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# Working Paper

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# Yield and dynamics of tri-trophic food chains

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## **Abstract**

Strong relationships between top productivity and dynamic behavior of tri-trophic food chains are pointed out by analyzing the classical Rosenzweig-MacArthur model. On one hand, food chains are subdivided into under-supplied and over-supplied, the first being those in which a marginal increase of nutrient supply to the bottom produces a marginal increase of mean top productivity. On the other hand, a detailed bifurcation analysis proves that dynamics complexity first increases with nutrient supply (from stationary to low-frequency cyclic regime and, finally, to chaos) and then decreases (from chaos to high-frequency cyclic regime). A careful comparison of the two analyses supports the conclusion that food chains cycling at high-frequency are over-supplied, while all others are under-supplied. A straightforward consequence of this result is that maximization of top productivity requires a chaotic regime. This regime turns out to be very often on the edge of a potential catastrophic collapse of food yield. In other words, optimality implies very complex and dangerous dynamics, as stated long ago for di-trophic food chains by Rosenzweig in his famous paper on the paradox of enrichment.

Simple relationships are established in this paper between the dynamics of tri-trophic food chains and the possibility of increasing top productivity through enrichment. Our result can be viewed as the most natural generalization of what is known since the early seventies for di-trophic food chains (Rosenzweig 1971).

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

If the superpredator is exploited, its mortality is the sum of basic mortality and harvesting effort, so that food yield (top productivity) is proportional to superpredator biomass. 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, while 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 which often influence only the prey carrying capacity (Oksanen et al. 1981; Abrams 1993). It is therefore possible to distinguish between under-supplied and over-supplied food chains. The first ones 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. Viceversa, over-supplied food chains are those that can be marginally improved through impoverishment. Hence, our food chains universe is subdivided into under- and over-supplied food chains. These two sets are separated by a critical set (of zero measure) composed of all food chains with top productivity 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 result is that coexistence of the three populations is possible and, depending upon parameter values, the dynamic regime is stationary, cyclic or chaotic. Moreover, food chains with time responses increasing from bottom to top, as the classical chains (plants - herbivores - carnivores), have cyclic regimes which are either low- or high-frequency. The geometry of the corresponding limit cycles is shown in Fig. 1. The low-frequency limit cycles (Fig. 1a) are characterized by relevant and slow variations of the superpredator, as well as by fast oscillations of prey and predators. On the contrary, high-frequency limit cycles (Fig. 1b) are characterized by almost steady superpredator populations. In conclusion, Rosenzweig-MacArthur food chains can 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 over-supplied and all other food chains are under-supplied. The most intriguing implication of this discovery is that food chains with maximum mean food production are on the edge of chaos. In other words, maximization of food production calls for the most complex dynamic behavior.

In management terms our results support two very simple decision rules:

- (i) if a food chain is stationary, cyclic at low-frequency or chaotic, then increase nutrient supply
- (ii) 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 take a decision even in the absence of information on system parameters.

The paper is organized as follows. First, we consider di-trophic food chains and show that Rosenzweig's paradox of enrichment can be formulated by stating that stationary food chains are under-supplied and cyclic food chains are over-supplied (the second statement is proved in the case of fast prey and slow predator). Then, we turn our attention to tri-trophic food chains and show the results 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 (McCann and Yodzis 1994; Abrams and Roth 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 over-supplied and all others are under-supplied. Such a result, obtained numerically, is then proved through a simple geometric approach in the case of food chains with superpredator characterized by high time responses. Finally, the robustness of the results with respect to various forms of enrichment and predator and superpredator behaviors is also shown. Merits and weaknesses of our findings, as well as possible extensions, are briefly discussed at the end of the paper.

## **Di-trophic food chains**

The Rosenzweig-MacArthur di-trophic food chain is composed by a logistic prey and a predator with Holling type II functional response. Under the assumption that predator mortality is proportional to predation rate the model is

$$\begin{aligned}\dot{x}_1 &= x_1 \left[ r \left( 1 - \frac{x_1}{K} \right) - \frac{ax_2}{b + x_1} \right] \\ \dot{x}_2 &= x_2 \left[ e \frac{ax_1}{b + x_1} - d \right]\end{aligned}\tag{1}$$

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 maximum),  $e$  is predator efficiency and  $d$  is predator death rate

(obviously  $ea > d$  since, otherwise, predator cannot persist).

As is well known, the parameter space can be divided into the following three regions

$$\begin{aligned}
 K &\leq \frac{bd}{ea-d} && \text{predator extinction} \\
 \frac{bd}{ea-d} &< K \leq \frac{bd+bea}{ea-d} && \text{stationary coexistence} \\
 K &> \frac{bd+bea}{ea-d} && \text{cyclic coexistence}
 \end{aligned}$$

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 di-trophic food chains are under-supplied.

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 is 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, makes use of the isoclines of the system. Fig.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 Fig.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 point 0 in Fig.2a, is composed by a first fast variation of the prey (horizontal segment 0 1) and then by a slow motion of prey and predator tending toward the equilibrium point along the isocline  $\dot{x}_1 = 0$ . In Fig.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 zero in a short time while the predator remains practically constant at the value  $x_{2\max}$ . Then in the absence of food, predator die off exponentially until the threshold biomass  $x_{2\min}$  is reached. Below this threshold prey are capable to quickly reproduce and grow 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), which is not reported here because not needed for our purpose. In fact Fig.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 Fig.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 to 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 not as sharp. Nevertheless the mean predator biomass decreases with respect to  $K$  for  $K$  bigger than  $K^*$ . This proves that cyclic food chains are over-supplied, as already argued by Rosenzweig (1971) and later confirmed by others on the basis of simulations.

We can conclude our discussion by noting that the above results suggest the use of the

following two operating rules

- (i) if a di-trophic food chain is stationary, then increase nutrient supply
- (ii) if a di-trophic food chain is cyclic, then decrease nutrient supply

The systematic use of these rules should slowly push exploited food chains to become insensitive to small perturbations of nutrient supply. This corresponds to food chains with  $K = K^*$ , i.e., to food chains which are on the edge of the cyclic behavior. In such conditions small errors in the calibration of the nutrient supply can give rise to dramatic losses of food yield as sketched in Fig.2 and noted by Rosenzweig (1971) 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”.

## Tri-trophic food chains

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

$$\begin{aligned}\dot{x}_1 &= x_1 \left[ r \left( 1 - \frac{x_1}{K} \right) - \frac{a_1 x_2}{b_1 + x_1} \right] \\ \dot{x}_2 &= x_2 \left[ e_1 \frac{a_1 x_1}{b_1 + x_1} - \frac{a_2 x_3}{b_2 + x_2} - d_1 \right] \\ \dot{x}_3 &= x_3 \left[ e_2 \frac{a_2 x_2}{b_2 + x_2} - d_2 \right]\end{aligned}\tag{2}$$

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 maximum predator rate, half saturation constant, efficiency, and death rate of predator ( $i = 1$ ) and superpredator ( $i = 2$ ).

Many simulation studies (Hogeweg and Hesper 1978; Scheffer 1991; Hastings and Powell 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 Fig. 1. McCann and Yodzis (1994) have pointed out that not all parameter values used in the above mentioned papers are biologically meaningful, but some of them are, like those used by Scheffer (1991) for plankton and 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 support 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) and then revised and completed by 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  $d_2$ , which can be varied by harvesting predator and superpredator or by contaminating or reclaiming their environments. By contrast, for our purpose, the analysis must be performed with respect to  $K$  and  $r$ , which are the two parameters that are 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 than those already detected by activating  $(d_1, d_2)$ . For this reason, the complete bifurcation diagrams are not reported (the interested reader can refer to Kuznetsov and Rinaldi (1996) for details on the methodology and on the bifurcation structure). We report here in Fig.3 only one diagram showing the regions with different modes of behavior in the space  $(K, r)$ . This diagram has been obtained by fixing predator and superpredator parameters  $a_i, b_i, e_i, d_i, i = 1, 2$  at the values specified in the caption. The boundaries of the various regions are bifurcation curves and would vary if the predator and superpredator parameters would be varied. The continuous lines refer to so-called catastrophic bifurcations, while the dashed ones to non-catastrophic 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. Fig.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 tea-cup strange attractors similar to the limit cycle shown in Fig.1a. By contrast, strange attractors close to the opposite border, resemble the high-frequency limit cycle shown in Fig.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 in full agreement with the conclusions of Abrams and Roth (1994) based on simulations carried out at constant  $r$ .

Let us now focus on mean food yield and on its dependence upon prey growth rate and carrying capacity. As for di-trophic food chains, we simply consider superpredator biomass as 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 upon  $K$  and  $r$ ; thus, in conclusion,

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

Although the function  $\Psi$  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 under-supplied. The computation of the mean superpredator biomass  $x_3$  for cyclic and chaotic food chains has been carried out numerically on a fine grid 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 interpolated in order to produce Fig.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 upon  $r$ , meaning that the optimum nutrient supply is almost independent upon 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



agree with the analysis performed by Abrams and Roth (1994) and reinforce Rosenzweig's conclusions.

We can actually derive sharper conclusions by more carefully analyzing our figures. For this, let us project the crest of the surface of Fig.4 on the horizontal plane, thus finding the sets of under- and over-supplied food chains in the space  $(K, r)$ , and then superimpose these sets to Fig.3. The result, reported in Fig.5, is surprisingly simple: the set of under-supplied food chains almost coincides with the union of the sets of stationary, cyclic at low-frequency and chaotic food chains, and, consequently, over-supplied food chains almost coincide with food chains cycling at high-frequency.

As for di-trophic 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 Fig.6 for two slightly different values of  $K$ .

In Fig.6a the food chain behaves on a low-frequency limit cycle. For a long period prey and predator oscillate at high-frequency while superpredator biomass slowly increases. The amplitudes of prey and predator oscillations decrease over time because higher superpredator biomass implies higher harvesting pressure on predator population. When 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, superpredator have no food and die of starvation. During this period (transition  $BC$  in Fig.6a) the food chains is practically disconnected because there is no energy flow from prey to superpredator. When superpredator population becomes sufficiently low, the few remaining predator can finally regenerate and reactivate the high-frequency prey - predator oscillations, thus closing a tea-cup 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 Fig.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  $E$  and this 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 Fig.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 Fig.5 the line separating under- and over-supplied food chains almost coincides with the line on which tea cup attractors suddenly become shorter by loosing the bottom of the cup.

Our findings support the two simple operating rules mentioned in the introduction, namely

- (i) if a food chain is stationary, cyclic at low-frequency or chaotic then increase nutrient supply
- (ii) if a food chain is cyclic at high-frequency, then decrease nutrient supply

These two rules could be used to guide any pragmatic “tatonnement” 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 yield production and gradually transform food chains with simple behavior into chaotic food chains. And this is true both for under- and over-supplied food chains.

## Robustness of the results

Up to now we have assumed that enrichment impacts only on prey carrying capacity because this is the assumption that is most often done in the literature. In reality, enrichment can also influence the biological process responsible of prey growth rate  $r$ . In fact, let us write prey growth per capita as the balance of natality  $n$ , basic mortality  $m$  and surplus mortality  $\gamma x$  due to intraspecific competition, i.e.,

$$\frac{\dot{x}}{x} = n - m - \gamma x$$

and assume that  $n$  and  $m$  are linearly related with nutrient supply  $S$ , i.e.,

$$n = n_0 + \alpha S \quad m = m_0 - \beta S$$

Under these assumptions (which are, indeed, quite reasonable) prey growth is described by the logistic equation

$$\frac{\dot{x}}{x} = (n_0 - m_0 + (\alpha + \beta) S) \left( 1 - \frac{x}{\frac{n_0 - m_0 + (\alpha + \beta) S}{\gamma}} \right)$$

which clearly shows that both  $r$  and  $K$  are influenced by nutrient supply. Actually this model indicates that  $K$  and  $r$  vary with nutrient supply  $S$  at a constant ratio,  $r/K = \gamma$ . This means that 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. It is therefore easy to determine under- and over-supplied food chains under this new assumption on enrichment. One has simply to look again at Fig.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 impacts on prey parameters in any forms ranging between the two extreme forms we have considered.

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 superpredator with low efficiency, predation rate, and death rate have fully confirmed our analysis. We have therefore varied the parameters in order to test cases with superpredator time responses comparable to prey and predator time responses, even if these cases are certainly a bit unrealistic, in particular in the context of exploited ecosystems. 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 Fig.7 which has been obtained with superpredator efficiency and death rate ten times bigger than in Fig.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 over-supplied food chains still approximates fairly well the right boundary of the chaotic region. Thus, it is still possible to conclude that in order 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 check we have performed, concerns some functional perturbations of the model. The first one takes care of a special kind of heterogeneity, namely the existence of a refugium where 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 with the functional response of the superpredator. In order to take into account that large superpredator have often 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 than the classical Monod form. In all these cases we have found results completely similar to those described in Figs.3-5. 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 Fig.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 to modify 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 has not yet been done and certainly requires a relevant computational effort. Nevertheless, the analysis of the dynamics of the fast components of the chain (nutrient, prey, and predator) for different constant values of superpredator biomass has already been accomplished, and has allowed us to verify that a catastrophe mechanism like that described in Fig.6 is present also in this case. This is a good argument for conjecturing that the conclusions obtained for the Rosenzweig-MacArthur model hold also for the chemostat food chain model. After all, this would not be too surprising since some sort of equivalence between the two models has already been pointed out (Gagnani and Rinaldi 1995).

## Conclusion

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

We like to stress that the enthusiasm for the general principle “optimality implies chaos” (already appeared in other fields of biology) 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 upon 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 resource 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 to destroy the validity of the principle ? In this respect, we are inclined to believe that the principle is relatively robust and, indeed, we have already shown that it survives to a number of functional and structural modifications of the model. But a great number of ecologically significant extensions still remain unexplored.



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## Figure legends

### Figure 1

Limit cycles of Rosenzweig-MacArthur food chain: (a) low-frequency cycle; (b) high-frequency cycle.

### Figure 2

Isoclines and trajectories of di-trophic food chain model (1) in the case of fast prey and slow predator. Single [double] arrow indicate slow [fast] transitions. In case (a)  $K < K^*$  (see text) and the system tends toward equilibrium  $E$ ; in case (b)  $K > K^*$  and the system tends toward the slow-fast limit cycle  $A T x_{2\max} x_{2\min}$ .

### Figure 3

The regions with different asymptotic regimes in parameter space  $(K, r)$ . The figure corresponds to the following parameter setting  $a_1 = 5/3$   $b_1 = 1/3$   $e_1 = 1$   $d_1 = 4/10$   $a_2 = 1/20$   $b_2 = 1/2$   $e_2 = 1$   $d_2 = 1/100$ . Transition from one regime to another are smooth when crossing a dashed line and catastrophic when crossing a continuous line.

### Figure 4

Mean superpredator biomass (proportional to food yield) vs. prey carrying capacity and growth rate. See caption of Fig.3 for parameter values.

**Figure 5**

The set (shaded region) of under-supplied food chains. Note the almost coincidence of the right border of the chaotic region with the boundary of the shaded region separating under- and over-supplied food chains.

**Figure 6**

Sketch of behavior of tri-trophic food chains with slow superpredator: (a) low-frequency limit cycle; (b) high-frequency limit cycle. Dashed lines indicate unstable equilibria of the prey-predator system with constant superpredator biomass.

**Figure 7**

The set (shaded region) of under-supplied food chains in the case of predator and superpredator with comparable time responses. The regions of low- and high-frequency cycles are melted in a single region.

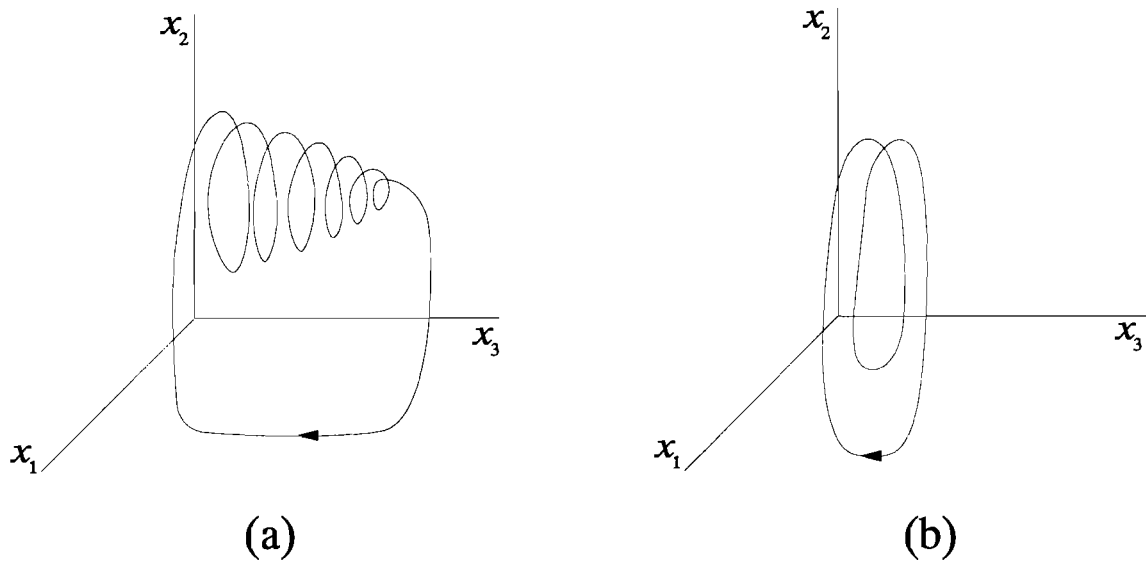


Figure 1

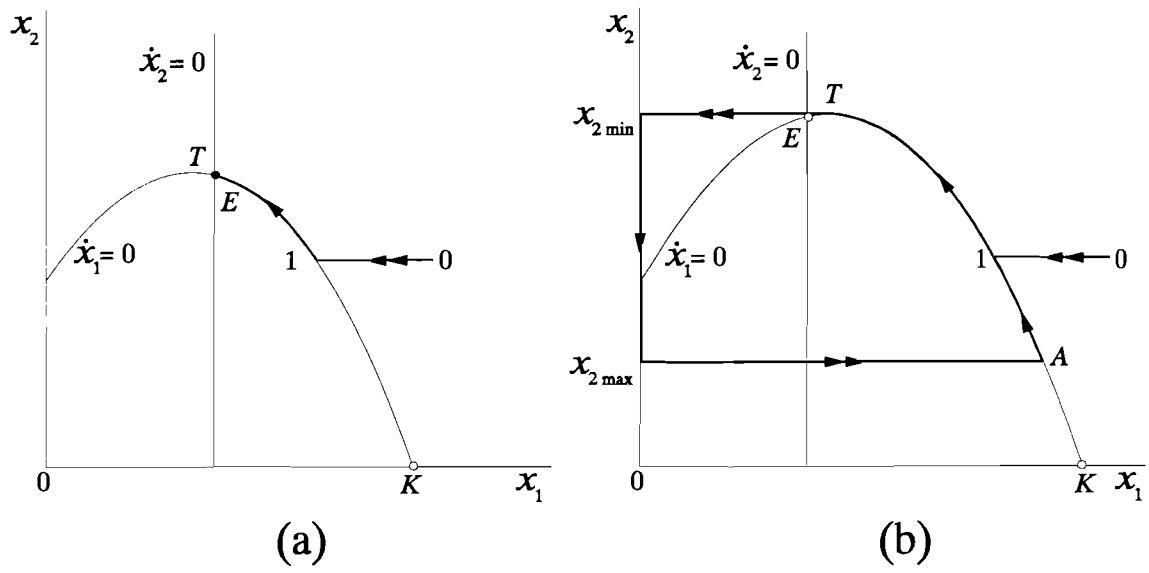


Figure 2



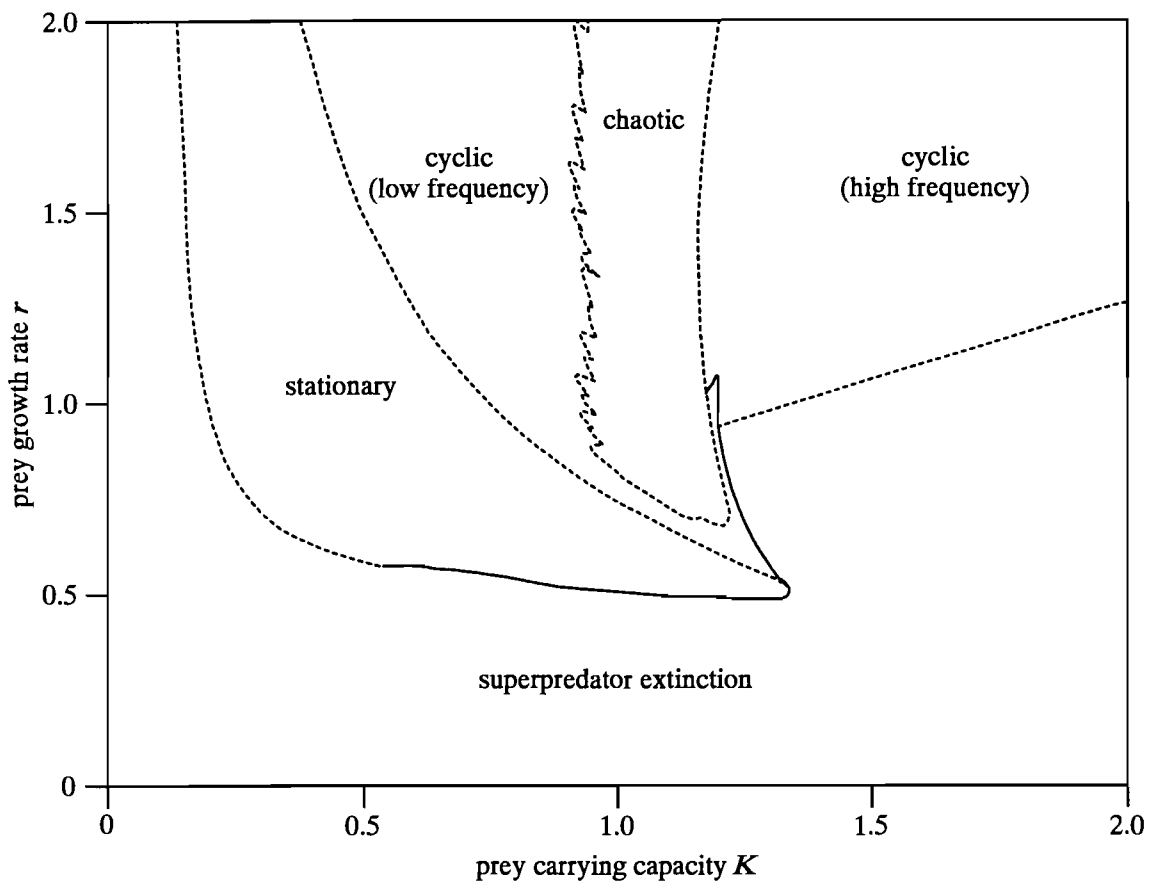


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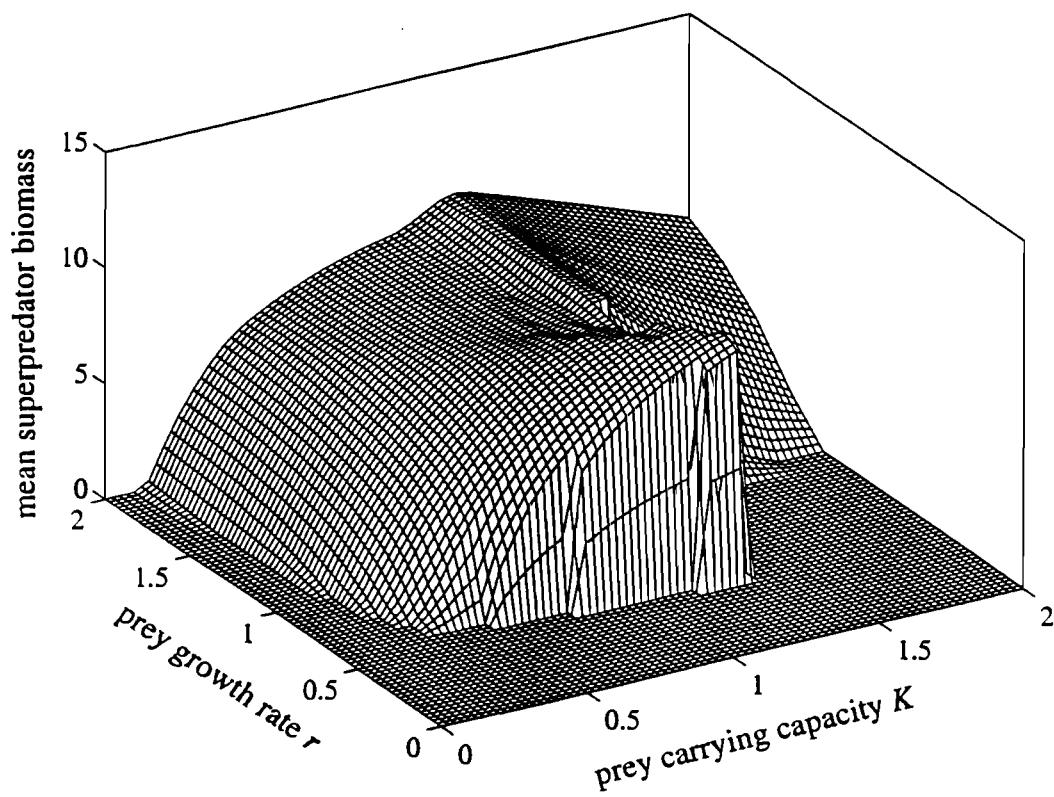


Figure 4

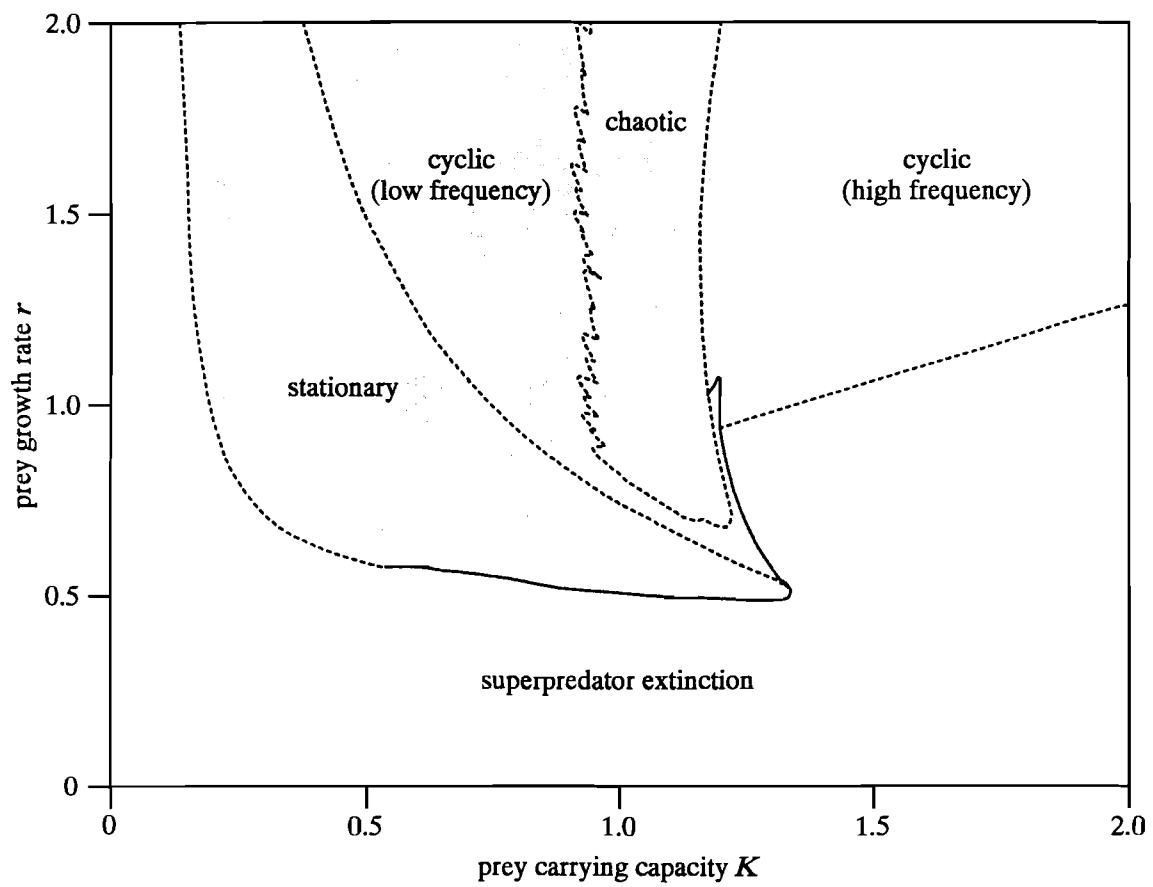


Figure 5

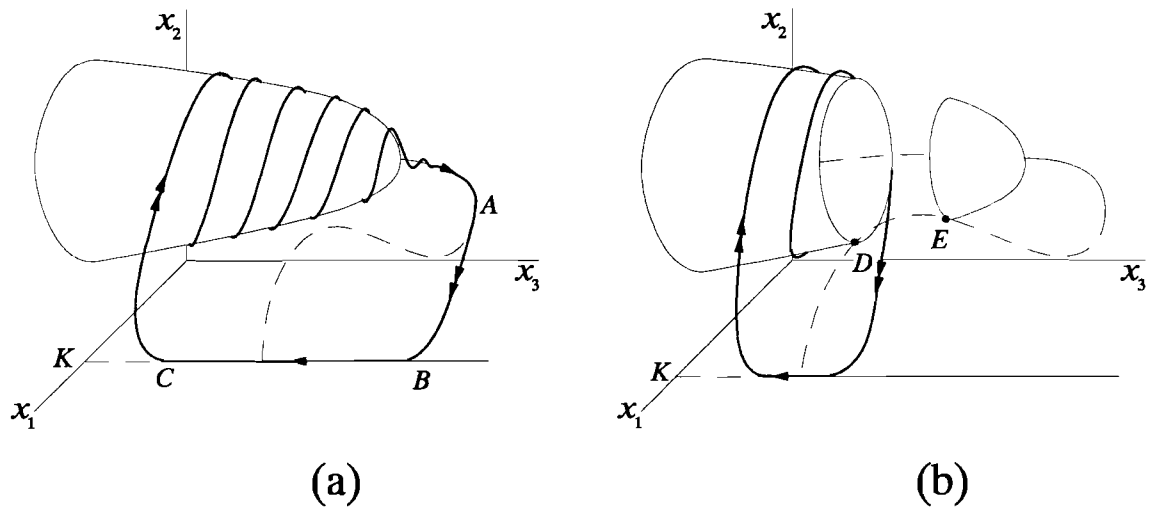


Figure 6

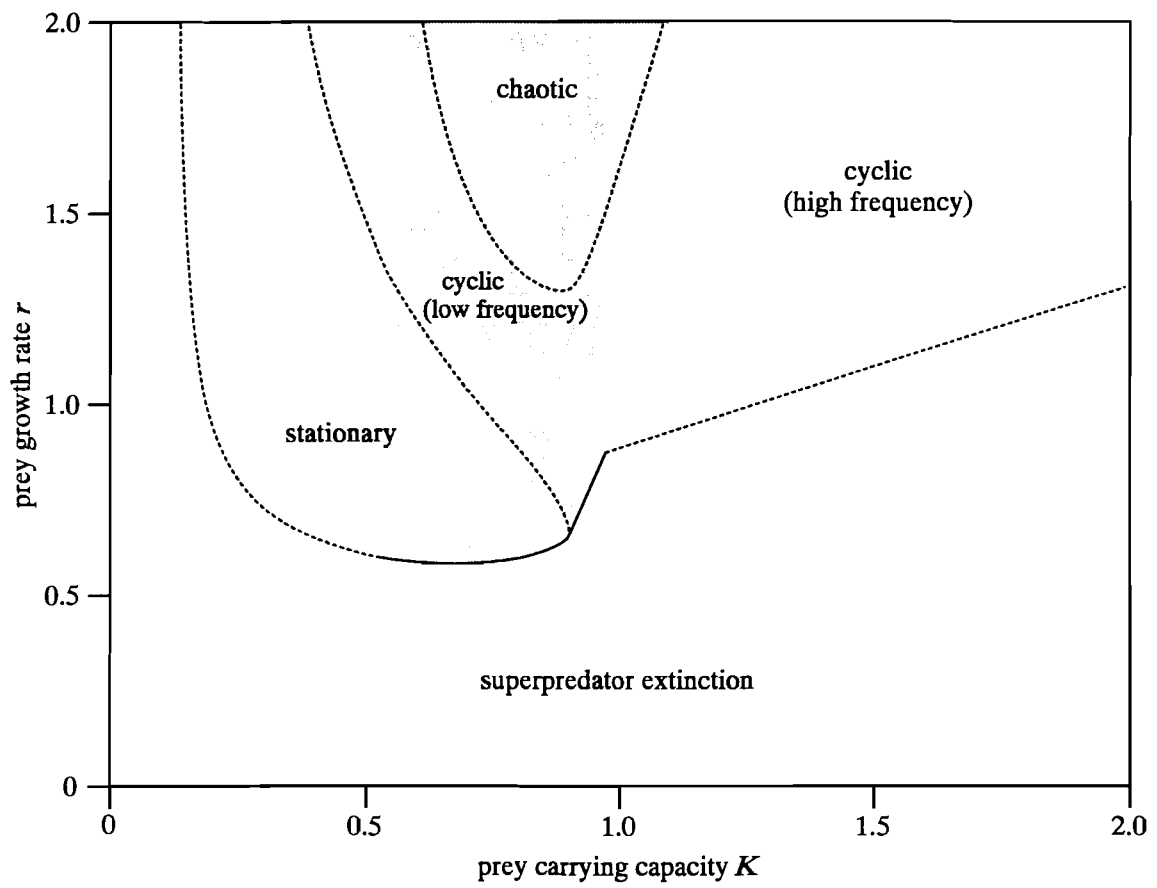


Figure 7