Biological Invasions (2005) 7: 845–861
DOI 10.1007/s10530-005-5213-y

Invasion of a top predator into an epipelagic ecosystem can bring a paradoxical top-down trophic control

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Received 11 October 2004; accepted in revised form 22 February 2005

Key words: biological invasion, marine ecosystem model, paradoxical trophic response, plankton, top predator, top-down trophic control

Abstract

We apply mathematical modeling to explore different scenarios of invasion of a top predator (carnivorous zooplankton or planktivorous fish) into an epipelagic plankton ecosystem. We use a ‘minimal’ model of three nonlinear ordinary differential equations (nutrient–phytoplankton–herbivores) with the top predator density as a time-dependent parameter. The ecosystem shows different types of response, which can be described in terms of top-down trophic control. Our investigation indicates that under certain conditions the plankton ecosystem model demonstrates a surprising kind of response: in a wide range of realistic ecosystem parameters the invasion of the top predator leads to a prominent increase in the average density of zooplankton and to a resulting decrease of phytoplankton density. This phenomenon is opposite to the ‘typical’ top–down control when the carnivore pressure decreases zooplankton density which, in turn, increases phytoplankton biomass. We call the revealed type of top-down control ‘paradoxical’. Examples of such a response in natural aquatic ecosystems were reported earlier but no clear explanation has been provided hitherto. In this paper, we analyze possible mechanisms of ‘paradoxical top–down control’ and show that it can occur in eutrophic epipelagic ecosystems subject to high rate of cross-pycnocline exchange.

Introduction

Understanding the possible consequences of a biological invasion is an issue of increasing importance in modern ecology (Drake et al. 1989; Shigesada and Kawasaki 1996; Sakai et al. 2001; Fagan et al. 2002). Invasion of exotic species can lead to catastrophic changes in the biomass and biodiversity of the community. An impressive example of invasion in a marine ecosystem is the invasion of the ctenophore *Mnemiopsis leidyi* into the Black Sea in the late 1980s (Vinogradov et al. 1989), which resulted in a drastic decrease of zooplankton biomass and density and nearly brought several fish species to extinction. The consequences of invasion can be especially dramatic when the invasive species constitutes a new trophic level of the ecosystem (Yodzis 1989) or when, as a result of invasion, one of the trophic levels is substituted by new species (McPeek 1998). In this paper, we consider different scenarios of invasion of a top predator (carnivorous zooplankton or planktivorous fish) into a marine plankton community when the 'new' predator appears to be a more effective consumer than the original top predator species.

The response of a plankton community to invasion of new carnivorous zooplankton or planktivorous fish species is subject to complex interactions between the principal trophic levels: limiting nutrient, phytoplankton as the primary producer, herbivorous zooplankton grazing phytoplankton, and the top predator consuming herbivorous zooplankton. The feedback between different trophic levels includes both positive and negative correlations. In particular, 'bottom–up' and 'top–down' types of trophic control have been described (Leibold et al. 1997; Shurin et al. 2002). An important example of 'bottom–up' control is the growth of phytoplankton biomass resulting from increased nutrient concentration (Eppley et al. 1979) which, in turn, can lead to the growth of zooplankton biomass. On the other hand, the consumer biomass can operate as the main factor controlling the biomass of its prey; in this case the negative correlation between these two trophic levels is called 'top–down' control (e.g., Brett and Goldman 1997; Worm and Myers 2003). In a more sophisticated case, an indirect impact of top predators on plants via herbivores is observed; this type of relation is called a 'trophic cascade'. Examples of trophic cascades have often been observed in freshwater aquatic ecosystems when introduction of planktivorous fish to lakes or fish ponds was negatively correlated with subsequent changes in zooplankton biomass and positively correlated with changes in phytoplankton biomass (Vanni and Layne 1997; Sarvala et al. 1998; Lammens 1999).

At the same time, in contrast to freshwater plankton communities, in marine ecosystems trophic cascades are usually weak (Shurin et al. 2002). For instance, the comprehensive study of marine fishery by Micheli (1999) indicated no significant correlation between phyto- and zooplankton densities. The absence of prominent trophic cascades in marine ecosystems is sometimes explained by a complex community structure, e.g., by the existence of parallel food chains (Stibor et al. 2004).

A 'typical' response of different ecosystems to an increase in carnivorous predators pressure consists in a decrease of the biomass of herbivores and an increase in the biomass of plants (Brett and Goldman 1997; Vanni and Layne 1997; Shurin et al. 2002). However, a more thorough analysis indicates that the situation is not as simple as it looks at first glance and ecosystems can exhibit other types of trophic response, too. An increase in fish trophic pressure sometimes leads to an increase in zooplankton biomass in lakes (Leibold et al. 1997). Removal of a top predator can result in a prominent decrease of the biomass of herbivores in a terrestrial ecosystem (Halaj and Wise 2001). Alimov (2000) reported a counter-intuitive phenomenon in epipelagic ecosystems that consisted of an increase of herbivorous zooplankton biomass resulting from an increased pressure of carnivores and fish. Below we call this type of feedback a 'paradoxical top–down control'.

Although 'paradoxical top–down control' in ecosystems is relatively rare, it has been repeatedly observed and reported in the ecological literature. However, no clear explanation of this phenomenon has been suggested so far and the mechanisms of 'paradoxical top–down control' are still poorly understood (Leibold et al. 1997). In this paper, we provide a possible explanation of 'paradoxical top–down control' in a marine epipelagic plankton community based on a conceptual mathematical model of a marine ecosystem.

The important fact for understanding the dynamics of marine ecosystems is that, apart from the complexity of trophic interactions, marine plankton communities are highly influenced by the physical environment, primarily by stratification of the water column. A typical marine pelagic ecosystem is restricted to the upper, well-illuminated (euphotic) ocean layer separated from the deeper layers by the pycnocline (the layer of sharp density gradient) which hinders the exchange between the layers. The nutrient flux from the deep layer stimulates phytoplankton growth; at the same time, some part of the organic matter produced sinks into the deep layer and is lost from the epipelagic food web. In this paper, we will show that these 'semi-transparent' ecosystem boundaries and the complexity of interactions between the system components can lead to new features of marine epipelagic plankton community which play an important role in the top–down relations between the trophic levels. As a result, the consequences of top predator invasion into an epipelagic community can be completely different from the intuitively expected pattern.

We describe the plankton community by a conceptual or 'minimal' model (cf. Edwards and Brindley 1996, 1999), consisting of three differential equations for nutrients, phytoplankton and herbivores, respectively, with the density of top predator as a time-dependent parameter controlling exploitation of herbivores. Similar approaches have been used by a number of authors (Evans and Parslow 1985; Caswell and Neubert 1998; Edwards and Yool 2000). Our numerical simulations show that, under certain conditions, the response of a plankton community to top a predator pressure becomes anomalous: in a wide range of system parameters the invasion of a top predator results in a prominent increase in the average zooplankton biomass and in a significant decrease in the average phytoplankton biomass. This 'paradoxical top–down control' is shown to appear for the parameters corresponding to eutrophic epipelagic ecosystems characterized by a high rate of cross-pycnocline exchange.

Model formulation

The functional structure of the model is shown in Figure 1. The original system, i.e., the system before invasion, is described in terms of three main compartments in a spatially homogeneous upper mixed layer: limiting nutrient, phytoplankton, and herbivorous zooplankton. The upward arrow indicates the nutrient influx due to inter-layer turbulent exchange, the downward arrows indicate the losses of matter due to its washing out of the system, other arrows indicate the fluxes of matter between the compartments. The invading top predator (carnivorous zooplankton or fish) is shown by the dashed ellipse.

First, we consider the model without a top predator. This consists of three ordinary differential equations for three dynamical variables, i.e., the densities of limiting nutrient (N), phytoplankton (P) and herbivorous zooplankton (Z) (cf. Steele and Henderson 1992; Edwards and Brindley 1996, 1999):

$$\frac{dN}{dt} = d(N_0 - N) - r\frac{N}{K_N + N}P + m_P P + \gamma m_Z Z + \alpha\mu\frac{P}{K_P + P}Z, \tag{1}$$

$$\frac{dP}{dt} = \omega r\frac{N}{K_N + N}P - m_P P - (d_1 + d)P - \mu\frac{P}{K_P + P}Z, \tag{2}$$

$$\frac{dZ}{dt} = \eta\mu\frac{P}{K_P + P}Z - m_Z Z. \tag{3}$$

Limiting nutrient N is transported into the upper mixed layer from the deeper layer, where its concentration N_0 is assumed to be constant. The rate

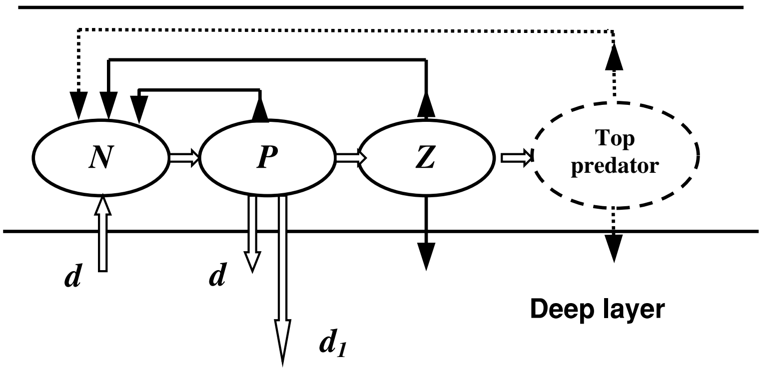

Figure 1. Structure of the nutrient–phytoplankton–herbivorous–fish/carnivorous model. The original system consists of three compartments: nutrient (N), phytoplankton (P), zooplankton (Z). Invasion of a top predator, carnivorous zooplankton or fish, is represented by the dashed ellipse. Arrows show flows of matter through the system.

of mixing between the two layers is described by the coefficient d. Phytoplankton consumes nutrient at the rate given by $rNP/(N+K\mathrm{N})$. The last three terms in Equation (1) describe the release of nutrient due to, respectively, decomposition of phytoplankton, decomposition of zooplankton and excretion of zooplankton, which is proportional to the rate of phytoplankton consumption with the coefficient α.

Phytoplankton growth is described by the first term in Equation (2), where K_{N} is the half-saturation nutrient density, r is the maximum growth rate and ω is the efficiency coefficient. Following Edwards and Brindley (1999), we further assume $\omega = 1$. For the sake of simplicity, we do not consider here the influence of illumination on photosynthesis. Phytoplankton biomass decreases due to natural mortality and respiration described by $m_{\mathrm{P}}P$, due to the outflow from the system via turbulent exchange between the two layers (dP), sinking (d_1P) and grazing described by the last term in Equation (2). We assume that zooplankton trophic response is Holling type II (cf. Scheffer 1991; Doveri et al. 1993) with maximum grazing rate μ and the half-saturation constant K_{P}. The efficiency of phytoplankton consumption by zooplankton is described by coefficient η, see Equation (3). Zooplankton biomass decreases due to its natural mortality and respiration processes described by the term $m_{\mathrm{Z}}Z$.

Below we refer to Equations (1–3) as 'N–P–Z model' or 'N–P–Z system'.

Note that, when considering the N–P–Z model, we do not necessarily assume that carnivorous zooplankton or planktivorous fish are absent in the system. Instead, we assume that the invasive top predator species is a more effective zooplankton consumer than the species constituting the top trophic level before invasion. The initial top predation is taken into account by means of additional mortality, i.e., included implicitly into the term $m_{\mathrm{Z}}Z$.

Biological invasion of a top predator (carnivorous zooplankton or planktivorous fish) into the original N–P–Z system is described in our model in the following way (cf. Edwards and Yool 2000; Scheffer et al. 2000). We do not consider the population of top predator explicitly; instead, we add in Equation (3), a term describing top predator pressure on zooplankton, described by trophic response of Holling type III (Scheffer 1991) and also add the corresponding excretion term into Equation (1). The model looks like this:

$$\begin{aligned}\frac{dN}{dt} &= d(N_0 - N) - r\frac{N}{K_{\mathrm{N}} + N}P + m_{\mathrm{P}}P \\ &\quad + \gamma m_{\mathrm{Z}}Z + \alpha\mu\frac{P}{K_{\mathrm{P}} + P}Z + \beta\delta(t)\frac{Z^2}{Z^2 + K_{\mathrm{Z}}^2}\end{aligned} \tag{4}$$

$$\begin{aligned}\frac{dP}{dt} &= r\frac{N}{K_{\mathrm{N}} + N}P - m_{\mathrm{P}}P - (d_1 + d)P \\ &\quad - \mu\frac{P}{K_{\mathrm{P}} + P}Z,\end{aligned} \tag{5}$$

$$\frac{dZ}{dt} = \eta\mu\frac{P}{K_{\mathrm{P}} + P}Z - m_{\mathrm{Z}}Z - \delta(t)\frac{Z^2}{Z^2 + K_{\mathrm{Z}}^2} \tag{6}$$

where δ(t) and K_{Z} are the parameters describing the top predation, β describes top predator excretion. Following Doveri et al. (1993), we assume top predator excretion β to be approximately equal to zooplankton excretion α.

Invasion of a top predator is not an instantaneous process; we assume that $\delta = 0$ for $t < 0$, then it gradually increases with time up to a certain δ_0. We choose the simplest way to parameterize the invasion using the piecewise linear function:

$$\delta(t) = \delta_0 t/t_0, \ \ t \in [0, t_0], \ \delta(t) = \delta_0, \ \ t > t_0 \tag{7}$$

where t_0 can be regarded as the characteristic time of top predator establishment.

We use realistic values of model parameters obtained from different sources and summarized in (Edwards and Brindley 1999; see Table 1), with nitrogen as limiting nutrient (with appropriate conversion into g carbon m^{-3} units, g C m^{-3}). Note that parameters δ_0 and K_{Z}, describing the intensity of top predation, are not given in Table 1, since δ_0, which is actually the product of the top predator density and the maximum top predation rate, can vary over a wide range. Similarly, the half-saturation constant K_{Z} for fish and zooplankton species varies as much as two orders of magnitude (Doveri et al. 1993). However, this is not a drawback of our model; on the contrary, it makes it possible to describe an invasion of different species with different characteristics.

Table 1. System parameters and ranges of their values for N–P–Z model.

Parameter	Symbol	Parameter range
Cross-pycnocline exchange rate	d	0.008–0.13 day^{-1}
Half-saturation constant for N uptake	K_{N}	0.02–0.15 g C m^{-3}
Half-saturation constant for Z grazing	K_{P}	0.02–0.10 g C m^{-3}
Regeneration of N from decomposition of Z	γ	0.5–0.9
N concentration in the deep layer	N_0	0.1–2.0 g C m^{-3}
P respiration rate	m_{P}	0.05–0.15 day^{-1}
Z respiration rate	m_{Z}	0.065–0.15 day^{-1}
Maximum P growth rate	r	0.2–1.5 day^{-1}
P sinking rate	d_1	0.032–0.08 day^{-1}
Z excretion coefficient	α	0.5–0.9
Z growth efficiency	η	0.2–0.5
Maximum Z growth rate	μ	0.6–1.4 day^{-1}

Results

In order to understand the consequences of the invasion of a top predator into a plankton system, we begin by considering the basic features of the N–P–Z system, i.e., the system without fish/carnivore trophic level.

Using standard analytical approaches (cf. Kuznetsov 1995), it is easy to show that the system (1–3), under some constraints on parameter values, possesses only one steady state in the first octant of the phase space ($N > 0$, $P > 0$, $Z > 0$); this state can be either stable or unstable.

However, for a system of nonlinear differential equations such as (1–3), analytical methods usually give only meager information. Numerical simulations of Equations (1–3) for parameters that are allowed to vary around the realistic values given in Table 1 show that this relatively simple plankton model exhibits complex dynamics, including multiple attractors and chaotic oscillations.

Extensive numerical study of the N–P–Z system was done by examining a few thousand different parameter sets. Among all regimes where at least one component does not go extinct, we found two main regimes of the system dynamics, i.e., periodic oscillations of N–P–Z densities along a stable limit cycle and relaxation of the densities to the globally stable steady state, which occurred altogether in more than 99% of computer experiments. Numerical simulations giving examples of these regimes are shown in Figure 2a (obtained for $d = 0.05$) and b ($d = 0.01$), respectively, other parameters are: $K_{\mathrm{N}} = 0.03$; $K_{\mathrm{P}} = 0.05$; $\gamma = 0.5$; $N_0 = 1$; $m_{\mathrm{P}} = 0.075$; $m_{\mathrm{Z}} = 0.1$; $r = 1$; $d_1 = 0.05$; $\alpha = 0.5$; $\eta = 0.25$; $\mu = 0.8$, units are given in Table 1.

Unfortunately, the large number of parameters in the system does mean that it is not possible to study its global bifurcation structure in the whole parameter space. Instead, we choose two controlling parameters of clear ecological meaning, N_0 and d, and study in detail the bifurcation structure of the N_0–d plane, keeping the other parameters fixed. The choice of N_0 and d is justified by the widely accepted fact that the dynamics of plankton systems is to a large extent governed by environmental conditions, in particular by the availability of nutrients. In our model, the availability of nutrients apparently depends on their concentration N_0 in the deeper layer and the intensity of inter-layer exchange d, thus high values and low values of N_0, d correspond to eutrophic and oligotrophic marine ecosystems, respectively.

This prediction is confirmed by the results of our computer experiments. Figure 2c represents two-parametric bifurcation portrait in the N_0–d plane; other parameters are the same as in Figures 2a and b. Here domain 1 corresponds to oscillatory dynamics and domain 2 corresponds to the globally stable steady state. In domain 3 below curve S, there is no attractor situated in the interior of the first octant so that zooplankton cannot survive, the globally stable steady state appears/disappears when crossing curve S via transcritical bifurcation. (Stability exchange takes

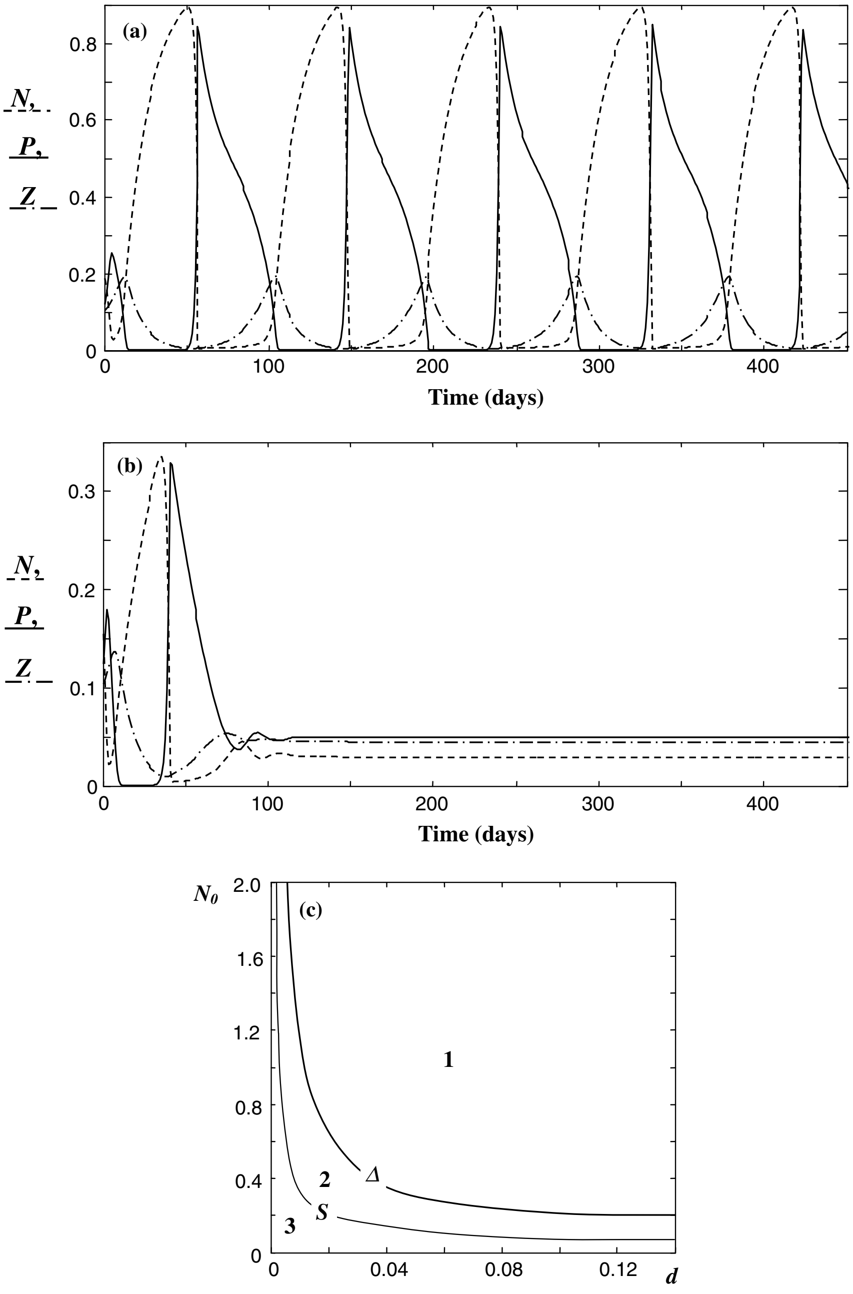

Figure 2. Dynamics of the N–P–Z system before introduction of top predator: (a) species density vs. time in the regime of stable periodical oscillations observed for $N_0 = 1$ and $d = 0.05$, other parameters are: $K_N = 0.03$, $K_P = 0.05$, $\gamma = 0.5$, $m_P = 0.075$, $m_Z = 0.1$, $r = 1$, $d_1 = 0.05$, $\alpha = 0.5$, $\eta = 0.25$ and $\mu = 0.8$, units are given in Table 1; (b) species density vs. time in the regime of relaxation to a stable stationary state observed for $N_0 = 1$ and $d = 0.01$, other parameters the same as above; (c) Map in N_0–d plane, parameters are the same as above. Domain 1 corresponds to periodic oscillations, domain 2 corresponds to a globally stable steady state, in domain 3 zooplankton goes extinct.

place between the trivial state (with $Z = 0$) and the nontrivial state, for which $Z < 0$ in domain 3 and $Z > 0$ in domains 1 and 2.) The transition from stationary stable state to oscillatory dynamics occurs across curve Δ via supercritical Hopf bifurcation, i.e., via the birth of a stable limit cycle. The cycle then grows in amplitude as d and N_0 increase.

Domain 1 thus corresponds to eutrophic ecosystems with large oscillations of species densities (prominent plankton blooms in the ocean are typical of eutrophic regions, Flynn et al. 1997; Lucas et al. 1999) and domains 2 and 3 correspond to oligotrophic ecosystems with stable dynamics where, for parameters from domain 3, the system productivity is too low to support zooplankton existence. Transition from domain 2 to domain 1 is followed by destabilization of the system dynamics and the appearance of large-amplitude oscillations. This phenomenon (called the 'paradox of enrichment') is typical of different aquatic systems and was studied theoretically (Rosenzweig 1971; Gilpin 1972) and observed experimentally (Luckinbill 1974).

Note that, although the diagram shown in Figure 2c is obtained for a particular parameter set (see Figures 2a and b), it remains qualitatively the same for most of the numerical experiments, as long as the parameter values stay within the ranges given in Table 1. In other words, the size of those domains (in the subspace of the other parameters: K_N, K_P, γ, m_P, m_Z, r, d_1, α, η, μ), which correspond to N_0–d diagrams with more complex behavior is extremely small.

Impact of top predator on system stability and complexity

Our numerical simulations show that invasion of a top predator significantly affects the system dynamics.

First, introduction of a top predator into the N–P–Z system remarkably increases the system's complexity. For the sake of simplicity, in this subsection we do not consider the transient stage and assume that the top predator has already invaded into the plankton community and attained its carrying capacity so that $\delta(t) = \delta_0$.

Figure 3 shows N_0–d diagram obtained for $K_Z = 0.03$ and $\delta_0 = 0.004$. Here Figure 3a shows the whole bifurcation portrait and Figure 3b gives more details of the part of the plane inside the thick-curve rectangle. Instead of single curve Δ (cf. Figure 2c), we now have a family of curves and a complicated structure where different domains correspond to different system properties. For ecological reasons, in order to classify different types of system dynamics below, we focus on attracting manifolds only, such as stable steady states, stable limit cycles and strange attractors, paying no attention to unstable equilibria and unstable limit cycles. For the parameters from domain 3, there is no attractor inside the first octant so that zooplankton cannot survive. In domains 2 and 2^* (the meaning of the asterisks will be explained below), the only attractor is a single, globally stable stationary state. Domain 4 is characterized by the coexistence of two stable stationary states. Domains 1 and 1^* correspond to oscillatory dynamics, either periodic or chaotic, with a single attractor. In domains 5 and 5^*, a stable stationary state coexists with either a stable limit cycle or with a chaotic attractor so that the system dynamics depends on initial conditions.

The nature of the bifurcation curves is as follows. The meaning of curve S and its position in the N_0–d diagram are the same as in the original N–P–Z system (cf. Figure 2c). The birth/disappearance of the steady states occurs when crossing the curves $\boldsymbol{l}_1$ and $\boldsymbol{l}_2$ (a 'fold bifurcation', cf. Kuznetsov 1995). $\boldsymbol{N}$ is the Hopf bifurcation curve. The two branches of the curves $\boldsymbol{l}_3$ show the boundaries of the region where chaotic and periodic oscillations alternate, the first period-doubling bifurcation occurs when crossing $\boldsymbol{l}_3$. However, inside the small domain bounded by curves $\boldsymbol{l}_4$ (see Figure 3b), oscillations disappear due to a homoclinic bifurcation when a single steady state becomes a global attractor; this domain is qualitatively similar to domain 2 on the left of $\boldsymbol{l}_1$ and thus bears the same number.

The meaning of the asterisks is as follows. Symbol 1^* means that the oscillations in the system become complex (after the first period-doubling bifurcation); in this domain chaotic oscillations alternate with windows of periodicity. In contrast, in domain 1 oscillations are purely periodical. Domain 5^* has a similar meaning but complex oscillations coexist with a stable steady state. Notation

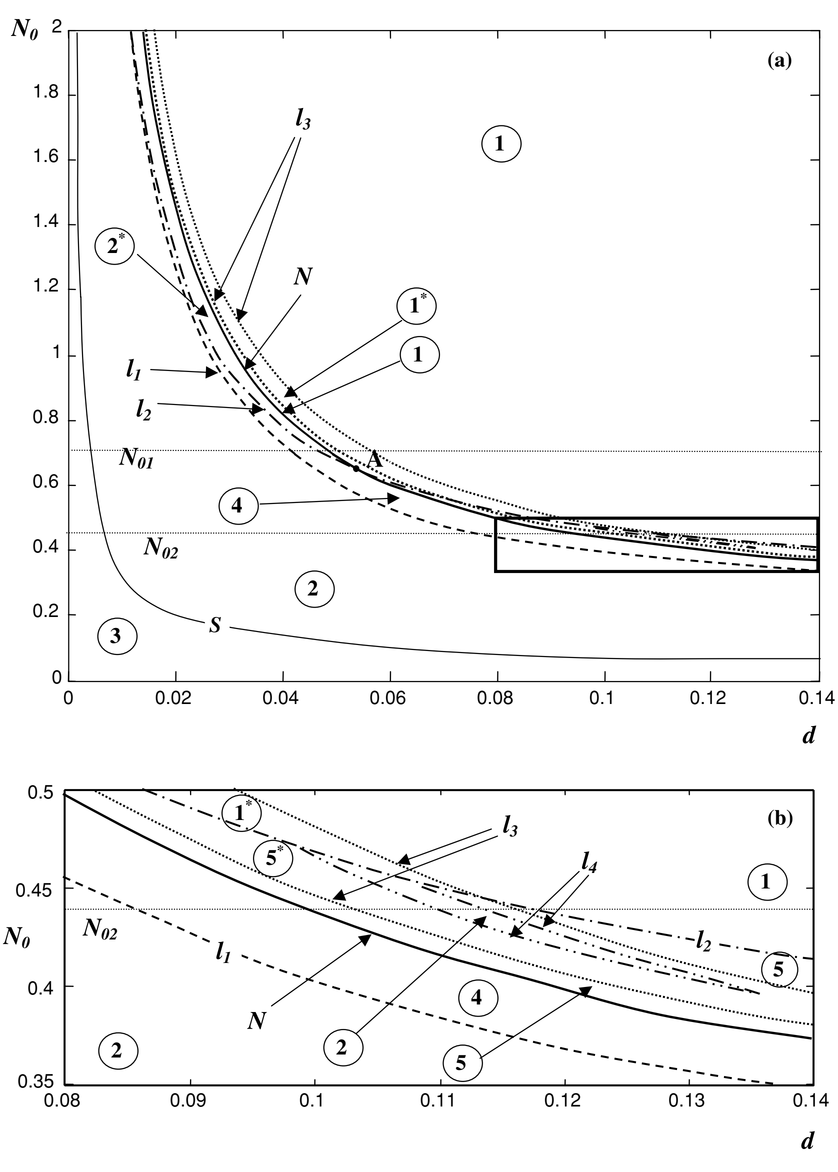

Figure 3. Map in N_0–d plane corresponding to the plankton system after the top predator invasion ($K_Z = 0.03$, $\delta_0 = 0.004$, other parameters are the same as in Figure 2c) shown (a) as a whole and (b) in more detail for the part of the plane inside the bold rectangle. The meaning of the curves and domains is given in the text.

2^* (see Figure 3a) corresponds to the situation when the lower stable stationary state disappears abruptly (when crossing l_2) and the upper stationary state becomes a global attractor in the system.

To clarify the bifurcation diagrams and the meaning of different domains, it is convenient to consider one-dimensional cross-sections of the N_0–d plane for N_0 = constant. Figures 4a and b show such cross-sections (cf. the dotted horizontal lines in Figure 3) obtained for $N_0 = 0.7$ and $N_0 = 0.44$, respectively, where the solid curves show stationary zooplankton density and the dashed curves show maximum and minimum values of oscillating zooplankton density vs *d*. The numbers in circles correspond to the domain numbers in the N_0–d plane. Coexistence of multiple attractors is readily seen in domains 4, 5 and 5^*. The composite curve consisting of the upper part of

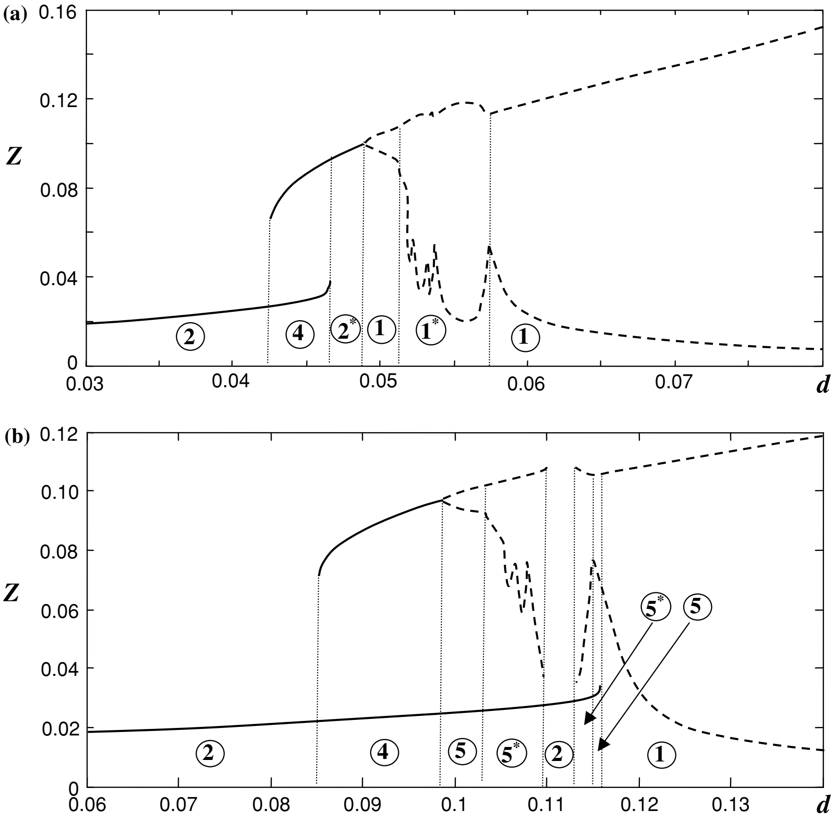

Figure 4. Bifurcation diagram of the system after invasion corresponding to the cross-section of N_0–d plane made for (a) $N_0 = 0.7$ and (b) $N_0 = 0.44$ (cf. the dotted horizontal lines in Figure 3a). Solid lines show stationary zooplankton density corresponding to stable steady states, the dashed lines show maximum and minimum of oscillating zooplankton density. Numbers in circles correspond to the domain numbers in Figure 3.

curve ***N*** (above point **A**) and the bottom part of curve $\boldsymbol{l}_2$ (below point **A**) separates the domain, where the system dynamics can only be oscillatory, either periodical or chaotic, from the domain where stable steady dynamics is possible. From below, the 'stability domain' is bounded by curve **S**.

An apparent increase in system complexity is not the only impact of the top predator. The invasion of top predator also results in stabilization of the plankton community dynamics: prominent oscillations of the species density observed in the N–P–Z system before invasion ($\delta = 0$) either become much smaller in amplitude or disappear entirely after the invasion ($\delta = \delta_0 > 0$).

Figure 5 shows the N_0–d diagram obtained numerically for $K_Z = 0.03$ and different values of the top predation intensity: $\delta_0 = 0$ (curve Δ), $\delta_{01} = 0.001$, $\delta_{02} = 0.002$, $\delta_{03} = 0.003$, $\delta_{04} = 0.004$, $\delta_{05} = 0.005$ and $\delta_{06} = 0.0055$. Other parameters are the same as in Figure 2c. For each δ, the corresponding curve separates the stability domain (below the curve), i.e., where at least one stable steady state exists, from the domain (above the curve), where the system dynamics is oscillatory. Apparently, the higher the intensity of top predation, the larger is the stability domain. From the left side, the stability domain is always bounded by curve ***S***.

Trophic response and paradoxical top-down control

The results described above show that invasion of a top predator can result in qualitative changes in plankton dynamics. From an ecological point of

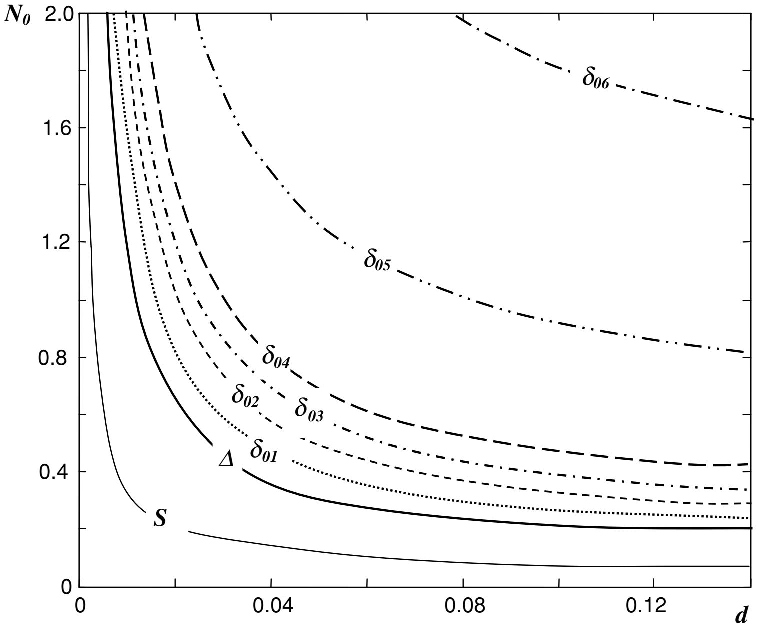

Figure 5. Map in N_0–d plane obtained for $K_Z = 0.03$ (other parameters are the same as in Figure 2c) and different values of the top predation intensity, $\delta_0 = \delta_{01} = 0.001$, $\delta_0 = \delta_{02} = 0.002$, $\delta_0 = \delta_{03} = 0.003$, $\delta_0 = \delta_{04} = 0.004$, $\delta_0 = \delta_{05} = 0.005$ and $\delta_0 = \delta_{05} = 0.0055$. Curve Δ corresponds to $\delta_0 = 0$. The 'stability domain' corresponding to existence of at least one stable steady state bounded by curve $\boldsymbol{S}$ and by curves δ_{0i}. Apparently, the stability domain grows in size with top predation intensity.

view, an important question is how the values of average plankton densities change when the top predation becomes more prominent. This issue is directly related to the problem of top–down trophic control.

In our extensive numerical study of system (4–6), we found two different types of the plankton system response to the invasion of a top predator; one of them can be considered as typical while the other looks rather paradoxical. Here the word 'typical' means that this type of response is frequently observed in nature, is well understood, and thus considered as a usual or typical top–down control (e.g., see Brett and Goldman 1997; Worm and Myers 2003).

Figure 6 gives two examples of the typical response of a plankton system to increasing intensity of top predation obtained for (a and b) $K_Z = 0.03$ and (c and d) $K_Z = 0.003$. Other parameters are the same as in Figure 2b and correspond to a well-balanced oligotrophic aquatic ecosystem with stable dynamics. We calculate the stationary densities of phyto- and zooplankton for different values of the top predation intensity δ_0. The invasion is described by Equation (7) with establishment time $t_0 = 365$ days. The initial conditions correspond to the stationary densities of the original N–P–Z system (cf. Figure 2b). As may be intuitively expected, an increase in δ_0 leads to a decrease in Z and to an increase in P. For different values of the half-saturation constant K_Z, the changes can be either gradual (see Figures 6a and b), or abrupt (discontinuous, see Figures 6c and d). A similar phenomenon of an abrupt drop in zooplankton density in response to top predation has been observed earlier in a simple two-component model (Scheffer et al. 2000) and reported for real aquatic ecosystems (McQueen and Post 1988).

However, the situation becomes essentially different when parameter values correspond to eutrophic ecosystem. Figure 7 shows phyto- and zooplankton densities vs. increasing top predation δ_0 (parameters are the same as in Figure 2a, $K_Z = 0.1$). Note that the value of K_Z is also important for the realization of this 'new' scenario, because it should be relatively high; this issue is discussed in detail later. Since in this case

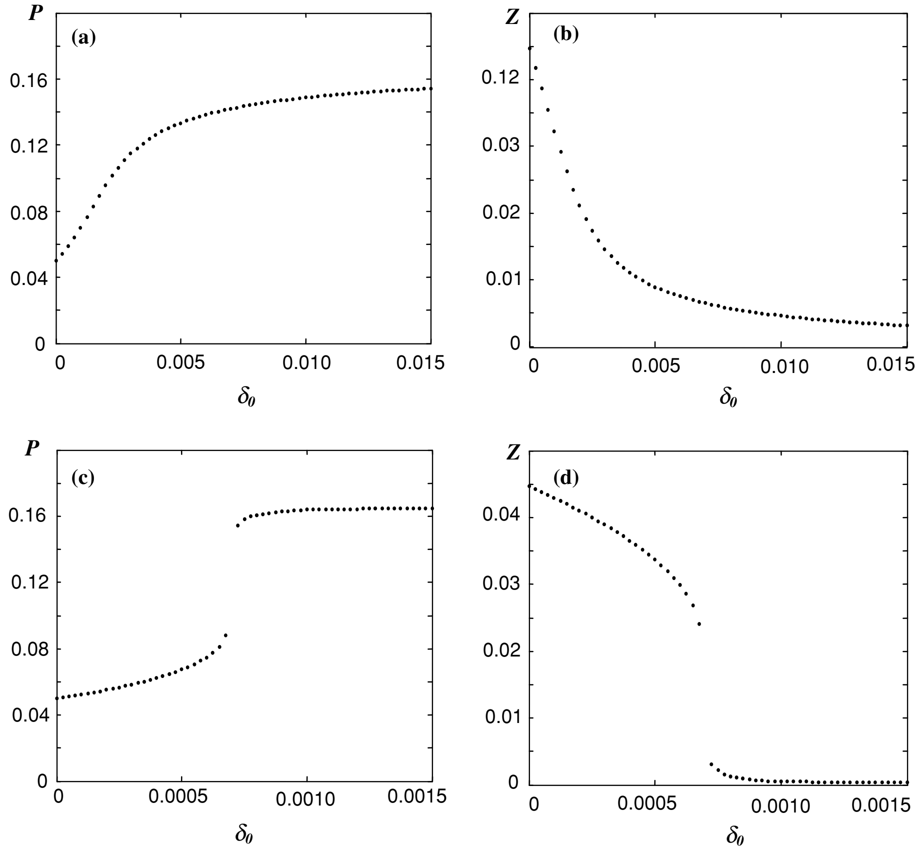

Figure 6. Stationary densities of phytoplankton (a and c) and zooplankton (b and d) calculated for different values of the top predation intensity in the case of the 'typical' responses of a plankton system to the top predator invasion. Here (a and b) and (c and b) are obtained for $K_Z = 0.03$ and $K_Z = 0.003$, respectively. Other parameters are the same as in Figure 2b and correspond to a well balanced oligotrophic ecosystem. A decrease in K_Z leads to an abrupt change in the plankton density in response to a small change in δ_0.

the original N–P–Z system and the system (4–6) for small values of δ_0 exhibit oscillations, we describe the system dynamics in terms of densities of P and Z averaged over 5 years starting from the moment when the top predation reaches its maximum value δ_0. The initial densities are the same for all δ_0 and belong to the limit cycle in the original N–P–Z system. For the values of δ_0 within the range 0.01–0.013, the averaged density of phytoplankton $<P>$ decreases and the averaged density $<Z>$ increases while the top predation grows (Figures 7a and b). Note that, when δ_0 becomes sufficiently large, the system response becomes 'typical' again, i.e., $<P>$ increases and $<Z>$ decreases.

From the ecological point of view, a substantial (more than double, cf. Figure 7b) increase in the averaged zooplankton density resulted from increasing top predation is surprising. The type of trophic response when the growing pressure of predator on its prey leads to an increase in the prey density is counterintuitive, which is why we call this type of top–down control 'paradoxical'.

Figures 7c and d show the corresponding bifurcation diagram, i.e., minima and maxima of the oscillating plankton density (dashed lines) and stationary plankton density (solid lines) vs. top predation intensity δ_0. It can readily be seen that an increase in δ_0 leads to a decrease in the

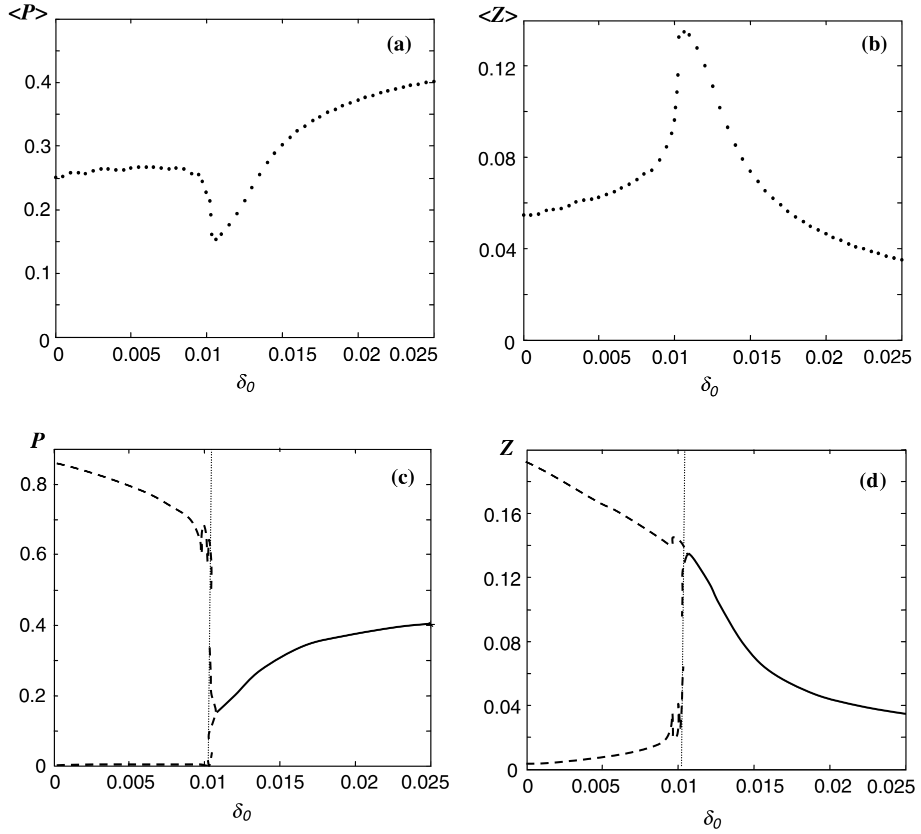

Figure 7. Average densities of (a) phytoplankton and (b) zooplankton calculated for different values of the top predation intensity in the case of the 'paradoxical' responses of a plankton system to the top predator invasion; (c) and (d) give the corresponding bifurcation diagrams, where solid lines show steady plankton density, dashed lines show maxima and minima of oscillating densities. Here $K_Z = 0.1$, other parameters are the same as in Figure 2a.

oscillation amplitude, first gradually and then abruptly through the transition from a big limit cycle to a small one, cf. vertical dotted line. Further increase in δ_0 turns oscillating dynamics to a stable equilibrium.

The changes in the average phyto- and zooplankton densities in response to the top predator pressure can be more sophisticated than that shown in Figures 6 and 7, when we change slightly the model parameters. In particular, Figure 8a and b show $<P>$ and $<Z>$ vs. increasing δ_0 obtained for $K_Z = 0.01$, $d = 0.03$ and $N_0 = 0.9$, other parameters the same as in Figure 2b. The corresponding bifurcation diagram is shown in Figure 8c and d. Solid lines show stable stationary states, dashed lines show maximum and minimum values of the oscillating densities. Due to the complex bifurcation structure of the system (cf. Figures 3 and 4), a small change in the top predation intensity δ_0 can lead to large, abrupt changes in the phyto- and zooplankton densities in the 'post-invasion' community. Note that we only show stable steady states and stable limit cycles, and not saddle points, so the fact that the left-hand side of the thick curves in Figure 8c and d terminates in nowhere actually means that the corresponding equilibrium states disappear in saddle-node bifurcations.

The results of our numerical simulations show that the increase of $<Z>$ in response to top predation intensity becomes more prominent if we diminish the maximum phytoplankton growth rate r. Since, for different values of r, the initial (i.e., for $\delta = 0$) values of average zooplankton

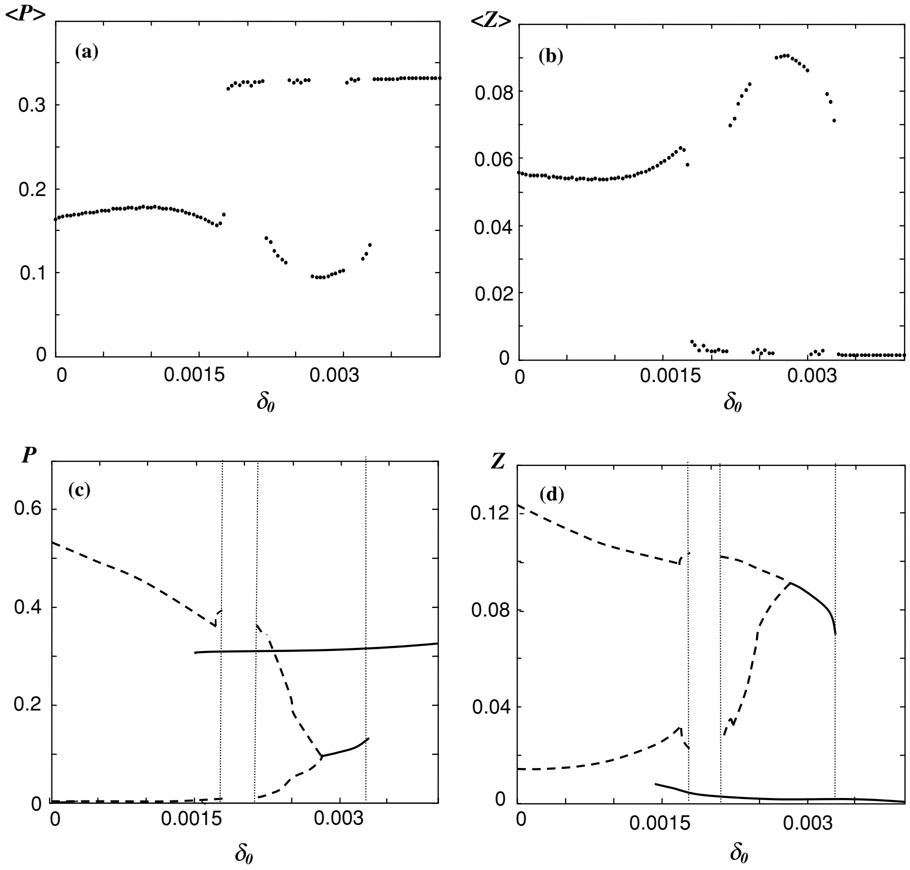

Figure 8. Example of the 'paradoxical' top–down control obtained for $K_Z = 0.01$; $d = 0.03$ and $N_0 = 0.9$, other parameters are the same as in Figure 2b: (a) and (b) show average phyto- and zooplankton densities calculated for different intensity of top predation; (c) and (d) give corresponding bifurcation diagrams. Existence of multiple attractors can result in different types of system response for close values of δ_0. Disappearance of the big cycles takes place via formation of homoclinic orbits.

density can be significantly different, it is convenient to use a scaled magnitude of the trophic response given by

$$\xi = \frac{<Z>}{<Z_0>}, \tag{8}$$

where $<Z_0>$ is the average zooplankton density in the original N–P–Z system. As in the previous computer experiments, averaging is done over 5 years.

Figure 9 shows the scaled magnitude of response ξ vs. δ_0 calculated for different values of the maximum phytoplankton growth rate: $r_1 = 0.3$, $r_2 = 0.4$, $r_3 = 0.6$, $r_4 = 0.8$, $r_5 = 1.0$, $r_6 = 1.2$, $r_7 = 1.4$, other parameters are the same as in Figure 2b. Thus, the magnitude of the paradoxical response is the larger the smaller r is. For small values of the maximum phytoplankton growth rate, an increase in the average zooplankton density caused by invasion of a top predator can be as large as five-fold!

Extensive numerical simulations performed for parameters varied around their realistic values have demonstrated the robustness of the phenomenon. The 'paradoxical top–down control' is observed inside a rather broad domain in the parameter space, provided that the values of N_0 and/or d are sufficiently high, which always corresponds to eutrophic ecosystems with large initial oscillations for $\delta_0 = 0$. For low values of N_0 and d, which corresponds to oligotrophic ecosystems, the trophic response of a plankton system to invasion of a top predator is always typical. Based on our numerical

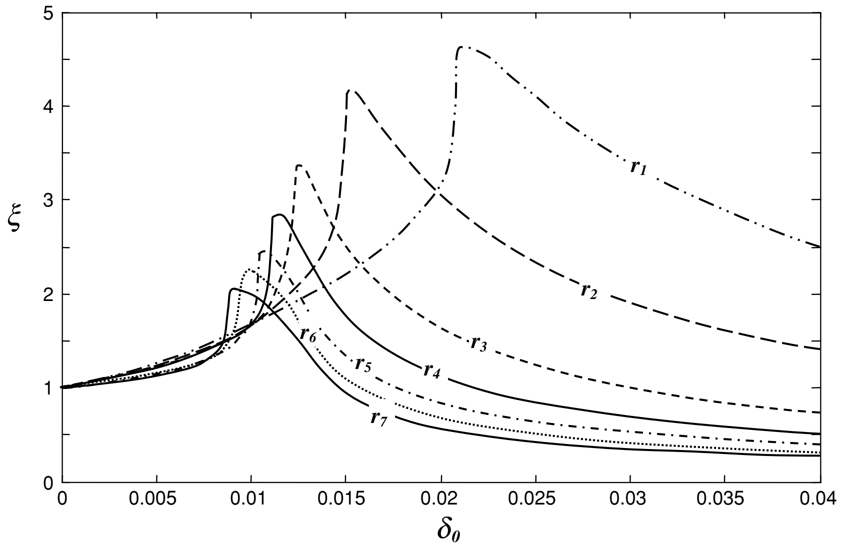

Figure 9. Scaled magnitude of the system response to the top predator invasion (cf. Equation (8)), calculated vs the intensity of top predation for different values of the maximum phytoplankton growth rate, $r_1 = 0.3$, $r_2 = 0.4$, $r_3 = 0.6$, $r_4 = 0.8$, $r_5 = 1.0$, $r_6 = 1.2$, $r_7 = 1.4$. Here $K_Z = 0.1$, other parameters are the same as in Figure 2b.

results (only a small part of them is shown above), we also conclude that, for both ecosystem types, the paradoxical response cannot be observed in case the top predator pressure is sufficiently high.

Another relevant question is whether it may be possible to reveal the dependence of the response type on the origin of the invading species, i.e., to distinguish between carnivorous zooplankton and fish. In order to address this issue, we analyzed

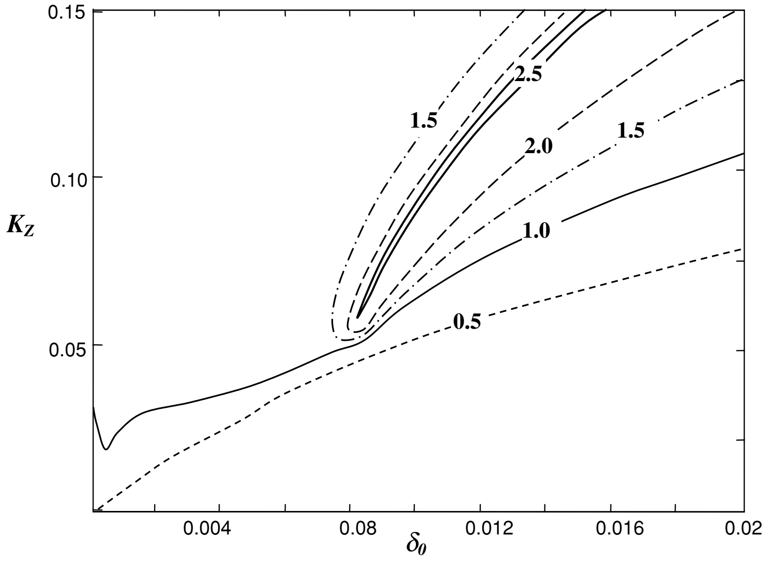

Figure 10. Dependence of the response type on the top predator half-saturation density K_Z. Different curves show the isoclines corresponding to different values of the scaled magnitude ξ of the response. Parameters are the same as in Figure 2b. Note that invasion of a top predator with small K_Z does not lead to the 'paradoxical top–down control'.

the impact of the top predator half-saturation constant K_Z on the plankton system dynamics. This parameter characterizes the top predator feeding ability and, according to Doveri et al. (1993), its value is significantly higher for planktivorous fish than for carnivorous zooplankton. Figure 10 shows the scaled magnitude of response ξ calculated for different values of K_Z and δ_0, other parameters are the same as in Figure 2a. The diagram shows that the 'paradoxical top–down control' becomes possible when the magnitude of K_Z is sufficiently high, which corresponds to planktivorous fish as a top predator. For small values of K_Z, corresponding to carnivorous zooplankton as a top predator, invasion of a top predator results in the typical top–down control, i.e., in a decrease in zooplankton density and an increase in phytoplankton density. Thus, it means that the availability of nutrients is not the only constraint for the 'paradoxical top–down control' to operate and it also can be species-specific.

Concluding remarks

In this paper, we have considered possible consequences of biological invasion in an epipelagic ecosystem when the invading species, e.g., carnivorous zooplankton or planktivorous fish, either constitutes a new, upper trophic level or appears to be a more effective zooplankton consumer than native species. A few important results have been obtained. First, we conclude that the introduction of top predator substantially increases the complexity of given plankton system (cf. Figures 2c and 3). Second, we show that an increase in the top predation intensity can result in system stabilization, i.e., in suppression of large-amplitude oscillations of population densities. This result is in a good agreement with conclusions drawn earlier based on other plankton models (Steele and Henderson 1992; Scheffer et al. 2000; Morozov 2003). Finally, we show that different types of top–down control in the community appear to be possible as a result of top predator invasion. In particular, we have shown that, along with the usual type of control when zooplankton density decreases as a response to increasing top predation, there can also exist another, a 'paradoxical' top–down control when an increase in top predation leads to a significant increase in average zooplankton density.

Although the paradoxical top–down control has been observed in both terrestrial and aquatic ecosystems (Leibold et al. 1997; Alimov 2000; Halaj and Wise 2001), it has been studied much less than the typical top–down control (cf. Abrams and Vos 2003). The anomalous trophic response is usually attributed to certain unknown indirect pathways. On the contrary, in our study we have shown that the paradoxical top–down control is possible in exactly the same population system, provided that the influx of nutrients into the system is sufficiently high.

A better understanding of the mechanisms underlying the paradoxical top–down control can be achieved from a comparison between the temporal variations of plankton densities in the systems with and without top predator. A significant increase in zooplankton density in response to an increase in top predation is observed for parameter values corresponding to eutrophic ecosystems. In a real sea or ocean, these ecosystems are not balanced and the species densities exhibit large amplitude oscillations resulting from a combined effect of seasonal variations of physical environment (Longhurst 1995) and the biological interaction of species (Truscott and Brindley 1994). Phytoplankton density can be very low during relatively long time intervals (cf. Figure 2a); during these periods zooplankton starves and its density diminishes substantially. At the end of these intervals of food shortage, when phytoplankton density increases, it takes a certain time for zooplankton to recover. As a result, the average zooplankton density is low.

Introduction of a top predator can balance the system. The top predator pressure does not allow zooplankton to gain high biomass during the periods of phytoplankton abundance and thus prevents phytoplankton from being overexploited. The intervals of low phytoplankton density become shorter and, on a longer time-scale, zooplankton also benefits from this stabilization: the maximum value of oscillating zooplankton density decreases but its density averaged over sufficiently long time (covering several population cycles) appears to be greater than it was before the top predator invasion. In terms of our model, this signifies that the shape of the orbits in the phase space and the speed along the orbits changes so that the trajectories spend less time at low values of Z while δ_0 is increasing.

A similar mechanism of trophic regulation by top predator in plankton communities was observed in natural epipelagic ecosystems. Hargrave et al. (1985) reported that the high predatory pressure by fish larvae on herbivorous zooplankton in summer prevented phytoplankton from being over-consumed and resulted in pronounced phytoplankton bloom in autumn; as a result, the zooplankton biomass also increased substantially during the bloom.

Another feature predicted by our model is that, for a relatively wide range of model parameters corresponding to the paradoxical top–down control, the increase of zooplankton density in response to increase in top predation was followed by abrupt collapse of zooplankton abundance (see Figures 8b and c). A qualitatively similar phenomenon was reported by Alimov (2000) for a natural marine ecosystem.

Other examples qualitatively similar to the 'paradoxical' response to top predation can be found in harvesting theory and fishery management. In particular, Abrams (2002) reported that a population under exploitation sometimes increases its size when harvesting increases. Matsuda and Abrams (2004) showed that the abundance of exploited fish population can become greater than in the absence of fishing and pointed at the initial overexploitation of the zooplankton as a possible explanation.

One of the reasons why the 'paradoxical top–down control' is relatively rarely observed in natural ecosystems is the fact that the observations on population dynamics are usually made on a short-time scale (Leibold et al. 1997). Our results, however, indicate that short-term observations may be misleading and the 'true' ecosystem response given by time-average species densities can only be revealed via sufficiently long time series. Moreover, our results show that the time necessary to reveal important changes in ecosystem properties can be much longer than the duration of the event causing them; in that sense our results are in agreement with the concept of 'extinction debt' (Tilman et al. 1994).

Our study leaves a few open problems. In this paper, we have studied the types of top–down trophic control in a plankton community using a conceptual three-component plankton model. Further progress can be made by taking into account other ecologically meaningful factors that we neglected here for the sake of simplicity. Such factors include seasonal variations in environmental conditions (Evans and Parslow 1985; Doveri et al. 1993), multi-species composition of each trophic level (Leibold et al. 1997), spatial heterogeneity (patchiness) of plankton distribution (James et al. 2003; Martin 2003), etc. An extension of the model in order to include any of these factors is likely to lead to a better understanding of biological invasion consequences and mechanisms of top–down control and will become a focus of our future work.

Acknowledgements

This research was partially supported by the Russian Foundation for Basic Research under Grants 03-04-48018 and 04-04-49649.

References

Abrams PA (2002) Will small population sizes warn us of impending extinction? American Naturalist 160: 293–305

Abrams PA and Vos M (2003) Adaptation, density dependence and the responses of trophic level abundances to mortality. Evolutionary Ecology Research 5: 1–20

Alimov AF (2000) Elements of Theory of Functioning of Aquatic Systems. Nauka, St. Petersburg, 147 pp [in Russian]

Brett MT and Goldman CR (1997) Consumer *versus* resource control in freshwater pelagic food webs. Science 275: 384–386

Caswell H and Neubert MG (1998) Chaos and closure terms in plankton food chain models. Journal of Plankton Research 20: 1837–1845

Doveri F, Scheffer M, Rinaldi S, Muratori S and Kuznetsov YA (1993) Seasonality and chaos in a plankton-fish model. Theoretical Population Biology 43: 159–183

Drake JA, Mooney HA, Fi Fdi Castri RH, Kruger FJ, Rejmanek M and Williamson M (1989) Biological Invasions: Global Perspective. Wiley, New York

Edwards AM and Brindley J (1996) Oscillatory behavior in a three-component plankton population model. Dynamics and Stability of Systems 11: 347–370

Edwards AM and Brindley J (1999) Zooplankton mortality and the dynamical behavior of plankton population models. Bulletin of Mathematical Biology 61: 202–339

Edwards AM and Yool A (2000) The role of higher predation in plankton population models. Journal of Plankton Research 22: 1085–1112

Eppley RW, Renger EH and Harrison WG (1979) Nitrate and phytoplankton production in the southern California coastal waters. Limnology and Oceanography 24: 483–494

Evans GT and Parslow JS (1985) A model of annual plankton cycles. Biological Oceanography 3: 327–347

Fagan WF, Lewis MA, Neurbert MG and van der Driessche P (2002) Invasion theory and biological control. Ecology Letters 5: 148–157

Flynn KJ, Fasham MJR and Hipkin CR (1997) Modelling the interaction between ammonium and nitrate uptake in marine phytoplankton. Philosophical Transactions of the Royal Society 352: 1625–1645

Gilpin ME (1972) Enriched predator-prey systems: theoretical stability. Science 177: 902–904

Halaj J and Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? American Naturalist 157: 262–281

Hargrave BT, Harding GC, Drinkwater KF, Lambert TC and Harrison WG (1985) Dynamics of the pelagic food web in St. Georges Bay, southern Gulf of St. Lawrence. Marine Ecology Progress Series 20: 221–240

James A, Pitchford JW and Brindley J (2003) The relationship between plankton blooms, the hatching of fish larvae and recruitment. Ecological Modelling 160(1–2): 77–90

Kuznetsov YA (1995) Elements of Applied Bifurcation Theory. Springer-Verlag, New York

Lammens EHRR (1999) The central role of fish in lake restoration and management. Hydrobiologia 395/396: 191–198

Leibold MA, Chase JM, Shurin JB and Downing AL (1997) Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28: 467–494

Longhurst A (1995) Seasonal cycles of pelagic production and consumption. Progress in Oceanography 36(2): 77–167

Lucas LV, Koseff JR, Cloern JE, Monismith SG and Thompson JK (1999) Processes governing phytoplankton blooms in estuaries. I. The local production-loss balance. II. The role of horizontal transport. Marine Ecology Progress Series 187: 1–30

Luckinbill LS (1974) The effects of space and enrichment on a predator–prey system. Ecology 55: 1142–1147

Martin AP (2003) Phytoplankton patchiness: the role of lateral stirring and mixing. Progress in Oceanography 57: 125–174

Matsuda H and Abrams PA (2004) Effects of predator–prey interactions and adaptive change on sustainable yield. Canadian Journal of Fisheries and Aquatic Sciences 61(2): 175–184

McQueen DJ and Post JR (1988) Cascading trophic interactions uncoupling at the zooplankton–phytoplankton link. Hydobiologia 159: 277–296

McPeek AM (1998) The consequences of changing the top predator in a food web: a comparative experimental approach. Ecological Monographs 68: 1–23

Micheli F (1999) Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science 285: 1396–1398

Morozov AY (2003) Mathematical modelling of ecological factors affecting stability and pattern formation in marine plankton communities, PhD thesis. Shirshov Institute of Oceanology, Moscow, 161 pp

Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystem in ecological time. Science 171: 385–387

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN and Weller SG (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332

Sarvala J, Helminen H, Saarikari V, Salonen S and Vuorio K (1998) Relations between planktivorous fish abundance, zooplankton and phytoplankton in three lakes of differing productivity. Hydrobiologia 363: 81–96

Scheffer M (1991) Fish and nutrients interplay determines algal biomass: a minimal model. Oikos 62: 271–282

Scheffer M, Rinaldi S and Kuznetsov YA (2000) Effects of fish on plankton dynamics: a theoretical analysis. Canadian Journal of Fisheries and Aquatic Sciences 57: 1208–1219

Shigesada N and Kawasaki K (1996) Biological Invasions: Theory and Practice. Oxford University Press, Oxford

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD and Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5: 785–791

Steele JH and Henderson EW (1992) The role of predation in plankton models. Journal of Plankton Research 14: 157–172

Stibor H, Vadstein O, Diehl S, Gelzleichter A, Hansen T, Hantzsche F, Katechakis A, Lippert B, Loseth K, Peters C, Roederer W, Sandow M, Sundt-Hansen L and Olsen Y (2004) Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. Ecology Letters 7(4): 321–328

Tilman D, May RM, Lehman CL and Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371: 65–66

Truscott JE and Brindley J (1994) Ocean plankton population as excitable media. Bulletin of Mathematical Biology 56: 981–998

Vanni MJ and Layne CD (1997) Nutrient recycling and herbivory as mechanisms in the "top–down" effect of fish on algae in lakes. Ecology 78: 21–40

Vinogradov ME, Shushkina EA, Musaeva EI and Sorokin PY (1989) A new invader to the Black Sea – ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora Lobata). Okeanologiya 29(2): 293–299

Worm B and Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top–down control in oceanic food webs. Ecology 84: 162–173

Yodzis P (1989) Introduction to Theoretical Ecology. Harper and Row, New York