versus changes in the K values for models with logistic resource growth.

All of these webs can be analyzed by the methods used above. Details of the less straightforward cases are presented in Appendix B. There are 12 cases (fig. 2) for which the changes in abundances of trophic levels all have a determinate sign, regardless of the details of the resource growth function g or the relative increases in inputs to different types on the bottom level. Eight of these 12 web structures produce the pattern predicted by OFAN: I, U, I. There are three other possible outcomes within the group of determinate outcomes: webs 4 and 5 produce an I, I, I response to productivity; web 17 produces a U, I, U pattern; web 26 produces I, I, U. In addition, there are 19 web structures that produce an indeterminate pattern of changes in abundances; that is, at least one of the trophic levels may increase or decrease in abundance with increasing inputs. Twelve of these 19 indeterminate webs produce the outcome I, U, (D,I); that is, the OFAN pattern may occur, or it may be altered by a decrease in the top level. These 12 webs all have connections between the top two trophic levels identical to webs 4 or 5 in figure 1 (two-level systems). The analysis in Appendix A again implies that increases in the top level are more likely to occur than are decreases; increases result in the OFAN pattern.

A total of 12 of the 27 theoretically conceivable outcomes are actually possible. This number would be increased if one added zero change as one of the possible outcomes when indeterminacy is indicated. However, in all such cases, zero change requires an extremely unlikely balancing of parameter values. It is very different from the zero change that occurs for all parameter values in webs such as 1.

The trickle-up theory is always valid for 13 web structures and may occur for

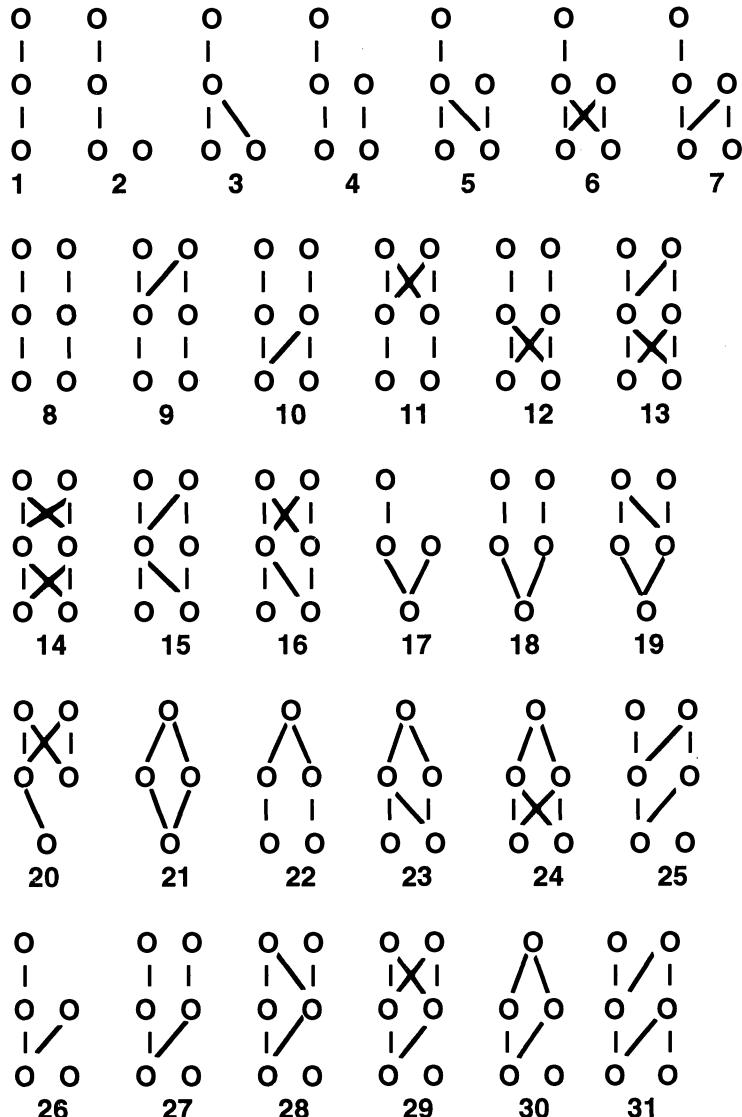


FIG. 2.—The 31 possible food web configurations with three trophic levels, no omnivory, and a maximum of two species per level. Subscripts 1 and 2 in the text are as in fig. 1. The outcomes of increased nutrient input on the abundances of each level can be described as follows for each of the numbered webs, where I denotes an increase; D, a decrease; and U, an unchanged abundance (changes are listed in order for the first [bottom], second, and third [top] levels; (D,I) indicates that decreases, increases, or no change are all possible): 1, I, U, I; 2, I, U, I; 3, I, U, I; 4, I, I, I; 5, I, I, I; 6, (D,I), I, (D,I); 7, (D,I), I, (D,I); 8, I, U, I; 9, I, U, (D,I); 10, I, U, I; 11, I, U, (D,I); 12, I, U, I; 13, I, U, (D,I); 14, I, U, (D,I); 15, I, U, (D,I); 16, I, U, (D,I); 17, U, I, U; 18, I, U, I; 19, I, U, (D,I); 20, I, U, (D,I); 21, U, (D,I), U; 22, I, (D,I), I; 23, (D,I), (D,I), (D,I); 24, (D,I), (D,I), (D,I); 25, I, U, (D,I); 26, I, I, U; 27, I, U, I; 28, I, U, (D,I); 29, I, U, (D,I); 30, I, (D,I), U; 31, I, U, (D,I).

another 14. The four web structures for which trickle-up is never valid are cases in which the abundance of the top level remains constant with increases in bottom-level input. Thus, there are no web structures for which the top trophic level must decrease with increasing inputs. On the other hand, these same results may be viewed as showing that there are exceptions to trickle-up in 18 of the 31 web structures.

Many of the three-level outcomes are easily understandable on the basis of the results for two-level systems presented above. The possibility of a decrease in the total abundance of the top level in webs 9, 11, 13, 14, 15, 16, 19, 20, 25, 28, 29, and 31 (in fig. 2) is explained by the same possibility in webs 4 and 5 in figure 1. Similarly, the possibility of a decrease in the middle level in webs 22, 23, and 24 in figure 2 follows directly from the possibility of a decrease in the lower level of web 3 in figure 1. The unique possibilities that have no analogue in the two-level systems are listed and explained briefly below; the details are relegated to Appendix B.

In webs 17 and 21 the change in abundances with productivity is the opposite of the OFAN pattern; the consumer (N) level changes abundance with increasing input while the other levels remain constant. In both cases the two equilibrium conditions for the consumer growth equations fully specify R and P , independently of input to the resources. In order for both consumers to exist, the two middle species must differ in susceptibility to the predator, and increasing nutrient inputs just increases the relative abundance of the predation-resistant consumer. The net result may be an increase or decrease in total consumer-level abundance.

Webs 6 and 7 also differ significantly from the patterns possible in two-level systems. Both have a midlevel species that has no predator but shares its food supply with the other consumer (which does have a predator). Increasing inputs can (but need not) alter the competitive advantage in favor of the predator-free consumer, which can clearly reduce the predator population. See Appendix B for more details.

Webs 22–24 are similar to web 3 in figure 1 in that the highest level has a single type feeding on both types on the level below. The analysis of the two-level system proves that the total abundance of the middle level in webs 22–24 may increase or decrease with increasing inputs. Because there is no interaction between the two consumers in web 22, it cannot exhibit any response of the top two levels that differs from web 3 in figure 1; this is proven in Appendix B. In webs 23 and 24, however, there is competition between the consumers, which is not present in the two-level analogue. The analysis in Appendix B shows that this makes it possible for top and/or bottom levels in these webs to decrease (or increase) with increasing productivity.

Figure 2 and the above discussion both assume that there are no extinctions of species as inputs to the bottom level are increased and that the webs have a stable equilibrium point. Extinction is possible in many of the web structures and can result in an abrupt qualitative change in the relationship between inputs and the abundances of levels (see discussion for two-level systems). Local stability analyses of three-level webs with five or more species are algebraically unwieldy, and complete exploration of parameter spaces for even a single web structure

would be very difficult. Simulations (assuming logistic resource growth) have been used to show that all of the webs illustrated can have stable equilibria for each of the possible outcomes listed under figure 2.

It is again of interest to know how the results with two species per level would change if more species were added. A complete analysis would require analysis of a huge number of webs with even three species per level and will not be presented here. However, it is clear that combining two or more of the web structures illustrated in figure 2 can lead to patterns of change that differ from any of these illustrated. The three-level webs in figure 2 may be combined with the two-level webs in figure 1 to yield more possibilities. It should be noted that it is possible for increased inputs to decrease all three trophic levels when there are more than two species per level; this can occur, for example, when there are subsystems corresponding to web 7 in figure 2 (in which the first and third levels often decrease with larger inputs) and web 21 in figure 2 (in which the second level may decrease while the others remain constant). This outcome could also occur if web 7 were combined with web 4 in figure 1. The number of additional productivity-abundance patterns possible with additional species per level represents an important unsolved theoretical problem.

Four or More Levels

There are many more possible web configurations when there are four trophic levels. However, the addition of a higher level is logically equivalent to the addition of a lower level (below resources). Addition of a lower level to a three-level system simply allows there to be exploitative competition between the two resources (which was assumed not to occur in the three-level systems). If competition were allowed in the three-level system, it would be possible for one of the two resource growth equations to decrease with increasing productivity. This increases the range of possible responses of the top two levels to increased inputs to the bottom of the system. In particular, the range of responses of the three-level systems without competition must be a subset of the possible responses of the top three levels in four-level systems (without competition on the bottom level) or in three-level systems with competition. The results from three-level systems are sufficient to identify many of the situations under which trickle-up may not occur; these include those four-level systems for which the top three levels have configurations that do not result in trickle-up when they are the only three levels present (e.g., web 7 in fig. 2).

The range of responses in the top three levels of four-level systems is greater than that revealed by the analysis of figure 2. For example, figure 3 shows a system whose top three levels correspond to web 4 in figure 2. Web 4 of figure 3 is characterized by an I, I, I response to increased productivity, but this is not true of the four-level system. An input to the left-hand resource (R_1) in figure 3 reduces the other (right-hand; R_2) resource. This implies a reduction in the predator at the top of the right-hand chain. Because the left-hand predator is maintained at a constant density by its top predator, this means a decrease in the total predator density. This possibility would also occur in the second-to-top level (N)

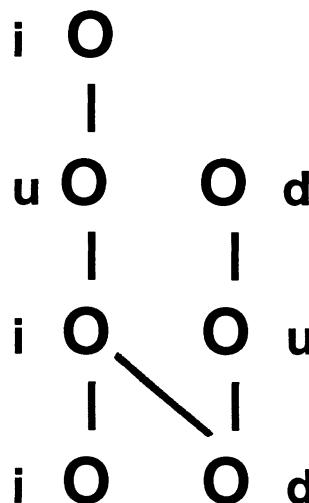


FIG. 3.—A four-level food web whose top three levels have the same structure as web 4 in fig. 2. The letters I, D, and U indicate the response of each species to an increase in nutrient inputs to the bottom left-hand species (R_i).

of the three-level system, if competition between species on the bottom level were permitted. A complete enumeration of all of the additional patterns possible in four-level systems is beyond the scope of this article.

Summary of Conditions under Which Trickle-Up Does Not Occur

This analysis reveals three mechanisms based on food web structure by which increased inputs to the bottom trophic level in a system may fail to increase the highest trophic level in that system; these are possible in any systems with three or more levels. The first mechanism is that increased inputs alter the competitive relationships between species on the top level in such a way that one competitor decreases by more than the other competitor increases (webs 9, 11, etc., in fig. 2). The second mechanism entails a generalist species on the next-to-highest trophic level that is invulnerable (or only slightly vulnerable) to predation and that effectively “siphons off” increases in productivity (webs 6, 7, and 17), which results in no increase or a decrease in the productivity base for the top level. Third, if there are coexisting species on the level below the top that share the same food and predators (webs 21, 23, and 24), then increased productivity results in the substitution of more predator-resistant types for less predator-resistant types, preventing increases in the top level.

As noted above, webs with more than two species per level can exhibit a greater range of responses of trophic-level abundances to increased nutrient input than do the two-species models considered here. However, wider food webs do not appear to exhibit any additional mechanisms for reversing the trickle-up effect beyond the three listed above.

DISCUSSION

Can Theory Predict the Relative Frequency of Patterns in Nature?

Ideally, we would like to predict the probability of occurrence of trickle-up or OFAN or other patterns of trophic-level changes in natural systems that are fertilized. There are several reasons why that is not yet possible.

The first reason is that the above analysis has restrictive assumptions about the food web structure—for example, no omnivory and the presence of only two trophic species per level. However, these limitations can easily be overcome by computer simulation of more complex systems (as in Jager and Gardner 1988).

The second reason is that more realistic population growth models (i.e., non-Lotka-Volterra models) may produce other patterns. Some of these possibilities are discussed briefly in the following section and could be analyzed more rigorously. However, here we run into the problem that we do not know the relative frequencies of occurrence of different types of growth functions in nature. For example, Pimm (1982) argues that negative effects of consumer population density on per capita growth rate, other than food depletion, are rare, while Arditi and Ginzburg (1989) and I (Abrams 1986) argue that they are extremely common.

The third and perhaps most fundamental problem is that we still do not know much about the structure of food webs in nature (but see Cohen et al. 1990). Many of the simple webs studied here have indeterminate responses to nutrient input; we would have to know the strengths of different links in the web to predict a response, but such information is seldom available. The number of qualitatively distinct web structures producing a particular set of productivity-abundance relationships cannot be translated into a probability of occurrence of the relationship. There are likely to be many more natural systems in which predators share prey than systems in which each predator has an exclusive prey (this is supported by the Cohen et al. [1990] collection of webs). Thus, webs such as 8 and 12 in figure 2 (in which each predator has an exclusive prey) are likely to be much rarer than the corresponding webs 11 and 14 (in which predators overlap in prey consumed). Unfortunately, we do not have a good enough data base of food web structure to know how much rarer. Existing catalogs of food webs (Cohen et al. 1990) probably do not represent a random sample of biological communities, and they are likely to have systematic biases and omissions (Polis 1991). Thus, their use in assessing the frequencies of occurrence of different types of web structures in nature is questionable.

Effects of Non-Lotka-Volterra Models on OFAN and Trickle-Up Predictions

The unifying theme in the above analysis is that the simplest models of food webs incorporating some heterogeneity within trophic levels may behave differently than models that assume homogeneous levels. However, the changes in trophic-level abundances with productivity can also be altered by adopting more elaborate models of homogeneous trophic levels. Three of the major factors known to affect the predictions of homogeneous models are omnivory, self-effects on the top trophic level, and adaptive foraging by individuals on intermediate

trophic levels. Of these, the first two alter the OFAN pattern but do not affect the trickle-up phenomenon. The third can result in a violation of both OFAN and trickle-up predictions. These assertions are discussed below. Because of these possibilities, observations that contradict OFAN or trickle-up predictions should not automatically be attributed to heterogeneity.

Trickle-up predictions are not greatly affected by omnivory in the broad sense of feeding on more than one trophic level, provided that the trophic levels are homogeneous. Models with omnivory, beginning with Menge and Sutherland's (1976) verbal treatment, have produced different patterns of change in trophic-level abundances from those in the HSS and OFAN models (Schoener 1989). However, they share the characteristic that the top trophic level must increase in abundance with increased productivity. This result can be demonstrated with a three- or four-level model of the Lotka-Volterra type used here, in which one of the levels feeds on the two below it. Schoener's (1989) analysis of terrestrial food chains suggests that such omnivory is common because of the ability of large carnivores to eat both herbivores and small carnivores (but Pimm et al. [1991] disagree).

It has long been known that direct negative effects of population density on the per capita growth rate of a consumer can result in a positive relationship between resource productivity and equilibrium resource abundance in the presence of the consumer (this can be shown by isocline analysis of predator-prey systems, e.g., Taylor 1984; it is discussed in Mittelbach et al. 1988). If a consumer's rate of food intake is a function of consumer population size, as in the "ratio-dependent" models of Arditi and Ginzburg (1989), there will also be negative self-effects, and population densities of all trophic levels are expected to increase (Oksanen et al. 1992). By the same token, if there are positive effects of consumer density on consumer per capita growth rate, this can result in a negative relationship between production and equilibrium resource abundance. In the three-level food chain, if the predator's death rate parameter, D , is replaced by $D - h(P)$, where h is a nondecreasing function of P , the equilibrium N will decrease with increasing nutrient inputs. However, neither positive nor negative self-effects of the predator reverse the trickle-up prediction.

The third factor that alters the OFAN and trickle-up predictions for homogeneous models is the presence of adaptive foraging by individuals on intermediate levels in the system. The top level may decrease if the foraging of all or most individuals on the second-to-highest trophic level decreases with increases in its food availability and lower foraging activity decreases the availability of second-level individuals to those on the highest level (Abrams 1984, 1991, 1992). Under these conditions, increased inputs may increase the abundances of the bottom two levels while decreasing the equilibrium abundance of the top trophic level. (It is also possible for all three levels to increase.) Thus, both the OFAN predictions and the trickle-up effect may be reversed by adaptive behavior. These models of adaptive consumer behavior differ from web 21 in figure 2 (which has heterogeneity only on the middle level) in assuming that there is a single optimum behavior rather than a polymorphic mix of behavioral types. If two or more species could be maintained on the middle level of a web by migration or intraspe-

cific density effects, the food web model with competition on the middle level could display the same behavior as the food chain model with adaptive behavior.

In addition to the above general factors, there are also explanations for exceptions to OFAN and/or trickle-up patterns that may be particular to certain types of systems. For example, in aquatic systems, if increasing nutrient inputs increase phytoplankton populations, the subsequent depletion of oxygen at lower levels due to decomposition of the dead phytoplankton may significantly reduce vertebrate populations at higher trophic levels. Other exceptions may occur when species switch their trophic status as they grow. Persson (1988) notes that the decrease in piscivorous fish in very productive lakes in Sweden is probably due to size-specific competition of juveniles (which are planktivores) with a very efficient plantivorous species.

The type of heterogeneity modeled here is not the only kind of heterogeneity that can affect the relationship between productivity and trophic-level abundances. Mittelbach et al. (1988) have shown that dietary differences between juveniles and adults can result in positive correlations between abundances of adjacent trophic levels. It has not been shown that such differences can reverse the trickle-up effect.

Finally, it should be noted that particular features of population dynamics can alter the magnitude of trickle-up, even if they do not eliminate it. Oksanen et al. (1981) pointed out that, if the consumer species has a saturating functional response and equilibrium resource abundance is high, increases in productivity in a three-level system will mainly increase the bottom level; very little increase will occur at the top.

Evidence from Nature

Both the OFAN pattern and trickle-up have been supported in several field studies (Oksanen 1983, 1988; Power 1990; Persson et al. 1992). This need not imply that trophic levels are homogeneous, since there is a wide variety of heterogeneous webs that produce the same patterns. In fact, one of the objections to the HSS hypothesis has been that the world is green not because of predation on herbivores, but because many plants are inedible (see, e.g., Murdoch 1966). This idea corresponds to web 2 in figure 2, which still results in the OFAN pattern of responses to productivity.

In addition, not all field studies have supported the OFAN predictions (Mittelbach et al. 1988; Leibold 1989). The most extensive observations and experiments on the relationship between productivity and trophic-level abundances comes from aquatic systems. Mills and Shiavone (1982), Mittelbach et al. (1988), and Leibold (1989) have all reviewed the results of a number of studies of productivity and correlations in the abundances of different trophic levels in aquatic communities. Virtually all of these studies have found increases in the abundances of all trophic levels with increasing productivity; that is, they support trickle-up, but not OFAN. The above analysis of heterogeneity suggests that there should be exceptions to both effects if all possible types of heterogeneity occur. This may mean that factors such as density dependence within trophic levels are responsible for the pattern or that only particular types of heterogeneity within levels are

common. Persson et al. (1992) criticize these surveys, since accurate measures of productivity and fish biomass are often unavailable. Their more rigorous survey of eleven Scandinavian lakes generally supports the OFAN pattern. However, as they note, the top two trophic levels in their productive systems each consist largely of a single species, so food chain models may be appropriate.

Analogues in Nonnatural Systems and Practical Implications

It may seem paradoxical that increasing nutrient inputs to a system could fail to increase, or actually decrease, the abundance of the top trophic level. In fact, it is possible for increased nutrients to decrease the abundances of all levels when there are more than two species per level, which is even more paradoxical. Similar phenomena have been discussed in other systems that can be described as networks of interconnected elements (Cohen 1988). For example, increasing the number of roads in a traffic network can decrease transit speed for all travelers (Cohen and Kelley 1990). These possibilities argue against the reliance on ecological models with homogeneous trophic levels (e.g., Crowder et al. 1988; DeAngelis et al. 1989; Kerfoot and DeAngelis 1989).

Fertilization, or nutrient input, is a pervasive element of human effects on the natural environment; it is usually intentional in terrestrial systems (to increase agricultural output), and unintentional in aquatic systems (a by-product of fertilizer runoff and atmospheric pollution). However, fertilization of the oceans has also recently been discussed as a possible mechanism for reducing the growth of atmospheric carbon dioxide. Before such steps are contemplated, it would be desirable to have a better understanding of effects on trophic-level abundances than we have today. Future work on heterogeneous models of food webs should contribute to such an understanding. Until our knowledge improves, the assumption that increased nutrient inputs will increase higher trophic levels is best regarded with the same suspicion as the "trickle-down" theory in economics; this theory failed to predict changes in monetary income of humans in the United States during the 1980s.

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APPENDIX A ANALYSIS OF TWO-LEVEL FOOD WEBS

This appendix analyzes changes in abundance of various trophic levels with increased nutrient input for the six web structures shown in figure 1. If there are two species on a level, the species in the left-hand position is species 1 and that on the right is species 2; population densities on different trophic levels are again labeled R and N . Web 1 has homogeneous trophic levels and therefore follows the OFAN predictions. Web 2 simply

adds a nonconsumed resource to web 1; the nonconsumed resource must increase if its inputs are increased, while the remaining two species follow the OFAN pattern.

Web 3 is the first of the three nontrivial cases. The equilibrium densities are determined by the equations

$$b_1 k_1 R_1 + b_2 k_2 R_2 = d, \quad (\text{A1a})$$

$$g_1(I_1, R_1) = k_1 N, \quad (\text{A1b})$$

and

$$g_2(I_2, R_2) = k_2 N, \quad (\text{A1c})$$

where I_i represents the input (of food or nutrients) to resource i , and the resource growth functions, g_1 and g_2 , increase with I_1 and I_2 and decrease with R_1 and R_2 . If increased inputs to the bottom level multiply both g functions by the same factor, the left-hand sides of equations (A1b) and (A1c) are multiplied by the same factor. This does not change equilibrium R values, but increases the equilibrium N . If the equilibrium R values are changed by increasing I_1 and I_2 , equation (A1a) ensures that one resource must increase and the other must decrease. If R_2 , for example, decreases, then the left-hand side of (A1c) must increase, because both $\partial g / \partial I$ and $-\partial g / \partial R$ are positive; equation (A1c) then implies that the equilibrium N must increase. Therefore, regardless of the relative changes in I_1 and I_2 , N must increase. Because of equation (A1a), the sum $R_1 + R_2$ will decrease with increasing inputs if R_1 increases and $b_1 k_1 > b_2 k_2$, or if R_1 decreases and the inequality is reversed. Thus, the top level must increase in abundance with increasing inputs, while the bottom level may increase or decrease.

Web 4 has two consumers, one a generalist and one a specialist. The equations specifying equilibrium densities are

$$b_{11} k_{11} R_1 + b_{12} k_{12} R_2 = d_1, \quad (\text{A2a})$$

$$b_{22} k_{22} R_2 = d_2, \quad (\text{A2b})$$

$$g_1(I_1, R_1) = k_{11} N_1, \quad (\text{A2c})$$

and

$$g_2(I_2, R_2) = k_{12} N_1 + k_{22} N_2. \quad (\text{A2d})$$

Equations (A2a) and (A2b) together completely specify equilibrium resource densities, so these must be independent of the inputs, I , to the lowest level. The possible effects of increased inputs to resources on the consumer trophic level can be seen by considering increased I_1 and increased I_2 in turn. Equation (A2c) implies that increased I_1 increases N_1 . Equation (A2d) then implies that N_2 must decrease, since the left-hand side of (A2d) is unchanged by I_1 . The total abundance of the consumer level will then decrease if $k_{22} < k_{12}$; total abundance will increase if the inequality is reversed. Similarly, one can show that, if I_2 alone is increased, N_2 must increase, while N_1 remains constant; that is, the entire trophic level increases. If both inputs increase, N_1 must increase, while N_2 may either increase or decrease; the total consumer abundance may increase or decrease.

Web 5 has web 4 as a limiting case, and the analysis is essentially identical. It is clear that the two consumer equilibrium conditions uniquely determine equilibrium resource densities, independently of productivities (assuming that a positive equilibrium exists). The effects of increased nutrient input on total consumer abundance can be positive or negative, as in web 4. It is possible to solve for the equilibrium consumer abundances in terms of the resource growth functions and consumption rate parameters. The results are

$$N_1 = (g_1 k_{22} - g_2 k_{12}) / (k_{11} k_{22} - k_{12} k_{21}), \quad (\text{A3a})$$

$$N_2 = (g_2 k_{11} - g_1 k_{12}) / (k_{11} k_{22} - k_{12} k_{21}), \quad (\text{A3b})$$

and

$$N_1 + N_2 = [g_2(k_{11} - k_{21}) + g_1(k_{22} - k_{12})]/(k_{11}k_{22} - k_{12}k_{21}). \quad (\text{A3c})$$

Because equilibrium R 's are independent of productivity, increased I 's simply increase the g functions. It is clear that proportional increases in both g functions must increase total consumer abundance, since this multiplies the numerator of equation (A3c) by a factor greater than one. It is also necessary that total abundance increase as a function of at least one of the g_i ; if it did not, total abundance would be negative. Total N decreases with g_i if $k_{ij} < g_i$, but this latter condition is constrained by the requirements for positive consumer densities; that is, $k_{ii}/k_{ij} > g_i/g_j > k_{ji}/k_{ij}$. Thus, total N decreases only if one particular productivity is increased much more than the other and if additional conditions on consumption rates and resource growth functions are met. Thus, an increase in total N seems more likely.

Web 6 is simply a tandem duplication of web 1, and must therefore have the same pattern of changes in the abundances of its trophic levels.

All of these analyses assume that there is an equilibrium with all species present. However, sufficiently large inputs to one resource may result in the exclusion of the other resource and/or one of the consumers. It is also possible that equal increases in inputs to both resources can cause exclusion. Consider web 3, for example. We know from equations (A1) that resource j will be excluded if

$$g_j(I_j, 0) < (k_j/k_i)g_i(I_i, (b_i k_i/d)). \quad (\text{A4})$$

Assume this inequality is not satisfied at a particular set of input rates. Increasing both I values proportionately will eventually result in the exclusion of resource j if the right-hand side of inequality (A4) increases faster with proportional changes in the I values than does the left-hand side. In the case of logistically growing resources, for example, this requirement translates into the following inequalities for eventual exclusion of resource 1 with continued proportional increases in both I values:

$$k_2 r_1 < k_1 r_2 \quad (\text{A5a})$$

and

$$K_2 > dk_1 r_2 / [b_2 k_2 (k_1 r_2 - k_2 r_1)]. \quad (\text{A5b})$$

This analysis has ignored the stability of the equilibria. In the cases of webs 1, 2, 3, 4, and 6, the webs are qualitatively stable (see, e.g., Pimm 1982). Web 5 is a two-consumer, two-resource system, which has been the subject of extensive work in competition models; it can be shown to be stable in the context of the assumptions made here whenever the resources have logistic growth (MacArthur 1970).

APPENDIX B

ANALYSIS OF THREE-LEVEL FOOD WEBS

This section examines only those webs in figure 2 that are discussed in the text as being qualitatively different from two-level systems. As before, when there are two species on a level, the species on the left-hand side is labeled species 1.

The webs that have the potential for exploitative competition between the two consumer (N) species have no precise analogue among the two-level webs. However, for many of these, the equilibrium values of both second-level species must remain constant at equilibrium (e.g., webs 9–16), on the basis of the equilibrium conditions for the two top-level species. Because of this lack of response in N , any increase in inputs to either or both resources results in an increase in the equilibrium resource abundance. The predator abundances in these webs may increase or decrease, on the basis of the results for webs 4 and 5 in figure 1.

The response of web 21 to greater productivity is very different from that of homogeneous food webs. The equilibrium conditions in web 21 are

$$B_1 C_1 N_1 + B_2 C_2 N_2 = D, \quad (\text{B1a})$$

$$g(I, R) = k_1 N_1 + k_2 N_2, \quad (\text{B1b})$$

$$b_1 k_1 R - d_1 - C_1 P = 0, \quad (\text{B1c})$$

and

$$b_2 k_2 R - d_2 - C_2 P = 0. \quad (\text{B1d})$$

The equilibrium densities are

$$P = (d_1 b_2 k_2 - d_2 b_1 k_1) / (b_1 k_1 C_2 - b_2 k_2 C_1),$$

$$R = (d_1 C_2 - C_1 d_2) / (b_1 k_1 C_2 - b_2 k_2 C_1),$$

$$N_1 = (D k_1 - B_1 C_1 g) / (k_1 B_2 C_2 - k_2 B_1 C_1),$$

and

$$N_2 = (B_2 C_2 g - D k_2) / (k_1 B_2 C_2 - k_2 B_1 C_1).$$

Note that P and R are independent of g ; they are determined by (B1c) and (B1d) alone. In order to have positive abundances of both P and R and both N 's, it is necessary that the consumer species j that has the larger value of $b_j k_j / C_j$ also have the larger value of d_j / C_j and the smaller value of $b_j k_j / d_j$. If the consumer species have equal d values, this implies that the consumer with the larger bk (efficiency of resource use) must have a larger C (predator vulnerability). The total abundance of the consumer trophic level is

$$N_1 + N_2 = [D(k_1 - k_2) + g(B_2 C_2 - B_1 C_1)] / (k_1 B_2 C_2 - k_2 B_1 C_1).$$

Assume without loss of generality that $k_1 B_2 C_2 > k_2 B_1 C_1$. Then N_1 decreases with increased I (increased g), and N_2 increases with I . The total consumer abundance may either increase or decrease with I ; it increases if $B_2 C_2 > B_1 C_1$ and decreases if this inequality is reversed. The general rule is that total consumer abundance increases with I if the species, j , with the larger value of $k_j / B_j C_j$ has the smaller value of $B_j C_j$. It is noteworthy that increased input decreases the summed abundances of all species in the web whenever it decreases the consumer trophic level. It is clear that a sufficiently large increase in g will drive the species with the larger k/BC value (i.e., the more vulnerable species, which is also the better exploiter) to extinction.

Web 17, which differs from web 21 only by the absence of a single link, can be analyzed without writing down equilibrium conditions. The single R must have an equilibrium abundance that is independent of productivity because it is the sole food of a nonconsumed species (N_2). Species N_1 must also have a constant equilibrium abundance for the same reason. For N_1 to remain at equilibrium with a constant R requires that the equilibrium P also be independent of productivity. Thus, only N_2 increases with productivity, and the middle level is therefore the only level that changes.

Web 7 has the following equilibrium conditions:

$$B_1 C_1 N_1 = D, \quad (\text{B2a})$$

$$g_1(I_1, R_1) = k_{11} N_1 + k_{21} N_2, \quad (\text{B2b})$$

$$g_2(I_2, R_2) = k_{22} N_2, \quad (\text{B2c})$$

$$b_{11} k_{11} R_1 - d_1 - C_1 P = 0, \quad (\text{B2d})$$

and

$$b_{21} k_{21} R_1 + b_{22} k_{22} R_2 - d_2 = 0. \quad (\text{B2e})$$

Equation (B2a) shows that N_1 is independent of productivity, but all of the other population densities may change as a function of nutrient inputs. Equation (B2d) shows that P and R_1 must change in the same direction, and (B2e) implies that R_1 and R_2 must change in opposite directions after a change in inputs. Because the equilibrium N_1 is independent of productivity, the group of R_1 , R_2 , and N_2 changes according to the same rules as web 3 in figure 1 (App. A). Thus, both N_2 and the sum $N_1 + N_2$ increase with greater inputs to the resources; the sum $R_1 + R_2$ may increase or decrease with increasing inputs. The resource population R_1 (and consequently P) must decrease if the increase in I_2 is sufficiently large relative to I_1 . Thus, the possible patterns of change are (1) resources decrease, consumers increase, predators decrease; (2) resources increase, consumers increase, predators decrease; (3) resources decrease, consumers increase, predators increase; and (4) all three levels increase. The fourth possibility occurs when the increase in I_1 is sufficiently large relative to I_2 . Web 6 has the same possible patterns of change in abundance as web 7 for the same reasons.

Webs 22, 23, and 24 are all analogous to web 3 in figure 1, and the changes in the top two levels of these webs must have at least as large a range of possible patterns of change in abundance as does that web. The equations for equilibrium densities in web 22 (the simplest of the three) are

$$B_1 C_1 N_1 + B_2 C_2 N_2 = D, \quad (\text{B3a})$$

$$g_1(I_1, R_1) = k_1 N_1, \quad (\text{B3b})$$

$$g_2(I_2, R_2) = k_2 N_2, \quad (\text{B3c})$$

$$b_1 k_1 R_1 - d_1 - C_1 P = 0, \quad (\text{B3d})$$

and

$$b_2 k_2 R_2 - d_2 - C_2 P = 0. \quad (\text{B3e})$$

Eliminating P from equations (B3d) and (B3e) shows that two resource densities must change in the same direction, while equation (B3a) shows that the two consumer densities must change in opposite directions. If the equilibrium P decreased with I_i , then both resource densities would have to decrease, according to equations (B3d) and (B3e). However, equations (B3b) and (B3c) would then imply that both consumer densities would have to increase to maintain equilibrium, which contradicts equation (B3a). Therefore, the equilibrium P and both R 's must increase with an increase in either or both I 's.

Webs 23 and 24 produce a similar range of responses, but 23 is slightly simpler, and only this web will be analyzed here. The equilibrium densities are specified by

$$B_1 C_1 N_1 + B_2 C_2 N_2 = D, \quad (\text{B4a})$$

$$g_1(I_1, R_1) = k_{11} N_1, \quad (\text{B4b})$$

$$g_2(I_2, R_2) = k_{12} N_1 + k_{22} N_2, \quad (\text{B4c})$$

$$b_{11} k_{11} R_1 + b_{12} k_{12} R_2 - d_1 - C_1 P = 0, \quad (\text{B4d})$$

and

$$b_{22} k_{22} R_2 - d_2 - C_2 P = 0. \quad (\text{B4e})$$

We know from the results for web 3 of figure 1 that it must be possible for the total consumer density to increase or decrease. Therefore, this analysis will focus on predator and resource densities. Equations (B4b) and (B4c) can be solved for the N 's in terms of the R 's, and these formulas substituted in equation (B4a) to give one relationship between R_1 and R_2 . Eliminating P from equations (B4d) and (B4e) results in another relationship between R_1 and R_2 . Implicit differentiation of these two relationships with respect to I_1 or I_2 yields formulas for the changes in resource densities with increased input. The formula

for the change in R_1 with I_1 is

$$\frac{\partial R_1}{\partial I_1} = \frac{(B_1 C_1 k_{22} - B_2 C_2 k_{21})(b_{22} k_{22} C_1 - b_{21} k_{21} C_2) \frac{\partial g_1}{\partial I_1}}{(B_2 C_2 k_{21} - B_1 C_1 k_{22})(b_{22} k_{22} C_1 - b_{21} k_{21} C_2) \frac{\partial g_1}{\partial R_1} - b_{11} B_2 C_2^2 k_{11}^2 \frac{\partial g_2}{\partial R_2}}. \quad (\text{B5})$$

The derivative of R_2 with respect to I_1 is given by the above expression multiplied by $C_2 b_{11} k_{11} / (b_{22} k_{22} C_1 - b_{21} k_{21} C_2)$. These formulas lead directly to conditions for the signs of trophic-level effects. For example, both resources will decrease as I_1 is increased if $b_{22} k_{22} C_1 > b_{21} k_{21} C_2$ and $B_1 k_{22} C_1 > B_2 k_{21} C_2$. In this case, P also decreases with I_1 , because the change in P must have the same sign as the change in R_2 , on the basis of equation (B4e). If both inequalities are reversed, R_1 will decrease with I_1 , while R_2 and P will increase; the net change in $R_1 + R_2$ may be positive or negative. A formula analogous to equation (B5) exists for the effects of increased I_2 . However, it should already be clear that increases and decreases are both possible responses of the top and bottom trophic levels.

Web 24, which simply adds one more link between consumers and resources, must exhibit at least the same range of responses to increased productivity as does web 23.

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