

Towards resolving the paradox of enrichment: The impact of zooplankton vertical migrations on plankton systems stability

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Abstract

Eutrophication, often resulting from human activity, is a serious threat to aquatic communities. Theoretical analysis of this phenomenon, based on conceptual mathematical models, leads to controversial predictions known as Rosenzweig's paradox of enrichment. At the same time, field observations demonstrate that real plankton communities exhibit various mechanisms of self-regulation which can buffer negative effects of enrichment. In this paper, we study potential effects of zooplankton vertical migration on stability of plankton systems functioning. We consider an intrinsically unstable plankton model, which is characterized by an unlimited phytoplankton multiplication and population oscillations of increasing amplitude, and investigate whether vertical migrations of zooplankton can stabilize such a system at low plankton densities. By means of developing two different models accounting for different ecological situations, e.g. deep waters and shallow waters, we show that vertical migrations of zooplankton can result in stabilization of eutrophic plankton systems. Thus, we show that this mechanism, rarely taken into account in models of plankton dynamics, may be important for resolving the paradox of enrichment in plankton communities.

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1. Introduction

A remarkable increase in eutrophication level associated with anthropogenic factors is widely regarded as a serious current threat to ecosystems all over the world. A theoretical analysis of its possible consequences leads, however, to controversial predictions known as the 'paradox of enrichment' (Rosenzweig, 1971; Gilpin, 1972; May, 1972). The paradox of enrichment predicts, as a response to an increase of nutrient input into the system, destabilization of a predator–prey system by means of inducing fluctuations of the population densities of increasing amplitude, which can potentially result in species extinction due to the impact of stochastic factors at low population density (Lande, 1993).

Although examples of such type of response were found in some experimental systems (Luckinbill, 1974; Morin and Lawler, 1995), for natural ecosystems an increase in nutrition does not often lead to system destabilization (McAllister et al., 1972; McCauley and Murdoch, 1990; Kirk, 1998). Apparently, natural ecosystems have some self-regulating mechanisms protecting them from negative effects of eutrophication. Different factors have been identified theoretically that can potentially increase the system stability such as the presence of invulnerable individuals in prey population (Abrams and Walters, 1996), the existence of 'unpalatable' prey (Genkai-Kato and Yamamura, 1999), the effect of a more complex functional trophic response for predator (Gross et al., 2004), the influence of mixotrophy (Hammer and Pitchford, 2005, 2006) and the impact of spatial heterogeneity (Jansen, 1995; Scheffer and De Boer, 1996; Petrovskii et al., 2004). However, up to now the question about the actual mechanisms of self-regulation in eutrophic ecosystems remains open.

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One advantage of the studies mentioned above is that they are based on very general ‘conceptual’ mathematical models and therefore the corresponding conclusions can be applied to virtually any ecosystem type. A reverse side of this generality is, however, that some important features of specific ecosystems have not been embraced at all. In particular, an immanent basic property of an aquatic ecosystem is that, due to the impacts of gravity and sunlight, there is obvious asymmetry between horizontal and vertical dimensions, referred to as stratification. Stratification results in very different environmental conditions in the upper photosynthetic layer and lower layer(s), and many aquatic species make use of this difference. Many freshwater and marine zooplankters are known to periodically move up and down within the water column by entering and leaving the upper layer where phytoplankton is concentrated (Ohman, 1990). This phenomenon is called vertical migration. A frequently observed example is given by diurnal vertical migrations: zooplankton descends during the daytime and ascends into the upper layer at dusk to graze on phytoplankton during the night (Cushing, 1951; Vinogradov, 1970; Lampert, 1992). The main factors stimulating herbivorous zooplankters to migrate are thought to be the risk to be consumed by carnivorous zooplankton or planktivorous fish in the upper layer during daytime (Murray and Hjort, 1912; Zaret and Suffern, 1976; Bollens and Frost, 1989) and an energetic gain in deeper waters due to low temperature (McLaren, 1963; Han and Straskraba, 1998).

Interestingly, in spite of generality of zooplankton vertical migrations in aquatic ecosystems, they are rarely taken into account in theoretical studies of plankton dynamics (but see Iwasa, 1982). In particular, to the best of our knowledge their potential impact on plankton system stability has never been addressed. Meanwhile, it is intuitively clear that such impact is probable because zooplankton is commonly regarded as a controlling factor for phytoplankton growth, e.g. (Raymont, 1980; Steele and Henderson, 1992). In this paper, we consider vertical migrations of zooplankton theoretically by means of developing and analyzing mathematical models and show that migrations can enhance system stability. We then place these results into a more general context of ecosystem response to eutrophication and show that zooplankton vertical migrations provide another potential mechanism of self-regulation of eutrophic plankton systems in oceans and lakes.

The paper is organized as follows. In the next section we give a general description of the modeling approach that will be used throughout the paper. In Section 3, we develop a conceptual model of plankton dynamics in deep waters taking into account vertical migrations of zooplankton species that usually inhabit deep layers and only ascend to the upper layer during the periods of food abundance. In Section 4, we develop a model of plankton dynamics in shallow waters when all zooplank-

ters feed in the upper layer and regularly migrate to deep layers, their migratory behavior being different subject to the amount of available food. In both cases, by analyzing the model properties we demonstrate that the impact of zooplankton vertical migrations can stabilize the system at intermediate phytoplankton densities. In the last section we provide a discussion of the results and show how they contribute to our understanding of the ‘paradox of enrichment’ in aquatic communities.

2. Outline of the modeling framework

What should be an appropriate model to study plankton dynamics continues to be a subject of intense discussions. Reported modeling approaches range from very simple ‘conceptual’ ones taking into account only basic features to very complicated ones accounting for many minor details. It is our opinion, however, that complexity of the model should arise as a compromise between the actual complexity of a given phenomenon and the goals of the study. The goal of this paper is to make an early insight into the impact and role of zooplankton vertical migration, which is a fairly basic property of aquatic ecosystems. Therefore, in order to make this impact clearly distinguishable and easily understood, a model appropriate for our purposes should include as few details as possible.

Some basic features of plankton dynamics can be described by a system of two ordinary differential equations (Scheffer, 1991; Steele and Henderson, 1992; Truscott and Brindley, 1994; Scheffer et al., 2000):

$$\frac{dP}{dt} = r(P)P - f(P, Z), \quad (1)$$

$$\frac{dZ}{dt} = kf(P, Z) - m_0Z. \quad (2)$$

Here P and Z are the phytoplankton and herbivorous zooplankton densities, respectively, averaged over a certain water volume. In order to exclude the impact of daily periodical oscillations in the sunlight availability, we regard P and Z as day-average values of plankton density rather than instantaneous ones. The function $r(P)$ stands for phytoplankton growth, $f(P, Z)$ describes grazing of zooplankton on phytoplankton, the term $m_0 Z$ stands for zooplankton mortality and k is the efficiency of food utilization.

However, a straightforward application of model (1)–(2) to eutrophic plankton systems leads to a meaningless result. In eutrophic systems, the algal per capita growth rate $r(P)$ is approximately constant over a wide range of phytoplankton densities P , $r(P) \approx r_0 = \text{const}$. (Note that here we do not consider massive algal blooms when limitation due to algae self-shading may start playing an important role.) Stability of the only existing nontrivial

stationary state is then determined by the type of trophic response (Bazykin, 1998). The stationary state can be stable if $f(P, Z)$ is of Holling type III and it is always unstable if $f(P, Z)$ is of Holling type II. In the latter case, all the system trajectories come from the unstable state and tend to infinity through a succession of oscillations of increasing amplitude, which cannot describe normal system functioning. Indeed, field observations show that in eutrophic systems phytoplankton densities are often restricted to intermediate values due to intensive zooplankton grazing (Raymont, 1980). On the other hand, the use of Holling type III is not always justified biologically since for many zooplankton species the trophic response is closer to Holling type II (DeMott, 1982; Mills and Forney, 1983; Scheffer 1991; Doveri et al., 1993).

Clearly, instability of the generic system (1)–(2) points out that some important processes have not been taken into account. In mathematical perspective, it means that Eqs. (1)–(2) are lacking some term(s) or factor(s). One possible solution of this problem can be found in adding a nonlinear function $F(Z)$ into the right-hand side of Eq. (2) describing either zooplankton self-grazing or a consumption of zooplankton by planktivorous fish (Van den Bosch et al., 1988; Steele and Henderson, 1992; Kohlmeier and Ebenhoh, 1995; Edwards and Yool, 2000; Scheffer et al., 2000; Morozov and Li, 2006). For instance, it was shown by Bazykin (1998) that adding a quadratic mortality term (corresponding to zooplankton self-grazing) into Eq. (2) resulted in the appearance of stable modes impossible otherwise. However, it does not answer the important questions whether a eutrophic phyto-zooplankton community is intrinsically unstable and/or whether cannibalism is the only ‘life-boat’ available in plankton systems. In the following sections we will show that no such assumptions are necessary if the zooplankton vertical migrations are taken into account.

In this paper, we are primarily concerned with diurnal vertical migrations. We assume that diurnal zooplankton migration is a manifestation of a certain foraging strategy; therefore, it can modify the normal pattern of phyto-zooplankton trophic interaction and affect the system stability. Indeed, numerous observations show that regularity of diurnal vertical migrations can be significantly perturbed by variations in phytoplankton abundance (Huntley and Brooks, 1982; Johnsen and Jakobsen, 1987; Hoenicke and Goldman, 1987; Dini and Carpenter, 1992; Dagg et al., 1997). In particular, the depth of the maximum of zooplankton vertical distribution and the average time spent by zooplankton in the upper layer change according to the food availability (Vinogradov, 1970). It was observed that, during periods of high phytoplankton density, zooplankton might cease a regular pattern of vertical migrations and stay in the upper layer in the daytime despite of high fish predation (Geller, 1986). These are the features that should be taken into account when developing a mathematical model.

3. Model I: vertical migrations in deep waters

3.1. Main equations

For modeling purposes, we consider that the whole pelagic water mass is split into two layers. For the sake of simplicity, we consider plankton densities to be homogeneous inside each layer. Phytoplankton is present only in the upper ‘subsurface’ layer. Some zooplankton species, with the total population density Z , grazes mostly in the upper layer; below we will call them the ‘zooplankton of the upper layer’. Other species, with the density Z_d , inhabit the deep layer where they graze on descending dead plankton and detritus (Vinogradov, 1970). We will refer to them as the ‘zooplankton of the deep layer’. We assume that, when the phytoplankton density in the upper layer increases, a portion of zooplankton ascends from the deep layer to graze on phytoplankton. When the food conditions in the upper layer deteriorate, zooplankton migrates back to the deep layer. The zooplankton species that spend part of their time in the surface zone and the other part in the deep zone are often called ‘interzonal species’, see (Vinogradov, 1970).

We want to emphasize that here we do not endeavor to model the patterns of regular diurnal vertical migrations explicitly, which is hardly feasible with a conceptual model (1)–(2). Instead, we consider the effects of averaged variations of zooplankton trophic pressure in the upper layer caused by the changes in zooplankton migratory behavior which, in turn, can result from variations of food availability in the upper layer.

We add a zooplankton migration term A into Eq. (2) and parameterize it in the following way. When the density of phytoplankton in the subsurface layer is low, $P < P_{cr}$ where P_{cr} is a certain threshold phytoplankton density, zooplankton migrates into the deep layer at a rate proportional to its concentration Z in the upper layer and to the food shortage $(P - P_{cr})$. In the case that the phytoplankton density is high, some amount of zooplankton migrates to the subsurface layer. This increase is assumed to be proportional to the abundance of food and to the zooplankton density in the deep layer. For the sake of simplicity, we consider the zooplankton density Z_d in the deep layer to be constant. We assume that the total amount of zooplankton in the deep layer is sufficiently larger than that in the upper layer; therefore, migration of a portion of zooplankton into the upper layer does not change this amount in any significant way. We also assume that the migration rate into the upper layer exhibits saturation at high phytoplankton densities. We consider that saturation actually occurs at a certain phytoplankton density P_s . The term A is then given as

$$A = \begin{cases} A_0(P - P_{cr})Z, & 0 < P < P_{cr}, \\ A_1(P - P_{cr})Z_d, & P_{cr} < P < P_s, \\ A_1(P_s - P_{cr})Z_d, & P > P_s. \end{cases} \quad (3)$$

Here and below, the trophic response of zooplankton is considered here to be of Holling type II:

$$f(P, Z) = K_Z \frac{PZ}{P + H}, \tag{4}$$

where H and K_Z are parameters with obvious meaning.

Thus, under all the above assumptions, from (1)–(2) we arrive at the following equations:

$$\begin{aligned} \frac{dP}{dt} &= r_0 P - K_Z \frac{PZ}{P + H}, \\ \frac{dZ}{dt} &= k K_Z \frac{PZ}{P + H} - m_0 Z + A. \end{aligned}$$

By means of introducing dimensionless variables,

$$P = \frac{r_0 H u}{k K_Z}, \quad Z = \frac{r_0 H v}{K_Z} \quad \text{and} \quad t = \frac{\tau}{r_0},$$

we obtain the following system:

$$\frac{du}{d\tau} = u - \frac{uv}{u\alpha + 1}, \tag{5}$$

$$\frac{dv}{d\tau} = \frac{uv}{u\alpha + 1} - \gamma v + A, \tag{6}$$

where A is now given by

$$A = \begin{cases} \lambda_1(u - u_{cr})v, & 0 < u < u_{cr}, \\ \lambda_2(u - u_{cr}), & u_{cr} < u < u_s, \\ \lambda_2(u_s - u_{cr}), & u > u_s. \end{cases} \tag{7}$$

System (5)–(7) contains six dimensionless parameters, i.e.,

$$\begin{aligned} \alpha &= \frac{r_0}{k K_Z}, \quad \gamma = \frac{m_0}{r_0}, \quad \lambda_1 = \frac{A_0 H}{k K_Z}, \quad \lambda_2 = \frac{A_1 Z_d}{k r_0}, \\ u_{cr} &= \frac{k K_Z P_{cr}}{r_0 H}, \quad u_s = \frac{k K_Z P_s}{r_0 H}, \end{aligned}$$

their value determining the system properties.

3.2. Analysis of the model

Model (5)–(6) has two stationary states. The trivial stationary state (0,0) exists for all parameter values and is always a saddle point. Under certain constraints, there can also exist a nontrivial stationary state (u_0, v_0) ; the equations for u_0 and v_0 are given in Appendix A. Depending on the system parameters, the nontrivial stationary state is either stable or unstable. The condition of stability is provided by expression (A10) from Appendix A.

Note that the right-hand side of Eq. (6) is a piecewise smooth function. The positive quadrant of the phase plane is divided into three domains; in each domain the function is analytical.

It is convenient to construct the global phase portraits of the model along with the construction of parametric diagrams. We consider the bifurcation curves in (u_{cr}, γ) plane, the other parameters being fixed (see Fig. 1). The sketches of the corresponding phase portraits are shown in

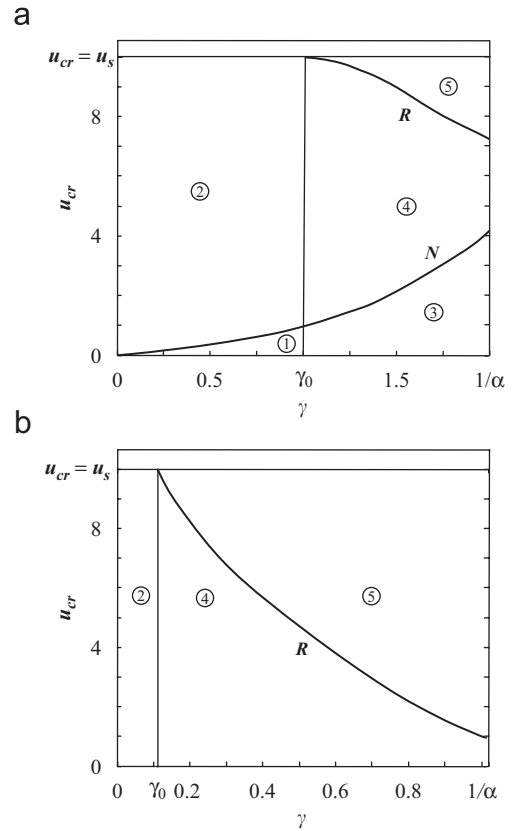


Fig. 1. Typical parametric diagrams of model I, see Eqs. (5)–(6), in the (u_{cr}, γ) plane: (a) in case $\lambda_2 > \alpha$ (shown for $\lambda_2 = 2$; $\alpha = 0.5$; $u_s = 10$); (b) in case $\lambda_2 < \alpha$ (shown for $\lambda_2 = 0.1$; $\alpha = 0.9$; $u_s = 10$). The meaning of the curves and domains is given in the text.

Fig. 2 by using Poincaré sphere representation (Kuznetsov, 1995; Bazykin, 1998). The domain numbers (in circles) in Fig. 1 correspond to the numbers of the phase portraits in Fig. 2. Note that the positions of the bifurcation curves do not depend on the parameter λ_1 .

The parametric diagram appears to have qualitatively different properties for $\lambda_2 > \alpha$ and for $\lambda_2 < \alpha$. A typical diagram in the case when $\lambda_2 > \alpha$ is shown in Fig. 1a for the parameters $\lambda_2 = 2$, $\alpha = 0.5$, $u_s = 10$. Here N is a neutrality curve; its position can be easily obtained from condition (A10) from Appendix A which gives

$$u_{cr} = \frac{(\alpha - \lambda_2)\gamma}{(\alpha\gamma - \alpha - 1)\lambda_2}. \tag{8}$$

When curve N is crossed in the direction from right to left, the stationary state loses its stability via a Hopf bifurcation. The scenario depends on the value of the first Lyapunov coefficient l_1 . We calculated l_1 by using the explicit analytical expression from Kuznetsov (1995). We found that on N we have everywhere $l_1 < 0$, i.e., the Hopf bifurcation is always supercritical so that a birth of a stable limit cycle takes place. The vertical line $\gamma_0 = 1/\alpha - 1$ separates domains 3, 4 and 5, where the trajectories in the phase plane can go to infinity (see Appendix A), from domains 1 and 2 where this type of behavior never

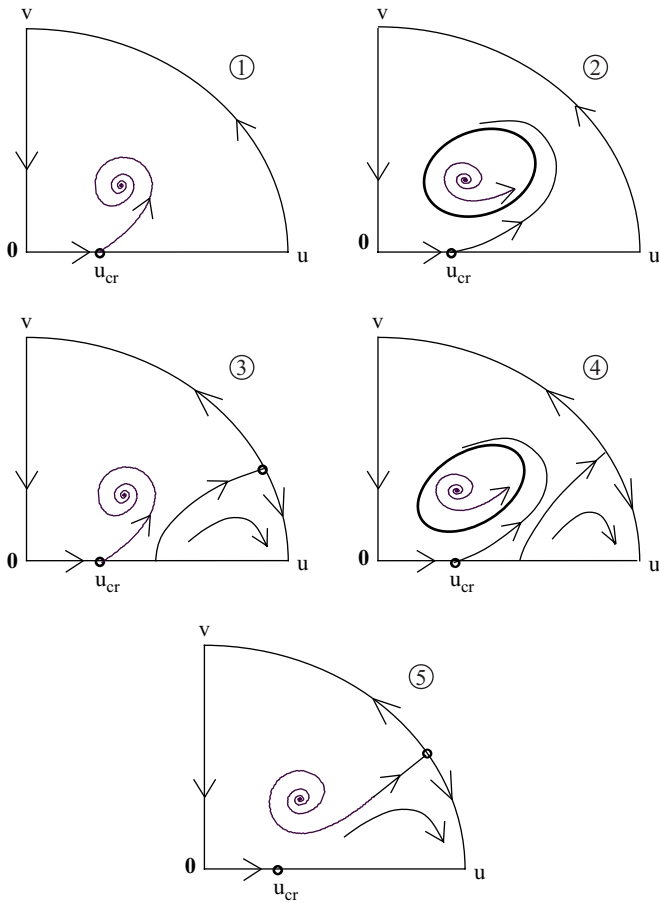


Fig. 2. The phase portraits of model I shown by using the Poincaré sphere representation. The portrait numbering corresponds to numbering of the domains in Fig. 1.

happens. Curve **R** corresponds to a disappearance of the ‘big’ limit cycle. The position of **R** is found numerically by means of solving (5)–(6) for various parameter values and identifying the type of the system behavior for each given parameter set.

The regimes 1 and 2 from Fig. 2 are thus characterized by existence of a globally stable mode, i.e., a stable stationary state or a stable limit cycle, respectively. For the regimes 3 and 4, stability takes place only for a part of the phase plane. Large initial densities of phytoplankton show a further unbounded exponential increase. Finally, the regime 5 is globally unstable; all trajectories go to infinity.

A typical diagram in the case when $\lambda_2 < \alpha$ is shown in Fig. 1b for $\alpha = 0.9$, $\lambda_2 = 0.1$, $u_s = 10$. The domain numbers have the same meaning as described above. The neutrality curve **N** now lies outside of the diagram and the stationary state is always unstable.

By considering the parametric diagrams and the phase portraits of the conceptual model (5)–(7), one can make an important conclusion. Here we should recall that the system (5)–(6) without the migration term is globally unstable for any parameter values. Introduction of the migration term changes the model properties in such a way

that the parameter space now contains a few domains where the system has either a stable equilibrium or stable limit cycle. Therefore, vertical migrations of zooplankton from the deep layer can lead to stabilization of initially unstable plankton community.

Interestingly, our model predicts that the aforesaid stabilization of plankton communities does not depend on the intensity of downward zooplankton migration. The latter is quantified by (dimensionless) parameter λ_1 which does not influence the parametric diagram properties in any significant way, only slightly affecting the size of the attractor basin.

Also, the model predicts that the chance for system stabilization is higher for $\lambda_2 > \alpha$. That can be seen from the comparison between the diagrams in Fig. 1 where regimes 1 and 2 of global stability become impossible for small λ_2 . Moreover, domain 5 of global instability grows in size with a decrease in λ_2 . By returning to the original parameters, from $\lambda_2 > \alpha$ we obtain that $A_1 K_Z Z_d > r_0^2$. In ecological terms, it means that stability in a plankton community is more probable for low rates of phytoplankton multiplication and/or for high rates of upward zooplankton migrations (given by a product of A_1 and Z_d). The latter seems to agree very well with intuitive expectations that vertical zooplankton migrations may act as a self-organized ecosystem response to the impact of destabilizing factors.

Moreover, stabilization of a plankton community depends to a large extent on the zooplankton mortality rate γ , which, in our model, is the sum of natural mortality rate and the rate of consumption of zooplankton by top predators (e.g., carnivorous zooplankton or planktivorous fish). The model shows that an increase in zooplankton mortality would likely result in a loss of stability when zooplankton is not able to control algal growth.

A question may arise here how important is the effect of saturation in the zooplankton migration rate, cf. the lines above Eq. (3). In order to address this issue, we considered a particular case of the model (5)–(6) (corresponding to $u_s \rightarrow \infty$) where saturation is neglected. Ecologically, it may mean that saturation does not take place until the phytoplankton density reaches very high values. We obtained that in this case the system has only three different phase portraits that are qualitatively similar to the portraits 1, 2 and 5 from Fig. 2. The parametric diagram is thus missing two domains, i.e., domains 3 and 4, where the system is stable for not very large initial phytoplankton density. Moreover, for the system without saturation, the domains corresponding to stable modes increase in size. Therefore, in agreement with the earlier inference, we conclude that saturation in the zooplankton migration rate decreases plankton system’s stability.

In conclusion of this section, we want to mention that a smooth version of the piecewise-linear parameterization (3) (or (7)) would lead to a system with essentially the same stability properties. Indeed, ‘smoothing’ of the system

(5)–(6) would imply applying a (small) structured perturbation to function (3) in a small vicinity of $u = u_{cr}$ and $u = u_s$; however, it is well-known that steady states and simple limit cycles are robust with respect to small perturbations of the right-hand side of the corresponding equations, cf. (Kuznetsov, 1995).

4. Model II: vertical migration in shallow waters

4.1. Main equations

The model considered in the previous section is essentially based on the assumption that some zooplankton species mostly live at considerable depth and only ascend to feed when the phytoplankton density in the upper layer is sufficiently high. In this section, we consider dynamics of a plankton community where all zooplankton species feed in the upper layer but may perform diurnal vertical migrations into deep waters to avoid predation. This situation seems to be more relevant in shallow lakes or shallow parts of the ocean.

We do not assume any more that the whole water mass is split into two layers. Instead, in order to quantify the migratory behavior of zooplankton, we introduce a factor η which gives the proportion of time spent by zooplankters in the upper part of the water column. Obviously, $0 \leq \eta \leq 1$; in particular, $\eta = 1$ means that all zooplankton remains concentrated in the subsurface waters and does not perform vertical migrations at all. The case $\eta = 0$ means that all zooplankton has descended to the depth and ceased its migration for a while, e.g., due to insufficient amount of food at the top of the water column. An intermediate value $\eta \approx 0.5$ corresponds to the case when zooplankton spends one half of the day in the upper waters and the other half in the deep waters.

Since there is considerable evidence that the intensity of zooplankton migrations is positively correlated with the availability of food, cf. (George, 1983; Hoenicke and Goldman, 1987; Dini and Carpenter, 1992; Sekino and Yamamura, 1999), we assume that η is a monotonically increasing function of P . Therefore, values of η close to 0 and close to 1 should correspond to relatively low and relatively high density of the phytoplankton density in the subsurface waters, respectively.

We then introduce a new variable $V = Z\eta$ where Z is the zooplankton density averaged over the whole water column. Since phytoplankton is mostly concentrated at the top, the consumption of phytoplankton by zooplankton is now described as $f(P, Z) = K_Z \eta Z P / (P + H) = K_Z V P / (P + H)$, i.e., it depends both on the total amount of zooplankton Z and on its presence η in the upper layer. It means that the left-hand side of the equation for the phytoplankton density, cf. (1), depends on V rather than on Z . Correspondingly, the generic system (1)–(2) can now be re-written in new variables P and V , provided we are able to derive an equation for V .

The rate of change in V is given as

$$\frac{dV}{dt} = \frac{d(Z\eta)}{dt} = \eta \frac{dZ}{dt} + Z \frac{d\eta}{dt}, \quad (9)$$

where $d\eta/dt = (d\eta/dP)(dP/dt)$ so that, making use of Eq. (1),

$$\eta'(t) = \left(r_0 P - K_Z \frac{\eta Z P}{P + H} \right) \eta'(P). \quad (10)$$

The equation for dZ/dt is essentially Eq. (2); however, we should now take into account that, in the subsurface waters, zooplankton predation by higher predators cannot be neglected:

$$\frac{dZ}{dt} = k K_Z \frac{P V}{P + H} - m_0 Z - m_1 V. \quad (11)$$

Here $m_0 Z$ and $m_1 V$ are the zooplankton natural mortality and its mortality due to the predation by top predator(s), respectively. The latter is assumed to depend on the time that zooplankton spends in the upper waters and thus depends on V rather than on Z . It should be also mentioned that, in a general case, predation by a top predator is described by a nonlinear function (Edwards and Yool, 2000); however, a linear function still can be a good approximation when the zooplankton density is not very high.

Since in eutrophic ecosystems zooplankton mortality is mostly caused by its predation by a higher predator (Jankowski et al., 2005), we can neglect the mortality term $m_0 Z$ for simplicity. From (9)–(11), we then obtain

$$\frac{dP}{dt} = r_0 P - K_Z \frac{V P}{P + H}, \quad (12)$$

$$\frac{dV}{dt} = \left(k \frac{K_Z V P}{P + H} - m_1 V \right) \eta(P) + V \left(r_0 P - \frac{K_Z V P}{P + H} \right) \eta'(P) / \eta(P). \quad (13)$$

Note that in the particular case $\eta(P) \equiv 1$ (i.e. when migrations are ‘switched off’ and all zooplankton is concentrated in the upper waters) Eqs. (12)–(13) are identical to the standard model (1)–(2) provided the same assumptions are made that the per capita phytoplankton growth is density independent and grazing is parameterized as (4). In a more general case $\eta(P) \equiv \text{const} < 1$, which means that zooplankton performs diurnal vertical migrations but their intensity is not affected by food availability, Eqs. (12)–(13) coincide with the model (1)–(2) up to a constant factor in the equation for the zooplankton density; in both cases the system remains globally unstable.

Introducing, for convenience, dimensionless variables

$$P = \frac{r_0 H u}{k K_Z}, \quad V = \frac{r_0 H w}{K_Z} \quad \text{and} \quad t = \frac{\tau}{r_0},$$

from (12) to (13) we arrive at the following system:

$$\frac{du}{d\tau} = u - \frac{uw}{u\alpha + 1}, \quad (14)$$

$$\frac{dw}{d\tau} = w \left(\frac{u}{u\alpha + 1} - \gamma \right) \eta(u) + \theta w \left(u - \frac{uw}{u\alpha + 1} \right) \eta'(u)/\eta(u), \tag{15}$$

where

$$\alpha = \frac{r_0}{kK_z}, \quad \gamma = \frac{m_1}{r_0} \quad \text{and} \quad \theta = \frac{r_0 H}{kK_z}$$

are dimensionless parameters.

4.2. Analysis of the model

System (14)–(15) has two stationary states. It is easy to prove that the trivial stationary state (0,0) is always unstable (a saddle point). The coordinates of the nontrivial stationary state (u_0, w_0) are given by

$$u_0 = \frac{\gamma}{1 - \gamma\alpha}, \quad w_0 = u_0\alpha + 1. \tag{16}$$

Applying standard linear stability analysis, it is readily seen that the nontrivial stationary state (u_0, w_0) is stable if and only if the following condition holds:

$$\frac{\eta'(u_0)}{\eta(u_0)} > \frac{\alpha}{\theta(u_0\alpha + 1)}. \tag{17}$$

From relation (17), we immediately arrive at an important conclusion: for any fixed value of the system parameters α , γ and θ , actual stability of the stationary state depends on how quickly the zooplankton migration intensity responds to a change in the phytoplankton density. Indeed, in the case that the relative increase in $\eta(u)$ (i.e., the weighted value η'/η) at the equilibrium is sufficiently large, the otherwise unstable stationary state becomes stable. Therefore, stabilization of an eutrophic plankton system in a shallow ocean or lake can appear as result of zooplankton vertical migrations. Note that this conclusion is made in a rather general case, i.e., without making any assumptions about specific form of function $\eta(u)$.

A more detailed analysis of system (14)–(15), such as limit cycle existence/nonexistence and construction of global phase portraits, can hardly be done without choosing a specific parameterization. For this purpose, we consider the following function:

$$\eta(u) = 1 - \eta_0 \exp(-u\omega). \tag{18}$$

Here parameter ω , is a measure of sensitivity of zooplankton migratory behavior with respect to a change in the phytoplankton density, the larger is ω , the quicker is the response. Parameter η_0 is auxiliary so that $(1 - \eta_0)$ gives the fraction of time that zooplankton spends in the upper waters in case of low phytoplankton density.

Stability condition (17) now takes a more specific form

$$\frac{\eta_0 \omega \exp(-u_0 \omega)}{1 - \eta_0 \exp(-u_0 \omega)} > \frac{\alpha}{\theta(u_0 \alpha + 1)}. \tag{19}$$

We consider the bifurcation curves of the system (14)–(15) with (18) in (ω, γ) parametric plane, all other

parameters being fixed. A typical diagram is shown in Fig. 3, which is obtained for $\alpha = 0.5$, $\theta = 2$ and $\eta_0 = 0.5$. The sketches of the corresponding phase portraits are shown in Fig. 4; the encircled numbers in Fig. 3 correspond to the numbers of the phase portraits in Fig. 4. The position of the neutrality curve N is obtained by means of numerical solution of (19). The nontrivial stationary state (u_0, w_0) is stable for domain 1 and unstable for the other domains. Loss of stability on N takes place either via a birth of a small stable limit cycle (supercritical Hopf bifurcation) when entering domain 2 or via disappearance of an unstable limit cycle (subcritical Hopf bifurcation) when entering domain 3. Domain 2 is characterized by a co-existence of unstable and stable limit cycles, the outer cycle being unstable. The cycles merge and disappear on curve J , which joints curve N at point O . For large values of ω , curves N and J gradually approach the vertical axis $\gamma = 0$. For parameters from domains 3 and 4, there exists

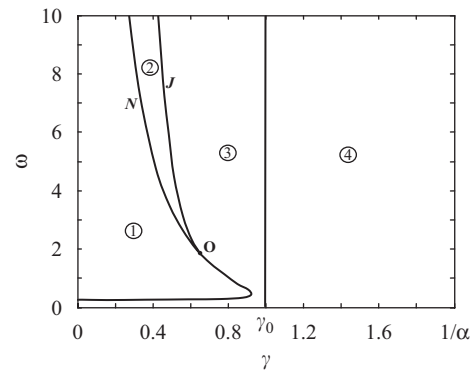


Fig. 3. A typical parametric diagram of model II, see Eqs. (14)–(15) with $\eta(u)$ given by (18), in the (ω, γ) plane (shown for $\alpha = 0.5$; $\theta = 2$; $\eta_0 = 0.5$). The meaning of the curves and domains is given in the text.

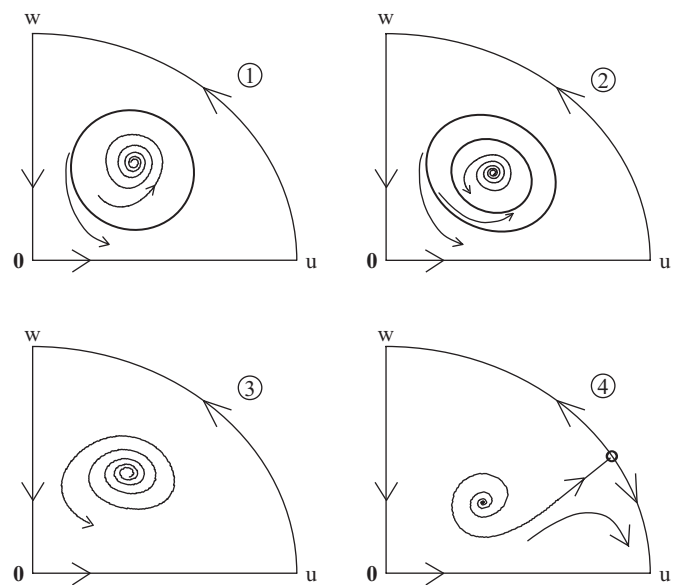


Fig. 4. The phase portraits of model II shown by using the Poincaré sphere representation. The portrait numbering corresponds to numbering of the domains in Fig. 3.

no attractor in the phase plane of the system and all trajectories tend to infinity either by unwinding in a spiral-like manner (domain 3) or by having $v/u \rightarrow 0$ for $u \rightarrow \infty$ (domain 4).

On the whole, the system may exhibit stable dynamics only in domains 1 and 2 where it has a stable steady state and a stable limit cycle, respectively. Let us recall here that the corresponding model without migrations (i.e., Eqs. (14)–(15) with $\eta(u) \equiv \text{const}$) is unstable for any parameter values. Therefore, stabilization of the system clearly occurs due to the impact of zooplankton vertical migration.

It should be mentioned, though, that the attractors of domains 1 and 2 are not globally stable; they are bounded by unstable limit cycles which gives the attraction basin boundary. In ecological terms, it means that for a large initial phytoplankton density zooplankton cannot control phytoplankton growth.

Considering the shape of curves N and J in Fig. 3, one can make an important conclusion that system stabilization can take place only when the value of ω is neither too small nor too large. Although it may seem somewhat counterintuitive, it agrees with heuristic argument. Indeed, small ω means that the intensity of zooplankton migratory behavior is hardly affected by availability of food at all. The system then becomes equivalent to the system without diurnal migrations, i.e., to globally unstable system (1)–(2). (We should recall here that P and Z give population densities averaged over 24 h rather than their momentary values, cf. the lines below Eq. (2).) On the contrary, large ω means that zooplankton overreacts to changes in phytoplankton density. From Eq. (18), we obtain that, in this case, $\eta \approx 1$ for virtually any value of u so that zooplankton is always concentrated in the upper waters (unless u is very small). This situation is described again by the unstable system (1)–(2).

An important question remains as to whether the above results are robust with respect to the choice of parameterization for $\eta(u)$. In order to address this issue, we considered the following piecewise-linear function:

$$\eta(u) = \begin{cases} \eta_0 + u\omega, & 0 \leq u \leq (1 - \eta_0)/\omega, \\ 1, & (1 - \eta_0)/\omega < u. \end{cases} \quad (20)$$

Unlike (18), for $\eta(u)$ given by (20) the saturation in migration intensity is reached suddenly when the phytoplankton density exceeds the threshold value $(1 - \eta_0)/\omega$.

The system (14)–(15) with (20) was studied both analytically and numerically. We have obtained that it possesses qualitatively similar properties. In particular, we found that system stabilization due to the impact of vertical migration can only take place for intermediate values of ω .

5. Concluding remarks

Ecosystem eutrophication is currently regarded as one of the most severe threats to populations and communities (Tilman et al., 2001). An effective management of this

threat apparently implies good understanding of causes and effects and, therefore, requires development of an appropriate theoretical background. The latter can be achieved by means of analysis of relevant mathematical models.

Different population systems may respond differently to eutrophication, though, and the mechanisms of self-regulation often remain obscure. Unfortunately, along with many serious and insightful studies, there has also been a tendency to simply ignore the problem rather than to search for its solution. In particular, Jensen and Ginzburg (2005) revisited the problem and suggested their own ‘solution’ by concluding that the Rosenzweig paradox of enrichment simply does not exist because extinction of species as a result of eutrophication is rarely observed in laboratory experiments, even when enrichment does lead to population oscillations of increasing amplitude. In contrast, although we admit that the problem as a whole may have somewhat different interpretation, it is our opinion that the main prediction of Rosenzweig’s analysis is system *destabilization* rather than species extinction. As a result of population oscillations caused by enrichment, the population density at times can fall to a progressively small value (May, 1972; Gilpin, 1972). Extinction, if any, then *may happen* due to the impact of stochastic perturbations, cf. (Lande, 1993). Apparently, the actual outcome of the system dynamics then depends on the nature of the perturbations and their magnitude. The latter is unlikely to be of any significant value in a laboratory experiment where most conditions are, by definition, controllable.

An invaluable contribution of Rosenzweig’s work to ecological theory is an emerging understanding that a generic predator–prey system, which is a basic element of any population community, is intrinsically unstable provided that the nutrient input is sufficiently high. It should be mentioned here that possible extinction is only one negative result of stability loss. At the other end of the same chain is a population outbreak, e.g., ‘algal bloom,’ and while extinction due to eutrophication is rarely observed in aquatic ecosystems, a massive increase in the phytoplankton density is quite typical. Therefore, identification of factors that can increase or decrease stability of ecosystem functioning is an issue of highest importance.

In our paper, by means of development and analysis of two conceptual mathematical models, we have shown that vertical zooplankton migrations, presumably affected by availability of food (i.e., phytoplankton), can be a factor that stabilizes plankton community and may buffer the negative impact of eutrophication.

Vertical migrations of zooplankton were considered earlier in few theoretical studies, cf. (Iwasa, 1982; Gabriel and Thomas, 1988; Sekino and Yamamura, 1999; Han and Straskraba, 1998; Liu et al., 2003). In those papers, the authors were mostly concerned with the question how food availability together with the top predator pressure could influence the migratory behavior of zooplankton as well as the variation of the depth of zooplankton density

maximum. However, the possible effect of zooplankton vertical migrations on plankton system stability has never been addressed.

A standard way to arrive, from the generic system (1)–(2), at a stable predator–prey model is to assume that the prey multiplication rate decreases when the population density increases, i.e., in the manner prescribed by the logistic growth: $r(P) = r_0(1 - P/P_{\max})$ where P_{\max} is the carrying capacity. Eqs. (1)–(2) with predation described by Holling type II function, see (4), then possess a non trivial steady state which is stable as long as the carrying capacity is not too large. Therefore, P_{\max} is a controlling parameter; in its turn it depends on a number of environmental factors. In particular, enrichment of the system increases the carrying capacity significantly. Field data on plankton blooms show that it may reach very high values, a few orders of magnitude higher than the plankton density observed during normal ecosystem functioning. Mathematically, this means that $P_{\max} \rightarrow \infty$. The growth rate then becomes approximately constant and the system loses its stability: the steady state is not stable any more. In a real ecosystem, however, enrichment does not always lead to system destabilization. That is where the impact of vertical migrations, probably along with some other factors, comes into play and stabilizes the otherwise unstable system.

Note that existence of unbounded trajectories should not be regarded as a drawback of the model. On the contrary, it makes it possible to analyze the influence of the vertical migration on the system stability in a heuristic way; trajectories going to infinity can be interpreted as the cases where the stabilizing impact of vertical migrations is not sufficient.

Obviously, our study leaves a number of open questions. First, in the above analysis we have assumed that the species horizontal distribution is homogeneous. In real ecosystems, it is not always so. Moreover, it is known that spatial heterogeneity is a factor that can, by itself, increase system stability with respect to eutrophication (Jansen, 1995; Petrovskii et al., 2004). Therefore, it would be interesting to check how vertical migrations can be modified by the impact of horizontal heterogeneity, which may require application of more complicated modeling approaches. Seasonality of the plankton dynamics is another issue (Giguere and Dill, 1980; Evans and Parslow, 1985; Doveri et al., 1993). Third, there are indications that, in some cases, the response of zooplankton migratory behavior to phytoplankton availability can occur in a more complicated manner, cf. (Hardy and Gunther, 1935; Vinogradov, 1970; Pearre, 1979; Dini and Carpenete, 1992; Dagg et al., 1997); in particular, zooplankton may sometimes stay longer in the subsurface waters even for very low phytoplankton concentration. Although this observation does not affect the results of our present analysis (because here we are concerned with the dynamics of a eutrophic system where plankton density is normally at an intermediate value), apparently, a different migration pattern can have different impact on system stability. This

issue should be further investigated. Finally, in our study we did not take into account different life stages of zooplankters. It is known, however, that earlier stages of zooplankton usually do not migrate downward and stay in the subsurface layer (Pearre, 1979), which can have implications for the system stability. These and other related problems will likely become the subject of our future research.

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Appendix A

The coordinates u_0 and v_0 of the non-trivial steady state of the system (5)–(7) are given by

$$1 - \frac{v_0}{u_0\alpha + 1} = 0, \tag{A1}$$

$$\frac{u_0}{u_0\alpha + 1} - \gamma + \lambda_1(u_0 - u_{cr}) = 0 \tag{A2}$$

when $u_0 < u_{cr}$, by the equations

$$1 - \frac{v_0}{u_0\alpha + 1} = 0, \tag{A3}$$

$$\frac{u_0v_0}{u_0\alpha + 1} - \gamma v_0 + \lambda_2(u_0 - u_{cr}) = 0 \tag{A4}$$

when $u_{cr} < u_0 < u_s$, and by the equations

$$1 - \frac{v_0}{u_0\alpha + 1} = 0, \tag{A5}$$

$$\frac{u_0v_0}{u_0\alpha + 1} - \gamma v_0 + \lambda_2(u_s - u_{cr}) = 0 \tag{A6}$$

when $u_s < u_0$.

For simplicity, we assume that parameter u_s , which quantifies saturation in the migration rate λ , satisfies the condition $u_s > u^*$ where u^* is the stationary density of phytoplankton in the absence of zooplankton migrations

$$u^* = \frac{\gamma}{1 - \gamma\alpha}. \tag{A7}$$

For biological reasons, we restrict our analysis to the parameter range where $u^* > 0$, i.e., to $\gamma < 1/\alpha$. The condition $u_s > u^*$ has a simple meaning that the migration rate is saturated at phytoplankton densities large compare to the characteristic density u^* .

It is readily seen that coordinates u_0 and v_0 are given by (A1)–(A2) if and only if the following condition holds:

$$u_{cr} > u^* = \frac{\gamma}{1 - \gamma\alpha} > 0. \tag{A8}$$

In this case we have $u_0 < u_{cr}$ and the value of u_0 is determined by (A2), although an explicit expression appears to be rather cumbersome.

For $u_{cr} < u^*$, we have $u_s > u_{cr}$; u_0 is now determined by (12)–(13) which gives $u_0 = (u_{cr}\lambda_2 + \gamma)/(1 - \gamma\alpha + \lambda_2)$.

On the other hand, it is easy to derive from (A5)–(A6) that u_0 should satisfy the following inequality:

$$u_0 = \frac{\gamma}{1 - \gamma\alpha} - \frac{\lambda_2}{1 - \gamma\alpha} < u^* < u_s. \quad (\text{A9})$$

It means that there cannot be a stationary state with $u_0 > u_s$. Note that, for the stationary states obtained from (A1)–(A4), we always have $u_0 < u_s$. This follows from the fact that if $u_0 < u_{cr}$ then $u_0 < u_s$; in the case $u_0 > u_{cr}$ we have $u_0 < u^*$ and $u_0 < u^* < u_s$.

Now let us consider stability of the nontrivial stationary state. Applying a standard linear stability analysis, it is easy to prove that for $0 < u^* < u_{cr}$ this state is always unstable. For $u^* > u_{cr}$, the stationary state may be either stable or unstable; stability takes place if and only if the following condition holds:

$$u_0 = \frac{u_{cr}\lambda_2 + \gamma}{1 - \gamma\alpha + \lambda_2} > \frac{\gamma}{1 - \gamma\alpha + \alpha}. \quad (\text{A10})$$

A complete analysis of the model should also include a study of its asymptotical properties at infinitely large values of the state variables. We considered the system behavior at infinity by applying a standard Poincaré method (Arnold, 1983). For the sake of brevity, we provide here only the result of this study. We found that, in the system (5)–(7), the trajectories tending to infinity (if any) have a stable zero slope, i.e., $u/v \rightarrow 0$, $u \rightarrow +\infty$, and no spiral-like trajectories with infinitely growing amplitude exist. Thus, loss of stability, when it happens, takes place in a different manner compare to the model without migrations.

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