

## Top-predator abundance and chaos in tritrophic food chains

Sergio Rinaldi<sup>1</sup> and Oscar De Feo<sup>2</sup>

<sup>1</sup>CIRITA, Politecnico di Milano,  
Via Ponzio 34/5 1–20133 Milano,  
Italy. E-mail:

rinaldi@elet.polimi.it

<sup>2</sup>DE-CIRC, Federal Institute of  
Technology (EPFL) CH-1015  
Lausanne, Switzerland.

### Abstract

Nonlinear models and laboratory experiments suggest that populations can be chaotic, whereas field data show that a fair proportion of observed populations are not too far from being chaotic. Thus, a natural question arises: do ecosystems enjoy special properties at the edge of chaos? By limiting the analysis to three classes of tritrophic food chains and to the role played by the nutrient available to the bottom of the ecosystem, we show that top-predator mean abundance is maximum at the edge of chaos. The geographical variability of species abundance along nutrient gradients and the dynamic complexity of observed natural populations are consistent with our findings. Effective guidelines for the sustainability of exploited ecosystems are also derived.

### Keywords

Chaos, dynamic complexity, enrichment, models, top-predator abundance, tritrophic food chains.

*Ecology Letters* (1999) 2: 6–10

### INTRODUCTION

A tritrophic food chain composed of prey ( $x$ ), predator ( $y$ ), and top-predator ( $z$ ) populations can be viewed, along with any other ecosystem, as an assembly of interacting plant and animal populations capable of transforming nutrient available in the environment into biomass. Of course, the amount of available nutrient affects the most important features of the ecosystem, among which are dynamic complexity and population abundance (Pimm *et al.* 1991; Abrams & Roth 1994a, b; Abrams *et al.* 1997; De Feo & Rinaldi 1997; Gragnani *et al.* 1998).

Dynamic complexity can be perceived in different ways. A food chain that settles to an equilibrium can be considered simple, but it can also be considered complex if transients toward equilibrium are wild. Here dynamic complexity will not refer to the transients, but only to the asymptotic mode of behaviour of the system, and more precisely to the dimension of its attractor (Strogatz 1994). Thus, there are at most three levels of complexity in tritrophic food chains, because our analysis shows that there are only three possible types of attractors in such systems, namely (from simple to complex) equilibria (stationary regimes), limit cycles (periodic regimes), and strange attractors (chaotic regimes). In order to be consistent with the above definition of dynamic complexity, the abundance will also be associated with the asymptotic regime and not with the transients. More precisely, the top-predator abundance will be that at

equilibrium or its mean value on a limit cycle or on a strange attractor.

Our analysis consists of a detailed study of three models, aimed at extracting common properties. A comparable study in the laboratory can be conceived but not performed, because the number of required experiments is simply too high (our analysis is based on about half a million simulations). Moreover, long experiments, like those required to evaluate mean abundance for different nutrient levels, are very difficult to keep under control, and the difference between a cyclic and a chaotic regime is often difficult (if not impossible) to ascertain (Perry *et al.* 1997).

### MODELS

The three food chain models used in this study are briefly described in this section. The first and the second are particularly suited for terrestrial and aquatic ecosystems, whereas the third one is a metapopulation model describing spatially heterogeneous systems. The equations of the models and the parameter values used in the analysis can be found in the cited references and are also available from the authors.

#### Model 1

The first model, the Rosenzweig–MacArthur model, is composed of a logistic prey and Holling type II predator

and top-predator (Hastings & Powell 1991; McCann & Yodzis 1994; Kuznetsov & Rinaldi 1996; De Feo & Rinaldi 1997). When top-predator dynamics are slow with respect to those of the two other populations, the model can behave chaotically (Hastings & Powell 1991). Moreover, its cycles and strange attractors have the form of a teacup or a cut teacup, as shown in Fig. 1 for increasing values of prey carrying capacity. Teacup cycles are low-frequency cycles involving slow, large swings of the top-predator as well as bursts of fast prey-predator oscillations (Muratori & Rinaldi 1992). By contrast, cut teacup cycles are high-frequency cycles characterized by limited variations of top-predator abundance and permanent fast prey-predator oscillations.

### Model 2

The second model (Kooi *et al.* 1997; Gragnani *et al.* 1998) is the natural extension to three trophic levels of the well-known ditrophic chemostat model proposed by Canale (1969). In such a model the prey feeds on a limiting nutrient ( $n$ ) available in the environment. This is the case of fresh water pelagic food chains, for example. The nutrient (e.g. phosphorus) available at the bottom of the chain is characterized by a mean residence time and is controlled by the nutrient concentration of the inflow. The nutrient equation is simply the balance between inflow, uptake, and outflow, and the uptake per unit of prey (e.g. algae) is assumed to be a Monod function of the nutrient concentration,  $\alpha n/(\gamma + x)$ . In the prey equation the natality is consistently proportional to nutrient uptake, while the predator (e.g. zooplankton) and top-predator (e.g. fish)

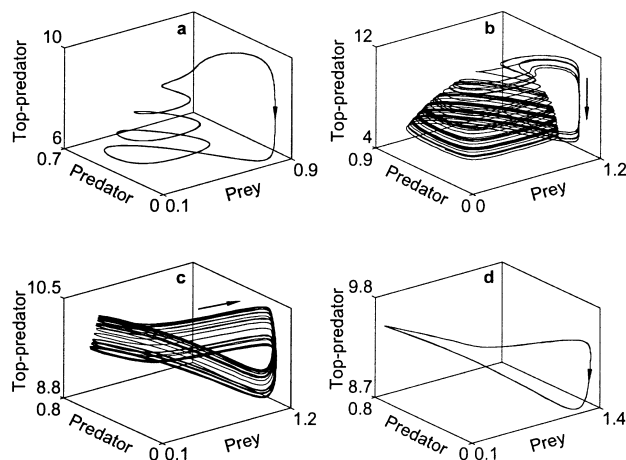
equations are as in the Rosenzweig–MacArthur model. Also, this model has low- and high-frequency cycles and strange attractors for suitable values of the demographic and environmental parameters (Gragnani *et al.* 1998).

### Model 3

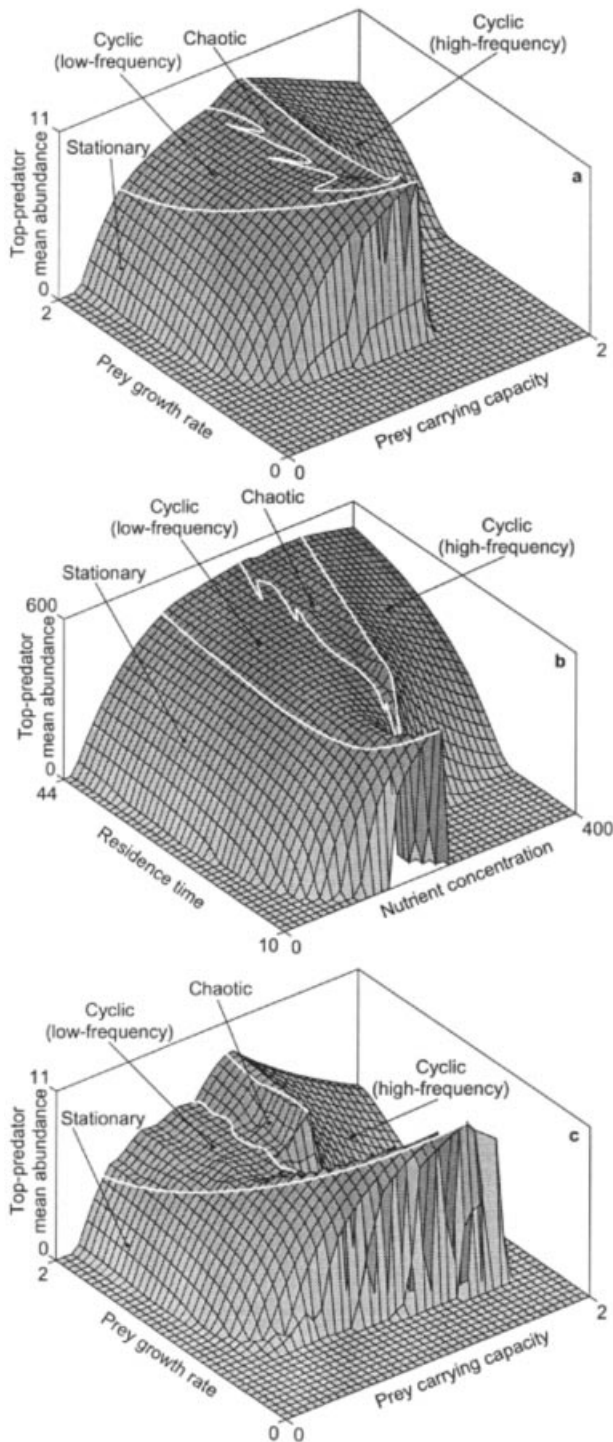
The third model is a fifth-order metapopulation model describing systems characterized by some degree of spatial inhomogeneity (Rinaldi *et al.* 1996). In this model,  $x$ ,  $y$ , and  $z$  are prey patches (e.g. leaves) that are, respectively, free, colonized only by predator (e.g. parasites), and colonized by predator and top-predator (e.g. insects), whereas the remaining two state variables  $Y$  and  $Z$  describe predator and top-predator dispersed in the environment. In the absence of predator dispersers ( $Y = 0$ ), free patches grow logistically toward their carrying capacity, whereas the rate of colonization of free patches is proportional to the abundance of predators dispersed in the environment ( $Y$ ) and to the probability that a disperser comes across a free patch. Such a probability, obviously increasing from zero to one with the density of free patches, is described by means of a Monod function,  $x/(\gamma + x)$ . Similar considerations hold for the rate at which patches occupied by predator are invaded by top-predator dispersers  $Z$ . Finally, the dynamics of  $Y$  and  $Z$  are simply the balance between the inflow rate due to the release of predators and top-predators into the environment from exhausted prey patches, and the mortality rate due to starvation (predation is possible only on patches).

### RESULTS

The results of our analysis are presented in Fig. 2, where the surfaces show how top-predator mean abundance  $\bar{z}$  depends upon two parameters, say  $p_1$  and  $p_2$ . For any pair  $(p_1, p_2)$  there is coexistence if  $\bar{z}(p_1, p_2) > 0$  and top-predator extinction if  $\bar{z}(p_1, p_2) = 0$ . The parameter  $p_1$ , increasing in a NE direction, is a measure of the amount of nutrient available to the ecosystem. This is obvious for the second diagram (aquatic food chain) where  $p_1$  is the nutrient concentration of the inflow, but is also true for the two other diagrams because prey-carrying capacity is positively correlated with the nutrient available to the bottom of the food chain (Oksanen *et al.* 1981; Abrams 1993). The parameter  $p_2$  (prey growth rate and mean residence time) increases in a NW direction and has been included in the analysis in order to prove the general validity of our results. In the first and third cases,  $p_2$  can also be influenced by the nutrient supply, but this possibility will not be considered because it is unimportant (De Feo & Rinaldi 1997).



**Figure 1** The attractor of a Rosenzweig–MacArthur tritrophic food chain for increasing values of prey carrying capacity: (a, d) limit cycles, (b, c) strange attractors; (a, b) low-frequency teacup attractors, (c, d) high-frequency cut teacup attractors.



**Figure 2** Top-predator mean abundance  $\bar{z}$  versus two parameters:  $p_1$  (increasing in a NE direction) and  $p_2$  (increasing in a NW direction). The parameter  $p_1$  is an indicator of the abundance of the nutrient available to the bottom of the food chain. Parts (a)–(c) refer to Models 1, 2, and 3 described in the text. The white curves separating different regimes are bifurcation curves. The figure shows that top-predator mean abundance first increases and then decreases with the abundance of nutrient ( $p_1$ ) and that the maximum is approximately at the edge of chaos.

Each diagram has been produced by simulating each model on a fine grid (10,000 points) in the parameter space ( $p_1, p_2$ ). For the pairs ( $p_1, p_2$ ) giving rise to alternative attractors, the attractor with the highest  $\bar{z}$  was selected because it usually has the largest basin of attraction. A method based on spectral analysis was used to compute the value  $\bar{z}$  associated with strange attractors. The white curves in Fig. 2 separate regions with different asymptotic regimes (i.e. with attractors of different kinds). They cannot be detected through simulation because limit cycles that are close to them are wild and can hardly be distinguished from strange attractors. These curves are the so-called bifurcation curves of a dynamical system (Strogatz 1994) and, indeed, they have been produced through bifurcation analysis, combining the theory of normal forms with powerful numerical continuation techniques (Kuznetsov 1995). The function  $\bar{z}(p_1, p_2)$  is discontinuous on a bifurcation curve if the bifurcation is catastrophic. In Fig. 2 some segments of the bifurcation curves separating chaotic regimes from top-predator extinction are catastrophic. This means that microscopic nutrient variations can trigger macroscopic transitions between different attractors.

The three surfaces shown in Fig. 2 share the following properties, which can be easily discovered if one observes how  $\bar{z}$  varies with respect to  $p_1$  (nutrient) for constant and sufficiently high values of  $p_2$ : (i) Dynamic complexity first increases with nutrient (from stationary to chaotic regimes passing through low-frequency cyclic regimes) and then decreases (from chaotic to high-frequency cyclic regimes); (ii) top-predator mean abundance first increases and then decreases with nutrient; (iii) top-predator mean abundance is maximum with respect to the nutrient at the edge of chaos, close to high-frequency cyclic regimes.

Of course, the surfaces in Fig. 2 vary with the parameter settings. Nevertheless, a great number of numerical experiments (not reported here) have shown that properties (i)–(iii) remain valid provided the time responses of the three populations increase from bottom to top.

## DISCUSSION

The above results satisfy the high level of synthesis that is required in population dynamics today. Even taking into account the scepticism that accompanies results derived from modelling exercises, properties (i)–(iii) are of great interest because they are valid in very common models used every day to interpret data, perform forecasts, and derive management policies for food chain systems. Nevertheless, different results might hold for different models.

Our discoveries can be used to support or derive other properties of ecosystems, e.g. the geographical variability

of species abundance. For this, let us assume that the amount of nutrient effectively available to the lowest trophic level of many aquatic and terrestrial food chains is determined by local geophysical and climatic characteristics, which, in turn, depend on latitude, altitude, and depth. Thus, even if all demographic parameters are constant in space, in view of property (ii) we should expect that species abundance varies in space. In particular, we should expect that top-predator mean abundance first increases and then decreases along gradients of basal productivity.

An intriguing property recently formulated by Ellner & Turchin (1995), namely the fact that observed field populations are chaotic or almost chaotic, is also consistent with our findings. In fact, let us assume that, in order to save time and effort, surveys are often performed at latitudes, altitudes, or depths where species are most abundant. Then, under these conditions our property (iii) would immediately imply that surveyed populations are chaotic or almost chaotic. Notice that in this way the result is derived without invoking evolutionary theories or thermodynamics principles (Ferrière & Gatto 1993; Kauffman 1993; Jorgensen 1995).

Finally, the properties (i)–(iii) have interesting consequences in the case of food chains exploited at constant effort, where managers can decide to enrich or impoverish the system by increasing or decreasing the supply of nutrient. In such a case, food yield is proportional to top-predator abundance and the model remains the same (module an increase of top-predator mortality). Therefore, plots like those in Fig. 2 can be regarded as plots of mean food yield. Thus, if the aim of the management is the maximization of mean food yield, statements (i)–(iii) suggest to enrich if the regime is stationary, cyclic at low-frequency, or chaotic, and to impoverish otherwise. Such a rule is very attractive because it can be applied in the absence of precise estimates of system parameters. Figure 2 shows, however, that the mean yield can collapse shortly after its maximum. Hence the maximization of the mean yield is risky, as pointed out by models of other exploited ecosystems and by dramatic failures experienced in natural resources management (Ludwig *et al.* 1993). Thus, a safer operational rule might be to enrich stationary food chains until some turbulence is detected in their dynamics. The systematic application of this rule would force the system to be suboptimal but increase the chances of its sustainability.

#### ACKNOWLEDGEMENTS

Support of the Italian Ministry of Scientific Research and Technology, contract Teoria dei sistemi e del controllo, and of Fondazione ENI Enrico Mattei (FEEM), Milano, Italy is gratefully acknowledged.

#### REFERENCES

- Abrams, P.A. (1993). Effect of increased productivity on the abundances of trophic levels. *Am. Naturalist*, 141, 351–371.
- Abrams, P.A. & Roth, J.D. (1994a). The responses of unstable food chains to enrichment. *Evol. Ecol.*, 8, 150–171.
- Abrams, P.A. & Roth, J.D. (1994b). The effects of enrichment of three species food chains with non-linear functional responses. *Ecol.*, 75, 1118–1130.
- Abrams, P.A., Namba, T., Mimura, M. & Roth, J.D. (1997). The relationship between productivity and population densities in cycling predator-prey systems. *Evol. Ecol.*, 11, 371–373.
- Canale, R.P. (1969). Predator-prey relationships in a model for the activated process. *Biotech. Bioengineering*, 11, 887–907.
- De Feo, O. & Rinaldi, S. (1997). Yield and dynamics of tritrophic food chains. *Am. Naturalist*, 150, 328–345.
- Ellner, S. & Turchin, P. (1995). Chaos in a noisy world: new methods and evidence from time series analysis. *Am. Naturalist*, 145, 343–375.
- Ferrière, R. & Gatto, M. (1993). Chaotic population dynamics can result from natural selection. *Proc. Royal Soc. London B*, 251, 33–38.
- Gagnani, A., De Feo, O. & Rinaldi, S. (1998). Food chains in the chemostat: relationships between mean yield and complex dynamics. *Bull. Math. Biol.*, 1, 1–16.
- Hastings, H. & Powell, T. (1991). Chaos in three species food chain. *Ecol.*, 72, 896–903.
- Jorgensen, S.E. (1995). The growth rate of zooplankton at the edge of chaos: ecological models. *J. Theor. Biol.*, 175, 13–21.
- Kauffman, S.A. (1993). *Origin of Order: Self Organization and Selection in Evolution*. Oxford: Oxford University Press.
- Kooi, B.W., Boer, M.P. & Kooijman, S.A. (1997). Complex dynamic behaviour of autonomous microbial food chains. *J. Math. Biol.*, 36, 24–40.
- Kuznetsov, Y.A. (1995). *Elements of Applied Bifurcation Theory*. New York: Springer-Verlag.
- Kuznetsov, Y.A. & Rinaldi, S. (1996). Remarks on food chain dynamics. *Math. Bioscience*, 134, 1–33.
- Ludwig, D., Hilborn, R. & Walters, C. (1993). Uncertainty, resource exploitation, and conservation: Lessons from history. *Science*, 260, 17–36.
- McCann, K. & Yodzis, P. (1994). Biological conditions for chaos in a three species food chain. *Ecol.*, 75, 561–564.
- Muratori, S. & Rinaldi, S. (1992). Low-and high-frequency oscillations in three-dimensional food chain systems. *SIAM J. Appl. Math.*, 52, 1688–1706.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Naturalist*, 118, 240–261.
- Perry, J.M., Woiwod, I.P., Smith, R.H. & Morse, D. (1997). Estimating chaos in an insect population. *Science*, 276, 1881–1882.
- Pimm, S.L., Lawton, J.H. & Cohen, J.E. (1991). Food web patterns and their consequences. *Nature*, 350, 669–674.
- Rinaldi, S., Dal Bo, S. & De Nittis, E. (1996). On the role of body size in a tri-trophic metapopulation model. *J. Math. Biol.*, 35, 158–176.
- Strogatz, S.H. (1994). *Nonlinear Dynamics and Chaos with Applications to Physics, Biology, Chemistry and Engineering*. Reading: Addison-Wesley.

Editor, M. Loreau

Manuscript received 3 August 1998

First decision made 19 August 1998

Manuscript accepted 31 August 1998

#### **BIOSKETCH**

Sergio Rinaldi is interested in theoretical population dynamics. At the moment he is involved in studies on tritrophic food chains, plankton dynamics, and forest ecosystems.