Yield and Dynamics of Tritrophic Food Chains

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YIELD AND DYNAMICS OF TRITROPHIC FOOD CHAINS

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Abstract.—Strong relationships between yield and dynamic behavior of tritrophic food chains are
pointed out by analyzing the classical Rosenzweig-MacArthur model. On the one hand, food
chains are subdivided into undersupplied and oversupplied categories, the first being those in
which a marginal increase of nutrient supply to the bottom produces a marginal increase of mean
yield at the top. On the other hand, a detailed bifurcation analysis proves that dynamic complex-
ity first increases with nutrient supply (from stationary to a low-frequency cyclic regime and,
finally, to chaos) and then decreases (from chaos to a high-frequency cyclic regime). A careful
comparison of the two analyses supports the conclusion that food chains cycling at high fre-
quency are oversupplied, while all others are undersupplied. A straightforward consequence of
this result is that maximization of food yield requires a chaotic regime. This regime turns out to
be very often on the edge of a potential catastrophic collapse of the top component of the food
chain. In other words, optimality implies very complex and dangerous dynamics, as intuitively
understood long ago for ditrophic food chains by Rosenzweig in his famous article on the para-
dox of enrichment.

Simple relationships are established in this article between the dynamics of
tritrophic food chains and the possibility of increasing yield through enrichment.
Our result can be viewed as contributing to the problem of enrichment raised in
the early seventies (Rosenzweig 1971).

The analysis is based on the Rosenzweig-MacArthur model, which assumes
that prey is logistic and that the predator and superpredator have a Holling Type
II functional response. We chose this model because of its adaptability to a great
variety of food chains (Yodzis and Innes 1992; McCann and Yodzis 1994) and
because of the richness of its behavior, covering the whole spectrum of dynamic
regimes, including chaos (Hastings and Powell 1991; Abrams and Roth 1994;
McCann and Yodzis 1994). The consequence of this choice is that each element
of our food chain universe is identified by a set of parameters describing the bio-
logical characteristics of the three populations (prey growth rate and carrying ca-
pacity, mortality, efficiency, maximum predation rate, and half-saturation con-
stant of predator and superpredator).

If the superpredator is exploited, its mortality is the sum of basic mortality
and harvesting effort, so that food yield is proportional to superpredator bio-

mass. If the chain is not stationary, superpredator biomass varies in time, and its mean value becomes the most simple indicator of food yield. In the case of cyclic regimes, the indicator is just the average value of superpredator biomass over one cycle; in the case of chaotic regimes, it is the average value of that biomass on a so-called strange attractor (Hastings et al. 1993).

Given a food chain, it is always possible, at least in principle, to enrich it or impoverish it by increasing or decreasing the supply of limiting nutrients to the bottom of the chain. This can be realized through many different interventions that often influence only the prey carrying capacity (Oksanen et al. 1981; Abrams 1993). It is therefore possible to distinguish between under- and oversupplied food chains. Undersupplied food chains are those for which a small increase of prey carrying capacity gives rise to a small increase of mean abundance of the top trophic level. Oversupplied food chains are those that can be marginally improved through impoverishment. Hence, our food chain universe is subdivided into under- and oversupplied food chains. These two sets are separated by a critical set (of zero measure) composed of all food chains with food yield marginally insensitive to nutrient (energy) supply. If yield maximization were the dominant mechanism of evolution, real exploited food chains should be close to this critical set or tend to approach it through long sequences of human interventions characterized by systematic increase (or decrease) of nutrient supply.

The dynamics of the Rosenzweig-MacArthur food chain have recently been classified by means of bifurcation analysis (Klebanoff and Hastings 1994; McCann and Yodzis 1995; Kuznetsov and Rinaldi 1996). The results are that coexistence of the three populations is possible and, depending on parameter values, that the dynamic regime is stationary, cyclic, or chaotic. Moreover, food chains with time responses increasing from bottom to top, such as phytoplankton-zooplankton-fish, have cyclic regimes of two different types called low- or high-frequency cycles (Muratori and Rinaldi 1992; Rinaldi and Muratori 1992; Kuznetsov and Rinaldi 1996). The distinction between these two types of cycles is mainly based on their geometry, as shown in figure 1. The low-frequency limit cycles (fig. 1A) are characterized by relevant and slow variations of the superpredator (x_3) as well as by fast oscillations of prey (x_1) and predators (x_2). On the contrary, high-frequency limit cycles (fig. 1B) are characterized by almost steady superpredator populations (x_3). Rosenzweig-MacArthur food chains can therefore be grouped into four sets (stationary, cyclic at low frequency, cyclic at high frequency, and chaotic), and the boundaries of such sets in parameter space can be explicitly found through numerical bifurcation analysis.

In principle, one should not expect any particular relationship between the two above classifications of food chains. In contrast with such an expectation, we will show that a very strong relationship exists; namely, high-frequency cyclic food chains are oversupplied, and all other food chains are undersupplied. The most intriguing implication of this discovery is that food chains with maximum mean food yield are on the edge of chaos. In other words, maximization of food yield calls for the most complex dynamic behavior.

In management terms, our results support two very simple decision rules: if a
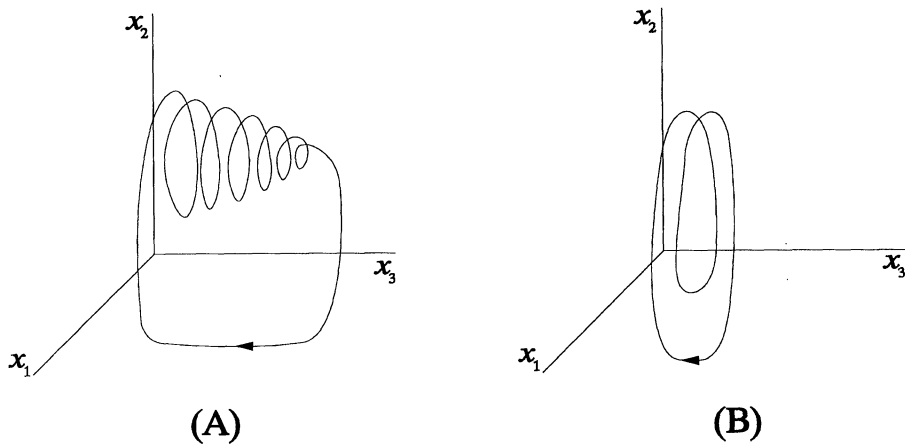
FIG. 1.—Limit cycles of prey (x_1), predator (x_2), and superpredator (x_3) in Rosenzweig-MacArthur food chain: (A) low-frequency cycle and (B) high-frequency cycle.

food chain is stationary, cyclic at low frequency, or chaotic, then increase nutri-ent supply; and if a food chain is cyclic at high frequency, then decrease nutrient supply. It is important to note that these rules are operational, in the sense that they allow one to make a decision even in the absence of information on system parameters.

This article is organized as follows. First, we consider ditrophic food chains and show that stationary food chains are undersupplied and cyclic food chains are oversupplied (the second statement holds in the case of fast prey and slow predator). Then, we turn our attention to tritrophic food chains and show the re-sults of a detailed numerical bifurcation analysis carried out with respect to prey growth rate and carrying capacity. The analysis is in agreement with previous findings and conjectures (Abrams and Roth 1994; McCann and Yodzis 1994) and clearly identifies the regions in parameter space where the dynamic regime is stationary, cyclic (at low and high frequency), and chaotic. By computing the mean food yield for all parameter values in the region of concern, we discover that high-frequency cyclic food chains are oversupplied and all others are under-supplied. Such a result, obtained numerically, is then proved to hold through a simple geometric approach in the case of food chains with a superpredator char-acterized by high time responses. Finally, the robustness of the results with re-spect to various forms of enrichment and predator and superpredator behaviors is also shown. Merits and weaknesses of our findings, as well as possible exten-sions, are briefly discussed at the end of the article.

DITROPHIC FOOD CHAINS

The Rosenzweig-MacArthur ditrophic food chain is composed of a logistic prey and a predator with a Holling Type II functional response. The model is

$$\dot{x}_1 = x_1 \left[r \left(1 - \frac{x_1}{K} \right) - \frac{ax_2}{b + x_1} \right],$$

and (1)

$$\dot{x}_2 = x_2 \left[e \frac{ax_1}{b + x_1} - d \right],$$

where x_1 and x_2 are prey and predator biomass, r and K are prey growth rate and carrying capacity, a is maximum predation rate, b is half-saturation constant (namely, prey biomass at which predation is half of the maximum), e is predator efficiency, and d is predator death rate that results from the sum of natural death rate and harvesting rate (obviously $ea > d$ since, otherwise, the predator cannot persist).

As is well known (see, e.g., Hsu et al. 1978), the parameter space can be divided into the following three regions:

$$K \leq \frac{bd}{ea - d} \quad \text{predator extinction},$$

$$\frac{bd}{ea - d} < K \leq \frac{bd + bea}{ea - d} \quad \text{stationary coexistence},$$

and

$$K > \frac{bd + bea}{ea - d} \quad \text{cyclic coexistence}.$$

Note that this partition does not involve prey growth rate r. Moreover, in the second region predator biomass at equilibrium is given by

$$x_2 = \frac{ber}{(ea - d)^2} \left(ea - d - \frac{bd}{K} \right)$$

and is therefore increasing with K (i.e., with nutrient supply). Thus, we can state, in our jargon, that stationary ditrophic food chains are undersupplied.

The computation of mean predator biomass in the third region is not possible analytically, because the prey-predator limit cycle is not known in closed form. However, if we assume that predator dynamics are slow with respect to prey dynamics, for example, because predator efficiency and death rate are low, we can use a very simple geometric approach (based on singular perturbation analysis) to approximate the limit cycle. This approach, first suggested by May (1977) in the context of population dynamics, uses the isoclines of the system. Figure 2 shows the isoclines of model (1) for two slightly different values of K, one just below (fig. 2A) and the other just above (fig. 2B) the critical value $K^* = (bd + bea)/(ea - d)$ separating stationary from cyclic food chains. In figure 2A the predator isocline is on the right of the top T of the prey isocline, and the intersection is a stable equilibrium. A trajectory starting from a generic point, like
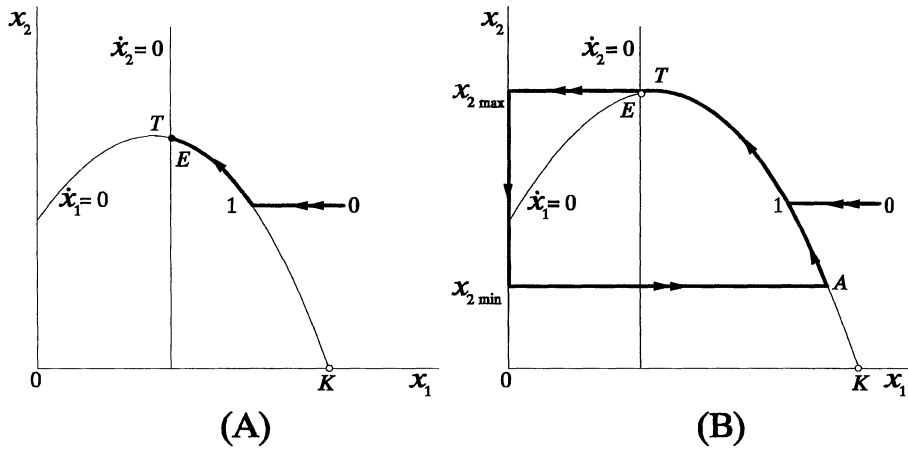
FIG. 2.—Isoclines and trajectories of ditrophic food chain model (1) in the case of fast prey and slow predator. Single- and double-headed arrows indicate slow and fast transitions, respectively. In case A, $K < K^*$ (see the text), and the system tends toward equilibrium E; in case B, $K > K^*$, and the system tends toward the slow-fast limit cycle $ATx_{2\,\max}x_{2\,\min}$.

point 0 in figure 2A, is composed first by a fast variation of the prey (horizontal segment 01) and then by a slow motion of prey and predator tending toward the equilibrium point along the isocline $\dot{x}_1 = 0$. In figure 2B the predator isocline is on the left of the top of the prey isocline so that their intersection is an unstable equilibrium point. After the first fast transition from 0 to 1, the trajectory develops at slow speed along the prey isocline. When the top of such isocline is reached, the prey collapses almost to 0 in a short time while the predator remains practically constant at the value $x_{2\,\max}$. Then in the absence of food, predators die off exponentially until the threshold biomass $x_{2\,\min}$ is reached. Below this threshold prey are capable of quickly reproducing and growing, and the consequence is a horizontal high-speed trajectory ending at point A, where a slow motion is again activated toward point 1, thus closing a cycle. The threshold $x_{2\,\min}$ can be determined by solving a simple integral equation (Rinaldi and Muratori 1992). Figure 2B implies that the mean value of predator biomass is somewhere between $x_{2\,\min}$ and $x_{2\,\max}$ and is therefore much lower than $x_{2\,\max}$. On the contrary, the predator biomass at equilibrium in figure 2A is approximately equal to $x_{2\,\max}$. This means that a switch of dynamic regime from stationary to cyclic, induced by a microscopic increase of nutrient supply, is associated with a macroscopic drop in food yield. Of course, if the time responses of prey and predator are not extremely diversified, the fall of predator biomass is sharp but not discontinuous. Thus, the mean predator biomass decreases with respect to K at least in some interval $K > K^*$. This proves that cyclic food chains with K slightly bigger than K^* are oversupplied, as already noticed in many simulation studies.

We can conclude our discussion by noting that the above results suggest the use of the following two operating rules in the vicinity of the point of maximum

mean yield: if a ditrophic food chain is stationary, then increase nutrient supply; if a ditrophic food chain is cyclic, then decrease nutrient supply.

The systematic use of these rules should slowly push exploited food chains to provide more and more yield until $K = K^*$. This corresponds to food chains that are on the edge of the cyclic behavior. In such conditions, small positive errors in the calibration of the nutrient supply (i.e., $K = K^* + \epsilon$) can give rise to dramatic losses of food yield as sketched in figure 2 and apparently intuitively understood by Rosenzweig (1971, p. 385), who stated, "Man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance."

TRITROPHIC FOOD CHAINS

The Rosenzweig-MacArthur tritrophic food chain is the following obvious extension of model (1):

$$\dot{x}_1 = x_1\left[r\left(1 - \frac{x_1}{K}\right) - \frac{a_1 x_2}{b_1 + x_1}\right],$$

$$\dot{x}_2 = x_2\left[e_1 \frac{a_1 x_1}{b_1 + x_1} - \frac{a_2 x_3}{b_2 + x_2} - d_1\right], \tag{2}$$

and

$$\dot{x}_3 = x_3\left[e_2 \frac{a_2 x_2}{b_2 + x_2} - d_2\right],$$

where r and K are prey growth rate and carrying capacity, and a_i, b_i, e_i, and d_i, $i = 1, 2$, are the maximum predator rate, half-saturation constant, efficiency, and death rate of the predator ($i = 1$) and superpredator ($i = 2$).

Many simulation studies (Hogeweg and Hesper 1978; Hastings and Powell 1991; Scheffer 1991; Rai and Sreenivasan 1993; McCann and Yodzis 1994; Wilder et al. 1994) have shown that model (2) can have chaotic dynamics and that the strange attractors resemble very much the low- and high-frequency limit cycles shown in figure 1. McCann and Yodzis (1994) have pointed out that not all parameter values used in the above-mentioned articles are biologically meaningful, but some of them are, such as those used by Scheffer (1991) for plankton and by Wilder et al. (1994) for gypsy moths. This fact, together with the analysis carried out by Abrams and Roth (1994) and McCann and Yodzis (1994) on food chains composed of vertebrates and invertebrates, strongly supports the conjecture that the irregular dynamics observed in many natural food chains might, indeed, be that of a strange attractor.

A formal classification of all stable modes of behavior of model (2) has been attempted by Klebanoff and Hastings (1994) and McCann and Yodzis (1995)
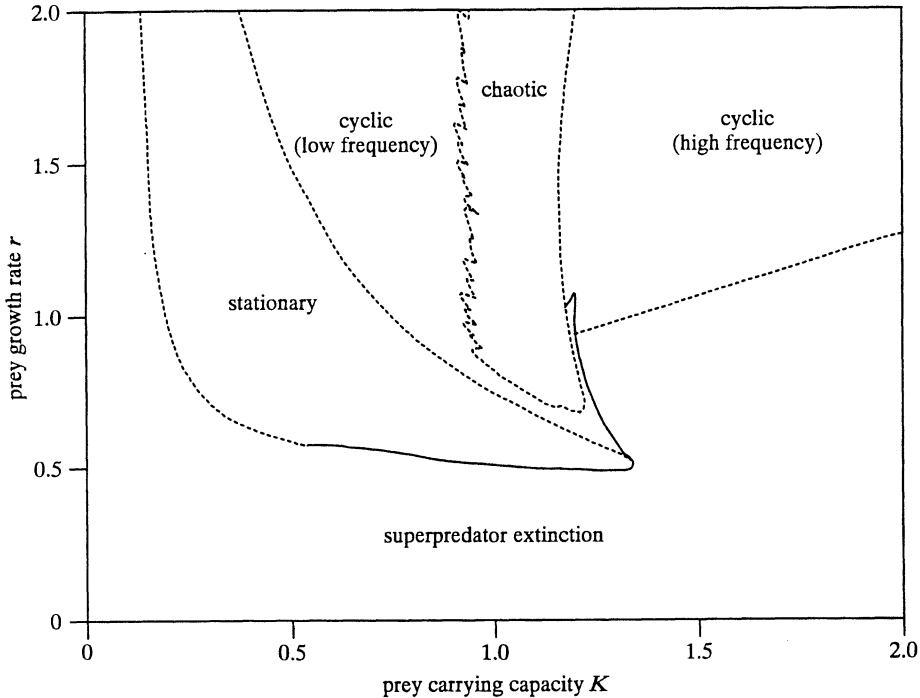
FIG. 3.—The regions with different asymptotic regimes in parameter space (K, r). The figure corresponds to the following parameter setting: $a_1 = 5/3$, $b_1 = 1/3$, $e_1 = 1$, $d_1 = 4/10$, $a_2 = 1/20$, $b_2 = 1/2$, $e_2 = 1$, and $d_2 = 1/100$. Transitions from one regime to another are smooth when crossing a dashed line and catastrophic when crossing a continuous line.

and then revised and completed (Kuznetsov and Rinaldi 1996) by means of specialized software for bifurcation analysis. In these studies, the discussion is mainly focused on the effects of two parameters, namely, d_1 and d_2. By contrast, for our purpose, the analysis must be performed with respect to K and r, which are the two parameters that are presumed to be correlated with nutrient supply to the bottom of the food chain. Thus, the bifurcation analysis has been repeated with respect to (K, r), and the result is that the bifurcations involved are essentially the same as those already detected by activating (d_1, d_2). For this reason, the complete bifurcation diagrams are not reported (for details on the methodology and bifurcation structure, see Kuznetsov and Rinaldi 1996). We report here in figure 3 only one diagram showing the regions with different modes of behavior in the space (K, r). This diagram has been obtained fixing predator and superpredator parameters a_i, b_i, e_i, d_i, $i = 1$, 2, at the values specified in the caption and looking only at the bifurcation of the most significant attractor, namely, that which has the highest mean yield. In other words, other attractors that coexist with the main one in some small regions of parameter space (see Kuznetsov and Rinaldi 1996) have been ignored. This simplification is justified by two

facts: the basins of attraction of the disregarded attractors are quite narrow, and their mean yields are much smaller than that of the main attractor. The boundaries of the various regions of the diagram reported in figure 3 are bifurcation curves and would vary if the predator and superpredator parameters would be varied. The continuous lines refer to so-called catastrophic bifurcations, and the dashed ones refer to noncatastrophic bifurcations. When a continuous line is crossed, the dynamic regime changes macroscopically. On the contrary, when a dashed line is crossed, there is no discontinuity, and the dynamic regime changes smoothly. Figure 3 gives a good idea of the influence of the prey parameters K and r on the dynamics of the food chain. In the lowest region, the superpredator goes extinct so that food yield is rigorously zero. In the remaining four regions, stable coexistence of the three populations is always possible but through different dynamic behaviors. More precisely, going from the left to the right (i.e., increasing prey carrying capacity), we have stationary coexistence, cyclic coexistence at low frequency, chaotic coexistence, and, finally, cyclic coexistence at high frequency. The chaotic region is a rather narrow and vertical band delimited by a regular curve on the right side. By contrast, its left boundary is a fractal set produced by a very complex bifurcation structure. Strange attractors close to this border are teacup strange attractors similar to the limit cycle shown in figure 1A. By contrast, strange attractors close to the opposite border resemble the high-frequency limit cycle shown in figure 1B. In conclusion, we can say that dynamic complexity first increases with prey carrying capacity (from stationary to chaotic regime) and then decreases (from chaos to cycles). These findings are only in partial agreement with the conclusions of Abrams and Roth (1994) based on simulations carried out at constant r. This is due to the fact that they have not used a sharp method to distinguish chaotic from cyclic regimes; in fact, in some cases they have classified a strange attractor as a cycle and vice versa. Under these conditions, it is rather obvious that they could not detect the results we have obtained through bifurcation analysis.

Let us now focus on mean food yield and its dependence on prey growth rate and carrying capacity. As for ditrophic food chains, we simply consider superpredator biomass as an indicator of food yield. For stationary food chains, the value of x_3 at equilibrium can be easily expressed in terms of x_1 and x_2. On the other hand, from the superpredator equation it follows that x_2 is independent of K and r; thus, in conclusion,

$$x_3 = \Psi[x_1(K, r), x_2].$$

Although the function Ψ is rather complex, it is possible to show that $\partial\Psi/\partial x_1$, $\partial x_1/\partial K$, and $\partial x_1/\partial r$ are positive for all parameter values (the proof, not reported here, is available on request). This implies that x_3 increases with K and r or, in our jargon, that stationary food chains are undersupplied. The computation of the mean superpredator biomass x_3 for cyclic and chaotic food chains has been carried out numerically on a fine grid (about 10,000 points) in the space (K, r). A special program, based on spectral analysis, has been used in the case of chaotic food chains. Finally, the results of these computations have been interpo-
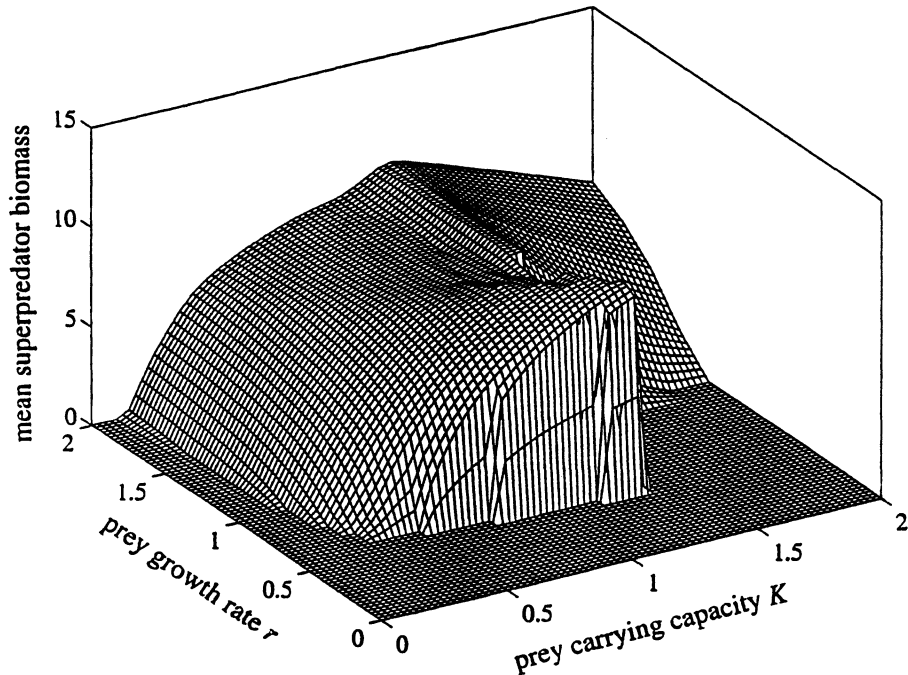
FIG. 4.—Mean superpredator biomass (proportional to food yield) versus prey carrying capacity and growth rate. See the legend to figure 3 for parameter values.

lated to produce figure 4. Obviously, food yield is zero in the region of superpredator extinction (see fig. 3), while it is first increasing and then decreasing with nutrient supply in the rest of the space. Moreover, the crest of the surface in the K direction is almost independent of r, meaning that the optimum nutrient supply is almost independent of prey growth rate. Finally, one can note that a small increase of K above its optimum value can have dramatic consequences on food yield if prey growth rate is low. All these features confirm some of Rosenzweig's intuitions and partially agree with the analysis performed by Abrams and Roth (1994), who, unfortunately, have simulated the system using too small a number of points (about 100 vs. our 10,000) and have poorly evaluated the mean yield (see, e.g., their figs. 1, 3, and 5, where they have indicated a range of possible values instead of a precise value).

We can actually derive sharper conclusions by more carefully analyzing our figures. For this, let us project the crest of the surface of figure 4 on the horizontal plane, thus finding the sets of under- and oversupplied food chains in the space (K, r), and then superimpose these sets to figure 3. The result, reported in figure 5, is surprisingly simple: the set of undersupplied food chains almost coincides with the union of the sets of stationary, cyclic at low frequency, and chaotic food chains, and, consequently, oversupplied food chains almost coincide with food chains cycling at high frequency.
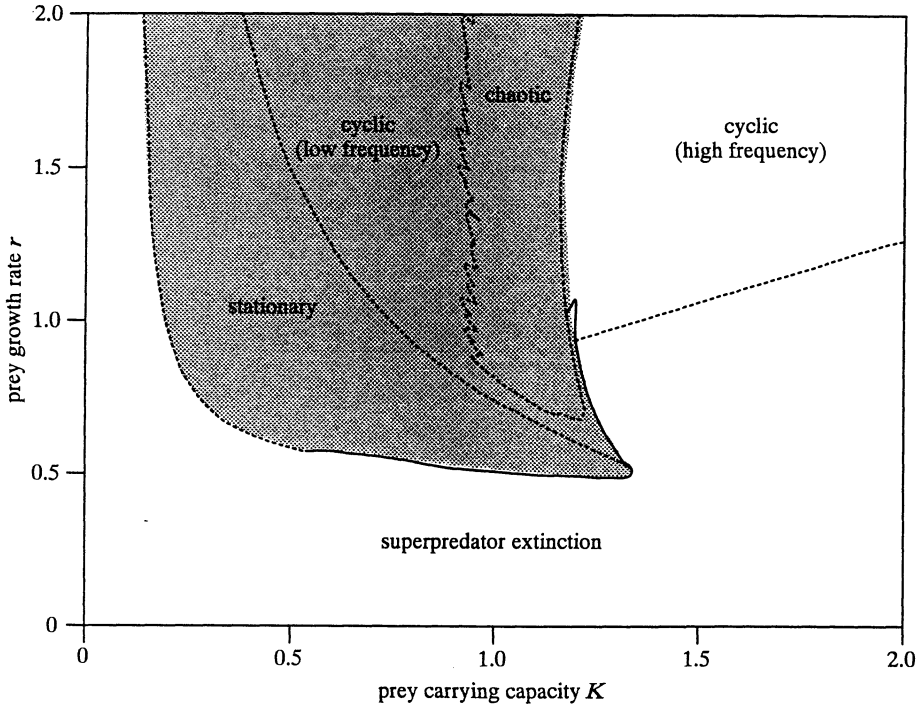
FIG. 5.—The set (*shaded region*) of undersupplied food chains. Note the near coincidence of the right border of the chaotic region with the boundary of the shaded region separating under- and oversupplied food chains.

As for ditrophic food chains, we can neatly support this result by analyzing food chains with superpredator growing at an extremely low rate with respect to prey and predator (Kuznetsov and Rinaldi 1996). In fact, in such a case one can first freeze superpredator biomass at a constant value and determine the corresponding asymptotic behavior of the (prey-predator) system. The result is a three-dimensional figure showing how the equilibria and limit cycles of the fast (prey-predator) system are influenced by superpredator biomass. Then, the slow dynamics of the superpredator can be superimposed, as shown in figure 6 for two slightly different values of K.

In figure 6A the food chain behaves on a low-frequency limit cycle. Prey (x_1) and predator (x_2) oscillate at high frequency for a long period, while superpredator biomass (x_3) slowly increases. The amplitudes of prey and predator oscillations decrease over time because higher superpredator biomass implies higher harvesting pressure on predator population. When the superpredator biomass is sufficiently high, prey and predator coexist at a slowly varying equilibrium until the pressure on the predator population becomes so high that such a population collapses, while prey population tends to carrying capacity (transition AB in fig. 6A). From this point on, the superpredator population has no food and dies of
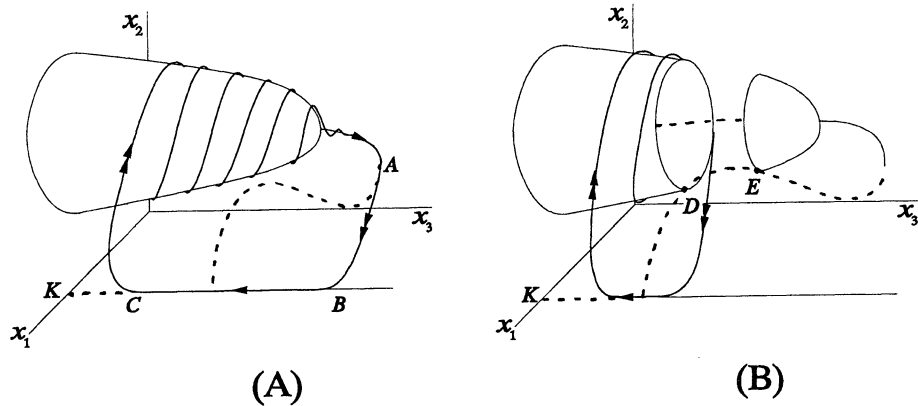
FIG. 6.—A sketch of behavior of tritrophic food chains with slow superpredator: (A) low-frequency limit cycle and (B) high-frequency limit cycle. Dashed lines indicate unstable equilibria of the prey-predator system with a constant superpredator biomass.

starvation. During this period (transition BC in fig. 6A), the food chain is practically disconnected because there is no energy flow from prey to superpredator. When the superpredator population becomes sufficiently low, the few remaining predators can finally regenerate and reactivate the high-frequency prey-predator oscillations, thus closing a teacup cycle. The mean value of superpredator biomass on this complex cycle is obviously somewhere between the x_3 coordinates of points B and C.

In figure 6B the carrying capacity K has been slightly increased. The consequence (see Kuznetsov and Rinaldi 1996) is that the line of the unstable equilibria of the fast (prey-predator) system touches the cycle manifold at two points, D and E, which implies that there are no limit cycles in the prey-predator system for a full range of values of superpredator biomass ($x_3^D < x_3 < x_3^E$). The collapse of the predator population occurs when $x_3 = x_3^D$ and is therefore anticipated with respect to figure 6A so that the whole cycle is characterized by much smaller values of superpredator biomass. In conclusion, a small increase of prey carrying capacity has produced a switch from a low-frequency cycle (fig. 6A) to a high-frequency cycle (fig. 6B), and this switch is accompanied by a remarkable reduction of mean food yield. This is why in figure 5 the line separating under- and oversupplied food chains almost coincides with the line on which teacup attractors suddenly become shorter by losing the bottom of the cup.

Our findings support the two simple operating rules mentioned in the introduction, namely, if a food chain is stationary, cyclic at low frequency, or chaotic, then increase nutrient supply; and if a food chain is cyclic at high frequency, then decrease nutrient supply. These two rules could be used to guide any pragmatic adjustment process aimed at improving food yield. Moreover, food chains with maximum yield (i.e., food chains corresponding to the crest of the surface in fig. 4) are on the edge of chaos. Thus, the systematic application

of the above operating rules should slowly improve mean yield and gradually transform food chains with simple behavior into chaotic food chains. And this is true both for under- and oversupplied food chains.

<center>ROBUSTNESS OF THE RESULTS</center>

Up to now we have assumed that enrichment has an impact on only prey carrying capacity K because this is the assumption that is most often done in the literature. In reality, enrichment can also influence the biological process responsible for prey growth rate r.

To clarify this point, let us first write the growth of the prey (x_1) in the absence of predator $(x_2 = 0)$ as a simple balance between natality (n) and mortality (m), that is,

$$\dot{x}_1 = x_1(n - m),$$

where n and m are per capita natality and mortality rates of the prey. Then, assume that

$$n = n_0 - \alpha x_1,$$

and

$$m = m_0 - \beta x_1,$$

where n_0 and m_0 are per capita natality and mortality rates at low prey densities and αx_1 and βx_1 are natality loss and surplus mortality due to intraspecific competition. Under these standard assumptions, the above balance equation is equivalent to the logistic equation (see model [2])

$$\dot{x}_1 = rx_1\left(1 - \frac{x_1}{K}\right),$$

with

$$r = n_0 - m_0,$$

and

$$K = \frac{n_0 - m_0}{\alpha + \beta}.$$

Of course, these formulas for r and K hold also when the per capita natality and mortality rates n_0 and m_0, as well as the intraspecific competition parameters α and β, are sensitive to a control parameter S, from now on called nutrient supply. In such a case, we must simply rewrite the formulas as follows:

$$r(S) = n_0(S) - m_0(S)$$

and

$$K(S) = \frac{n_0(S) - m_0(S)}{\alpha(S) + \beta(S)}.$$

Affirming that the nutrient supply S has beneficial influence on prey natality and mortality is equivalent to assuming that n_0 increases with S and m_0, α, and β are decreasing functions of S; that is,

$$n_0'(S) \geq 0,$$

$$m_0'(S) \leq 0,$$

$$\alpha'(S) \leq 0,$$

and   (3)

$$\beta'(S) \leq 0.$$

As expected, from these inequalities it follows that

$$r'(S) \geq 0,$$

and

$$K'(S) \geq 0.$$

The above formulas for $r(S)$ and $K(S)$, together with inequalities (3), imply something more, namely, that the ratio

$$\frac{r(S)}{K(S)} = \alpha(S) + \beta(S)$$

is a decreasing function of S. In other words, when a food chain is enriched (i.e., when S is increased starting from a given value $\overline{S}$), the point $P = (K(S), r(S))$ in parameter space moves upward and to the right starting from point $\overline{P} = (K(\overline{S}), r(\overline{S}))$ (because $r' \geq 0$ and $K' \geq 0$). But point P remains in any case, below the straight line with slope $r(\overline{S})/K(\overline{S})$ passing through the origin and point $\overline{P}$ (because the ratio $r(S)/K(S)$ decreases with S).

   Up to now, we have studied the extreme case in which enrichment has an impact only on prey capacity (i.e., $r'(S) = 0$). From the prior discussion, it follows that this extreme case corresponds to $n_0'(S) = m_0'(S) = 0$, namely, to the rather common case of prey populations with individuals competing for a resource S but scarcely influenced by it at low numbers. Another extreme case, $\alpha'(S) = \beta'(S) = 0$, corresponds to populations in which individuals do not compete for S, which is therefore biologically less significant. This happens, for example, when S is a measure of the quality of the habitat, namely, a resource for which individuals do not compete but that could influence their natality and mortality at low densities.

   The above simple interpretations of the relationships between nutrient supply S and prey parameters (K, r) suggest that for most food chains the first extreme

assumption (K varies with S, and r is constant) should better interpret the real impact of enrichment. But let us determine, in any case, what would be the consequence of the second extreme assumption, when a small increase of nutrient supply can be viewed as a small step in the parameter space (K, r) along the straight line passing through the origin. Under- and oversupplied food chains can be easily determined under this new assumption on enrichment. One has simply to look again at figure 4 and determine the crest of the surface along all rays through the origin. The result is obvious: the new crest practically coincides with the old one, because the yield is much more sensitive to K than to r. This means that all our findings are valid provided that enrichment has an impact on prey parameters in any form ranging between the two extreme forms we have considered (i.e., in any form satisfying conditions [3]).

A second check of the robustness of our conclusions has been conducted by repeating for different parameter settings the analysis presented in the previous section. In accordance with the geometric interpretation based on slow-fast dynamics (see fig. 6), all the cases corresponding to a superpredator with low efficiency, predation rate, and death rate have fully confirmed our analysis. We have therefore varied the parameters to test cases with superpredator time responses comparable to prey and predator time responses. Under these conditions, one should expect that the distinction between low and high frequency is not possible anymore. Intuition has been confirmed by the analysis, as shown by figure 7, which has been obtained with superpredator efficiency and death rate 10 times bigger than in figure 5. The regions of low- and high-frequency cyclic behavior are now melted in a single region surrounding the region of chaotic behavior. The line separating under- from oversupplied food chains still approximates fairly well the right boundary of the chaotic region. Thus, it is still possible to conclude that to improve the yield when prey growth rate is high, one should force the ecosystem to behave chaotically. By contrast, food chains with low prey growth rate cannot be chaotic, and the maximization of their yield is obtained with a cyclic regime. This means that the two operating rules formulated in the previous section should only be slightly adapted to fit with this special case.

The last and possibly most interesting checks we have performed concern some functional perturbations of the model. The first one takes care of a special kind of heterogeneity, namely, the existence of a refugium where the prey population cannot be predated and is therefore at carrying capacity. For this we have added in the prey equation a small diffusive inflow proportional to the difference between carrying capacity and prey density. This simple modification of the Rosenzweig-MacArthur model has been recently proposed by Scheffer and De Boer (1995) in the context of plankton dynamics. The second modification we have considered is related to the functional response of the superpredator. To take into account that large superpredators often have alternative sources of food and switch to a specific one only if it is not too scarce, we have substituted the Holling Type II functional response $a_2 x_2/(b_2 + x_2)$ with a Holling Type III (sigmoid) functional response $a_2 x_2^2(b_2^2 + x_2^2)$. Finally, we have also considered the case in which the functional responses have Ivles's exponential form instead of
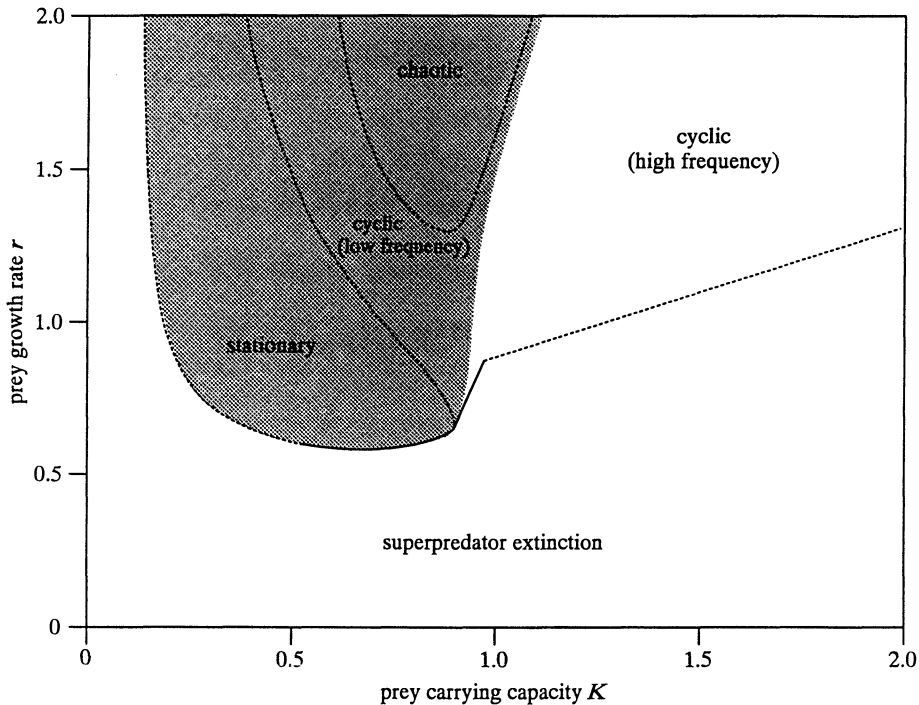
FIG. 7.—The set (*shaded region*) of undersupplied food chains in the case of a predator and superpredator with comparable time responses. The regions of low- and high-frequency cycles are melted in a single region.

the classical Monod form. In all these cases we have found results completely similar to those described in figures 3 and 5. The reason for this is that the above modifications do not substantially alter the geometry of the attractors of the fast components of the system. In other words, these attractors vary with superpredator biomass roughly as in figure 6, so that the mechanism responsible for the sudden yield collapse is still present.

Another possible modification is to add to model (2) one differential equation describing nutrient dynamics. This obviously requires modifying the prey equation by substituting the logistic growth rate with the balance between a nutrient uptake rate and a mortality rate. The new food chain model would then be a fourth-order chemostat model in which enrichment is realized by increasing either the flow rate or the concentration of the nutrient inflow. The classification of all the dynamic modes of behavior of this model requires a relevant computational effort and has not yet been published. But the analyis of the dynamics of the fast components of the chain (nutrient, prey, and predator) for different constant values of superpredator biomass is easily accomplished and allows one to verify that a catastrophe mechanism like that described in figure 6 is present also in this case. This implies that the conclusions obtained for the Rosenzweig-

MacArthur model hold also for the chemostat food chain model. This is not surprising since some sort of equivalence between the two models has already been pointed out (Gragnani and Rinaldi 1995). The details of the analysis concerning bifurcations, chaotic behavior, and maximization of mean yield of the chemostat model will be published elsewhere.

CONCLUSION

We have shown that a strong relationship exists between dynamic behavior and abundance of the top component of tritrophic food chains. In a sense, this article can be considered as the natural follow-up of a study by Abrams and Roth (1994), who concluded that often mean abundance of the top species first increases and then decreases with nutrient supply to the bottom species and that chaotic regimes are obtained for intermediate values of nutrient supply. Our study confirms these two facts and shows that they are actually tied together because mean abundance of the top species is maximum at the edge of chaos. This very sharp and intriguing property was not discovered by Abrams and Roth (1994, p. 1129), who only noticed that "chaos occurs for a range of carrying capacities close to those producing the maximum population size of the top species."

More precisely, we have discovered that food chains that tend to behave at equilibrium, on a low-frequency limit cycle, or on a chaotic attractor are undersupplied, in the sense that the mean abundance of their top component (or their food yield in the case of the top predator being harvested) can be marginally increased by slightly enriching the bottom of the chain. Conversely, food chains with high-frequency cyclic behavior should be impoverished to improve top abundance. These conclusions have been obtained by comparing the results of a detailed bifurcation analysis identifying all dynamic modes of behavior, with the results of a systematic simulation analysis aimed at determining the dependence of top abundance on prey growth rate and carrying capacity. The same results have also been formally proved for the special but important case of food chains characterized by a top predator growth rate much lower than that of the prey and predator. One important consequence of our findings is that maximization of top abundance requires a special chaotic regime, which is very often on the edge of a potential catastrophic collapse. In other words, optimization requires very complex and very dangerous dynamics, as intuitively perceived long ago by Rosenzweig (1971) in his famous article on ditrophic food chains.

These findings might be of great importance for understanding community evolution due to exploitation or gradients of primary productivity. For example, they might be used for explaining the catastrophic collapse of too heavily enriched resources or the differences in abundance of various species at different latitudes, altitudes, and depths.

We like to stress that the enthusiasm for the general principle "optimality implies chaos" has already appeared in other areas of biology (e.g., brain activity, Rapp et al. 1985; cardiac function, West and Goldberger 1987; metapopulations, Allen et al. 1993; evolution, Ferrière and Gatto 1993; Kauffman 1993; ecosys-

tems, Jorgensen 1995) and should be counterbalanced by the consciousness of the limits of the approach we have followed to derive it. In fact, our findings are not supported by field or laboratory experiments, which would in any case require a paramount effort. Moreover, our derivation relies on a specific model, in which the complexity of plant and animal behaviors and trophic interactions are kept at a minimum. Thus, it is perhaps more honest, and certainly more appropriate, to say that the standard assumption of logistic growth of the prey and Holling Type II functional response of predator and superpredator point out the principle "optimality implies chaos." The problem then becomes the following: Are some of the neglected properties of the three populations involved so strategic as to destroy the validity of the principle? In this respect, we have already shown that this principle survives a number of functional and structural modifications of the model. But a great number of ecologically significant extensions still remain unexplored.

Finally, at a more abstract level, it would also be interesting to explore whether any relationship exists between the principle "optimality implies chaos" and other general principles of evolution, adaptation, self-organization, thermodynamics, and information in biological systems that have recently been used to support the idea that ecosystems are on (or should tend toward) the edge of chaos.

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