



Emergence of Holling type III zooplankton functional response: Bringing together field evidence and mathematical modelling

Andrew Yu. Morozov^{a,b,*}

^a Department of Mathematics, University of Leicester, UK

^b Shirshov Institute of Oceanology, Moscow, Russia

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ABSTRACT

Food-web population models are rather sensitive to parameterization of functional response in predation terms. Theoretical studies predict enhancing of ecosystems' stability for a functional response of sigmoid type (Holling type III). The choice of a correct type of response is especially important for modelling outcome of grazing control of algal blooms by zooplankton in nutrient-rich ecosystems. Extensive experiments on zooplankton feeding in laboratories show non-sigmoid nature of response for most herbivorous zooplankton species. As a consequence, there is a strong opinion in literature that the implementation of Holling III type grazing in plankton models is biologically meaningless. I argue, however, that such an 'evident' claim might be wrong and sigmoid functional responses in real plankton communities would emerge more often than was suggested earlier. Especially, this concerns plankton models without vertical resolution, which ignore heterogeneity in vertical distribution of species. Having conducted extensive literature search of data on zooplankton feeding *in situ*, I show that vertical heterogeneity in food distribution as well as active food searching behaviour of zooplankton can modify the type of functional response. In particular, the rate of food intake by the whole zooplankton population in the column, as a function of total amount of food, often exhibits a sigmoid behaviour, instead of a non-sigmoid one postulated previously based on laboratory experiments. This conceptual discrepancy is due to the ability of zooplankton to feed mostly in layers with high algal density. I propose a generic model explaining the observed alteration of type between overall and local functional responses. I show that emergence of Holling type III in plankton systems is due to mechanisms different from those well known in the ecological literature (e.g. food search learning, existence of alternative food, refuge for prey).

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1. Introduction

Dynamics of food-web population models largely depends on parameterization of functional response in predation terms (Oaten and Murdoch, 1975a,b; Hassell and Comins, 1978; Murdoch et al., 1998; Gross et al., 2004). This is especially true for modelling of eutrophic aquatic ecosystems, where the choice of type of zooplankton functional response becomes crucial for predicting the outcome of grazing control of algae (Truscott and Brindley, 1994; Hernández-García and López, 2004; Fussmann and Blasius, 2005). Implementation of an appropriate type of functional response for herbivorous zooplankton and, in particular, the correctness of the use of Holling type III (a sigmoid-shaped) response has provoked a vivid discussion in the literature (Rothhaupt and Lampert, 1992; Scheffer and De Boer, 1995; Murdoch et al., 1998; Jeschke et al., 2004; Sarnelle and Wilson,

2008). In this paper, I will consider the current problem from a different angle.

The zooplankton functional response is usually defined as the specific food intake rate (i.e. per zooplankton biomass, per unit of time) as a function of ambient food density. Conventionally, there exist three main types of functional response known as Holling types (Jeschke et al., 2002; Gentleman et al., 2003). These are Holling type I (linear response), Holling type II (concave upward response) and Holling type III (sigmoid response having a concave downward part at low food density). Note that replacing a functional response in a model with another one of a different type would completely modify models' properties (e.g. Gross et al., 2004; Fussmann and Blasius, 2005). For instance, some models of plankton blooms simply do not 'work' properly in the case of replacing Holling type III with a non-sigmoid one (e.g. Truscott and Brindley, 1994; Hernández-García and López, 2004; Malchow et al., 2005). It is important to add as well that theoretical studies predict enhancing of ecosystems' stability in the case where functional response of predator is of

* Correspondence address: Department of Mathematics, University of Leicester, UK.
E-mail address: morozov_andrew@yahoo.com

sigmoid type (Oaten and Murdoch, 1975a; Scheffer and De Boer, 1995).

What is the most frequently observed type of functional response for herbivorous zooplankton? The conventional way of determining the type of response consists in laboratory experiments on zooplankton feeding, which are usually carried out in small-sized containers or bottles. A huge amount of literature exists on this topic. Experiments reveal non-sigmoid types (i.e. Holling types I and II) for most herbivorous zooplankton species (e.g. DeMott, 1982; Hansen et al., 1990; Hirst and Bunker, 2003; Jeschke et al., 2004). As a result, a rather strong opinion in the literature is that implementation of Holling III type in plankton models is biologically meaningless (DeMott, 1982; Scheffer and De Boer, 1995; Murdoch et al., 1998). On the other hand, there are a number of papers claiming exactly the opposite, i.e. that it is Holling type III that we should use in modelling of grazing by herbivorous (Frost, 1975; Chow-Fraser and Sprules, 1992; Gismervik and Andersen, 1997; Sarnelle and Wilson, 2008). More surprisingly, the latter statement is sometimes based on revisiting previous laboratory experiments that had demonstrated non-sigmoid response for a given species (e.g. Sarnelle and Wilson, 2008). Thus, the question of adequacy of implementation of Holling type III response in models is far from being solved.

I would say, however, that the above discussion on the existence (or non-existence) of type III functional response in feeding experiments might be of little practical importance when one wishes to model zooplankton feeding in real ecosystems. This is especially true for plankton models without vertical spatial resolution, dealing with average over column species densities. The point is that in all models without explicit vertical space, the grazing rate of zooplankton in the column (per unit volume) is computed as

$$E = f(\bar{P})\bar{Z}, \quad (1)$$

where \bar{P} and \bar{Z} are the average (over the column) densities of phytoplankton and zooplankton, respectively; $f(P)$ is the functional response found previously in laboratory experiments.

However, the mean-field approach based on (1) provides satisfactory results only in the case where vertical distribution of plankton is close to homogenous. On the other hand, it is well known that real vertical distribution of plankton is often highly heterogeneous, especially during phytoplankton blooms and this can seriously affect the behaviour of plankton models (e.g. Poggiale et al., 2008). Moreover, herbivorous zooplankton is capable of adjusting its vertical location and feeding at depths of high food concentrations (Townsend et al., 1984; Napp et al., 1988; Castro et al., 1991; Seuront, 2008). As such, the grazing rate E in all models with implicit vertical space should be given by $E = F/H$, where F is the consumption of food in the entire water column and H the depth of the column. The grazing rate (1) can be re-written in the following way:

$$E = \frac{F}{HZ} \bar{Z} = g[P(h), Z(h)]\bar{Z}, \quad (2)$$

where the ratio $F/(HZ)$ is replaced with the function $g[P(h), Z(h)]$, which is a 'true' functional response, i.e. the amount of food consumed in the column per zooplankton biomass.

In this paper, I show that the functional response g (which I call further the overall functional response) might be of sigmoid type even though local grazing is described by a non-sigmoid response. Note that the overall response g is not a function in a strict mathematical sense but it is a function of functions (i.e. a functional) since it depends on vertical distributions of phyto- and zooplankton $P(h)$ and $Z(h)$, which are functions themselves. However, in this paper, I will consider the case $g = g(\bar{P})$, where \bar{P} is the space average density of phytoplankton in the column. The correctness of such assumption will be discussed

in Section 4. Note that such an assumption is made in *all* models without explicit spatial resolution. As a result, the grazing rate of zooplankton is given by $E = g(\bar{P})\bar{Z}$, i.e. as in expression (1). However, the laboratory functional response (or the local functional response) $f(\bar{P})$ should be replaced with the overall response $g(\bar{P})$. I will show that the difference between $f(\bar{P})$ and $g(\bar{P})$ might imply an alteration of *type* of response, in particular, it might result in a Holling type III overall response.

As a part of the current study, I have conducted a rather comprehensive literature search on patterns of zooplankton feeding *in situ*. The results show evidence of alteration of *type* of the response between the overall $g(\bar{P})$ and the local $f(\bar{P})$ functional responses. In particular, by applying a straightforward test, I demonstrate the emergence of Holling type III overall response for herbivorous zooplankton for a number of ecosystems. Surprisingly enough, sigmoid overall responses are obtained for species usually exhibiting non-sigmoid responses (local responses) in laboratories. Such discrepancy is not due to some errors in previous laboratory studies, but is a result of complex foraging behaviour of zooplankton in real ecosystems.

Further, I suggested a simple generic plankton model explaining the observed alteration of type of functional response. The model shows emergence of Holling III type for the overall response $g(\bar{P})$ with a non-sigmoid local response of zooplankton $f(P)$ within a large range of parameters. The obtained Holling type III becomes possible due to a mechanism different from those well known in the literature to be responsible for a sigmoid-shaped response (e.g. learning in food searching, existence of alternative food, refuge of prey). The model predicts the crucial role of light attenuation by phytoplankton and depth of the column in shaping the zooplankton functional response.

2. Evidence for Holling type III zooplankton functional response *in situ*

First, a rather detailed example of emergence of the overall response of sigmoid type from the local non-sigmoid one can be found in Morozov et al. (2008). The ecosystem under study was the central Barents Sea. Here I provide another example of such alteration of types based on field data from Bautista and Harris (1992). The results are presented in Fig. 1. Fig. 1A shows the overall functional response g for *Calanus helgolandicus* (large-sized copepod species) plotted versus average chlorophyll density \bar{P} in the water column ($H=50$ m). In other words, the specific consumption of food of the whole population of *C. helgolandicus* is plotted versus average food density in the column. Note that the constructed functional response corresponds to the pre-bloom and the beginning of the bloom periods (March–April 1989). Such a restriction is needed due to the fact that a succession among different algal groups occurs at the peak of the bloom as well as during the post-bloom period (Bautista and Harris, 1992). As such, different algal groups have different nutrition properties and constructing the functional response as a function of *total* amount of chlorophyll does not make any sense in this case.

To demonstrate that the functional response Fig. 1A is close to Holling type III, the data were fitted with the power functions $g = \alpha\bar{P}^\gamma$ (with $\gamma \geq 1$). The latter fitting can be considered as the first term of expansion of the sigmoid response given by $\alpha P^\gamma / (1 + \beta P^\gamma)$, which is well adapted in the literature (see Gentleman et al., 2003 and references therein). In Section 3.3, some theoretical background will be given for approximation of the overall response by a power function. Non-linear regression analysis based on the least square method (LSM) has been applied to provide the best parameters (which are given in legends of Fig. 1). The analysis shows that non-linear responses given

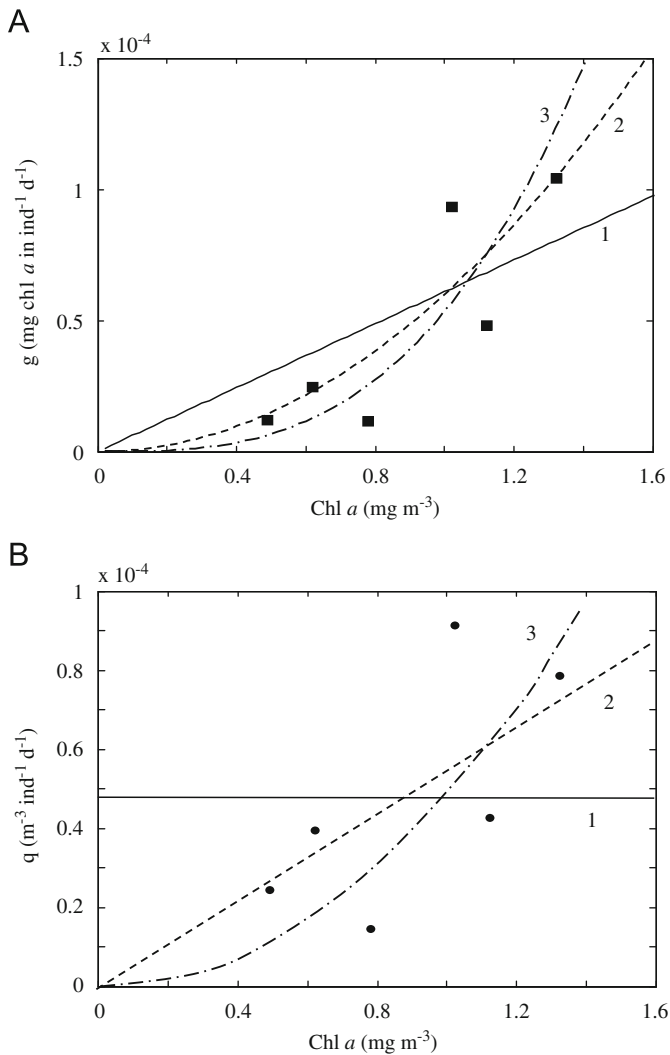


Fig. 1. (A) Overall functional response g of copepods (*Calanus helgolandicus*) measured *in situ*. The data are taken from Bautista and Harris (1992). The fitting functions are: (1) linear function $g(\bar{P}) = a\bar{P}$, $a = 6.1 \times 10^{-5}$; (2) parabolic function $g(\bar{P}) = a\bar{P}^2$, $a = 6.0 \times 10^{-5}$ and (3) cubic function, $g(\bar{P}) = a\bar{P}^3$, $a = 5.4 \times 10^{-5}$. (B) Clearance rate $q = g/\bar{P}$ calculated based on (A). The fitting functions are: (1) $q(\bar{P}) = a$, $a = 4.8 \times 10^{-5}$; (2) $q(\bar{P}) = a\bar{P}$, $a = 5.5 \times 10^{-5}$ and (3) $q(\bar{P}) = a\bar{P}^2$, $a = 5.0 \times 10^{-5}$.

by $g = \alpha\bar{P}^\gamma$ fit the data better than the linear one (for the linear response $R^2 = 0.52$, $\gamma = 1$; for the non-linear responses: $R^2 = 0.706$, $\gamma = 2$; $R^2 = 0.707$, $\gamma = 3$). In each case, the parameter γ was fixed at the indicated values. Note that fitting both parameters α and γ simultaneously results in large values of confidence intervals for γ .

As a result, the overall response of the zooplankton population shown in Fig. 1A is concave upward, i.e. it is of Holling type III. It is interesting that for the same species (*C. helgolandicus*) in laboratory, the functional response (the local response) is closer to Holling type II (e.g. Schnack, 1983). The possible explanation of such alteration between the responses consists in changing in feeding strategies of zooplankton with an increase of total amount of food in the system (Bautista and Harris, 1992). In particular, major grazing takes place at depths with high food abundance.

To make the conclusion about the Holling type III response in Fig. 1A more convincing, I plotted as well the clearance rate of zooplankton, which is determined by $q = g/\bar{P}$. Note that the clearance rate of a sigmoid response increases with an increase of food density at low food densities whereas the clearance rate of non-sigmoid response either always decreases (Holling type II)

or remains constant for Holling type I (Chow-Fraser and Sprules, 1992). Fig. 1B demonstrates an increase of the overall clearance rate q with an increase of food, which is in support of sigmoid shape of functional response. Based on the previous approximation of g by power functions, I considered fitting of q as $q = \alpha\bar{P}^{\gamma-1}$. This gives $R^2 = 0$ for the linear functional response ($\gamma = 1$); $R^2 = 0.47$ for parabolic functional response ($\gamma = 2$) and $R^2 = 0.40$ for a response parameterized by a cubic parabola ($\gamma = 3$). Note also that implementation of Akaike information criteria tells us that the linear response has substantially less support compared with responses with $\gamma > 1$. This takes place for approximation of response function g and clearance rate q .

Surprisingly, there is a notable scarcity of data in the plankton literature that could allow construction of overall functional responses of zooplankton *in situ* similar to the one constructed above. This is especially true for data on zooplankton feeding during pre-bloom and beginning of bloom periods. Note that these are exactly those periods where one can distinguish between sigmoid and non-sigmoid responses since all responses behave in a similar way at high phytoplankton densities, exhibiting saturation. However, the mentioned difficulty can be partially settled in the case where one is interested in demonstrating only the existence of Holling type III response without plotting the response itself.

In this paper, I suggest a simple straightforward test to demonstrate the emergence of Holling type III response in real plankton communities. To implement the test, one needs to plot the ratio of the overall functional responses g_2/g_1 versus the ratio P_2/P_1 of the total amounts of food at any two stations. Note that the environmental conditions (e.g. temperature, hydrological regimes, etc.) at the two stations should be very close to each other. The results can be easily interpreted with the help of $(g_2/g_1, P_2/P_1)$ diagram (see Fig. 2A). In such a representation, Holling type I would correspond to points lying on the dotted line $g_2/g_1 = P_2/P_1$, i.e. an increase of consumption rate would be proportional to the increase of amount of food. Points related to Holling type II response should get inside the domain situated below the dotted line. Note that, the same concerns Holling type III response after saturation. Finally, the domain corresponding to Holling type III (before saturation) is situated above the dotted line since an increase in food amount by the factor of m would result in an increase of average specific grazing rate by the factor of $n > m$. Note that we consider that $P_2/P_1 > 1$; otherwise, the location of domains for Holling type II and III will be the opposite.

Implementation of the above test demonstrates evidence for Holling type III overall response in different ecosystems (see Fig. 2B). I used literature field data on grazing of copepods in oceans, making sure that there was no pronounced succession among different algal groups with different nutrition characteristics during the considered periods. One can see from Fig. 2B that for the considered ecosystems, points in the diagram are situated well above the dotted line, showing an increase in grazing rate (per unit zooplankton biomass) more rapid than linear. Details regarding the data sets used in Fig. 2B are given in the figure legend. Thus, the responses $g(P)$ of the whole zooplankton populations in the column as functions of the total amount of food were of sigmoid type. On the other hand, it is to be emphasized that grazing of each of those species in laboratories shows a non-sigmoid 'local' response.

3. Modelling the emergence of Holling type III zooplankton functional response

3.1. General idea of the method

The central idea of the method implemented below is the following. A plankton model with *explicit* vertical resolution is

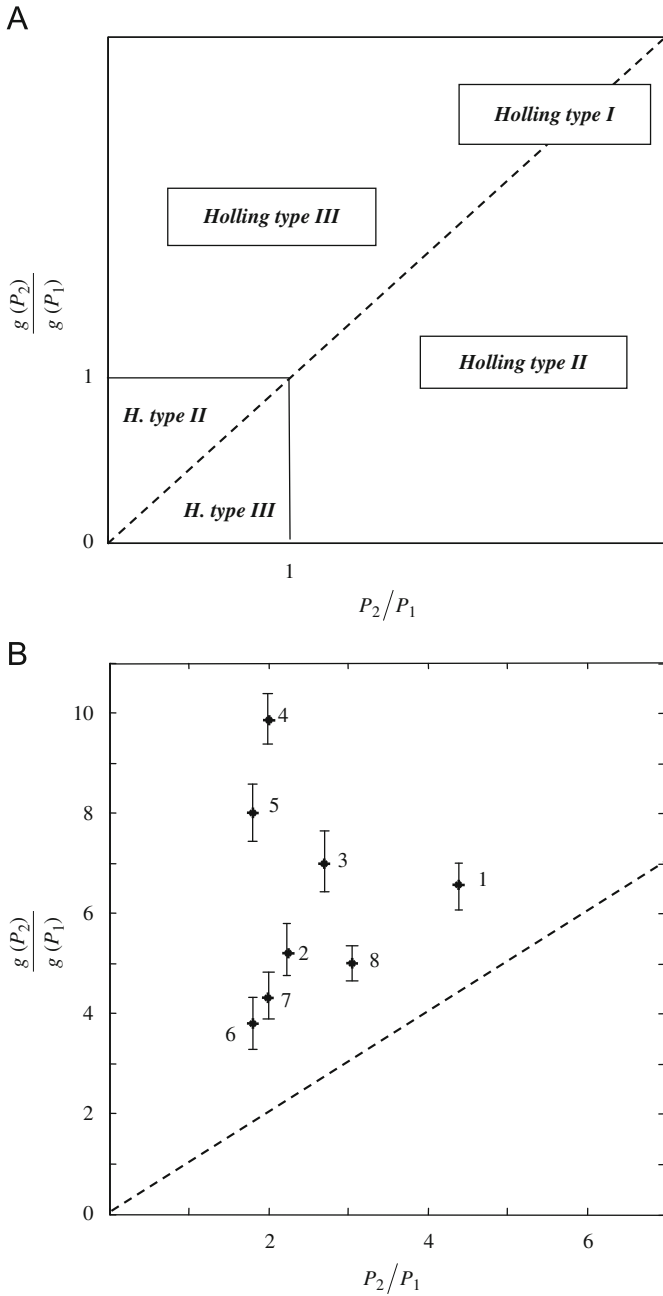


Fig. 2. (A) Determining the type of functional response based on $(g_2/g_1, P_2/P_1)$ diagram, where P_2/P_1 is the relative increase of total amount of food and g_2/g_1 the relative increase in specific consumption rate of a zooplankton population. (B) Evidence for sigmoid functional response in real plankton communities. The points are situated well above the dotted line $g_2/g_1 = P_2/P_1$, which supports a sigmoid-like behaviour of the responses. The data represent feeding of marine copepods in the following ecosystems: (1, 2) Barents Sea, May and July 2003, 2005 (Morozov et al., 2008); (3) coastal waters off Plymouth, March–April 1989 (Bautista and Harris, 1992); (4) coastal waters off Plymouth, March–April 1990 (Bautista et al., 1992); (5) Faroe Shelf, May 2004 (Debes et al., 2008); (6) Western Mediterranean, June 1986 (Saiz and Alcaraz, 1990); (7) Bering Sea, May 1979 (Dagg et al., 1982) and (8) Eastern Barents Sea (Arashkevich, unpublished data). The bars in the figure show error bars.

used to obtain the overall functional response. Based on the vertical distribution of species given by the model's equations, the specific intake rate of the whole zooplankton population is plotted versus the average density of food in the column. The overall functional responses obtained in such a way might be used when constructing plankton models with *implicit* vertical space.

To compute the intake rate in a model with vertical resolution, one needs to know the distribution of food in the column as well as that of grazers. It is important to emphasize that one needs the vertical distribution of *actively* grazing zooplankton, which can be different from the actual distribution of zooplankton in the column. The point is that feeding of zooplankton organisms such as copepods includes periods of active grazing and non-active periods (see Leising et al., 2005 and references therein). As such, one needs to take into account the grazing impact only of those animals that are currently in the active phase of a feeding cycle and neglect those that are in the non-active phase of feeding (Morozov and Arashkevich, 2010). Let us denote the density of actively grazing zooplankton at a depth h by $Z(h)$ and suppose that consumption of active grazers at a depth h can be described via a local functional response $f_h(P(h))$. Then the overall response g of the whole population (per unit biomass) will be determined by

$$g = \frac{\int_0^H f_h(P(h))Z(h)dh}{HZ_0}, \tag{3}$$

where Z_0 is the average zooplankton density (HZ_0 gives the total biomass of zooplankton in the column per unit area) and H the depth of the column. The shape of the overall response g can be revealed by plotting g versus space average of food density \bar{P} .

Note that g might not be a unique function of average food density \bar{P} , since it depends on distributions $P(h)$ and $Z(h)$ rather than on \bar{P} . In the case where $P(h)$ and $Z(h)$ are functions of time given by a dynamical model, the 'number' of model's trajectories will be infinite and this would result in an infinite number of functional responses (3). To settle (at least partially) this problem, a possible solution can be considering the functional response after all transients die out and the system trajectories lie on attractors. In the case where attractors are not stationary states but non-damped oscillations (regular or chaotic), values of $P(h)$, $Z(h)$ in (3) should be understood as time average species densities. Note, however, that such an approach can provide only a few points for a fixed set of parameters (corresponding to the number of attractors). This, definitely, cannot be used for plotting $g(\bar{P})$. To obtain a continuous range of \bar{P} , a system parameter is to be varied. In this paper, growth rate of phytoplankton is chosen as a control parameter. This would allow modelling of an ecologically important case of occurrence of algal blooms arising as a response to an increase of water temperature, light intensity, etc. (e.g. Truscott and Brindley, 1994).

3.2. Model formulation

I assume the total amount of zooplankton in the column to be constant; however, the vertical distribution of actively grazing zooplankton $Z(h)$ can vary depending on phytoplankton distribution. The influence of variation in the total amount of zooplankton on shape of functional response is discussed in Section 3.3. The dynamics of phytoplankton in the column is described by the following equation:

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial h^2} + r(h, P)P - f_h(P)Z(h), \tag{4}$$

where D is the coefficient of vertical turbulent diffusion and r the growth rate of phytoplankton.

Following Morozov and Arashkevich (2010), I shall assume that the distribution of actively grazing zooplankton follows the ideal free distribution (i.e. it is proportional to food density in the column):

$$Z(h) \equiv Z(P) = \frac{P}{\bar{P}} \theta Z_0. \tag{5}$$

The total number of actively grazing zooplankton in the population given by $H0Z_0$ is assumed to be constant, where θ is a coefficient ($0 < \theta < 1$).

To parameterize phytoplankton growth rate, the logistic function $r(1-P/K)$ is used, K being the carrying capacity. Thus, depletion of nutrients in the column is not modelled explicitly. The vertical heterogeneity in phytoplankton growth rate in the model arises due to light shading. I considered the scenario where attenuation of light in the column is due to self-shading of phytoplankton in deep layers by phytoplankton of surface layers. This can be parameterized by multiplying the algal growth rate by $\exp(-vB_h)$, where B_h is the integral biomass of phytoplankton located between the water surface and depth h ; v is a positive coefficient (Herman and Platt, 1983). Note that including absorption of light by water in the generic model (4) does not influence the main results (see the end of Section 3.3).

After having parameterized the functions in (4), we arrive at the following equation:

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial h^2} + r_0 \exp\left(-v \int_0^h P dx\right) P \left(1 - \frac{P}{K}\right) - \frac{1}{\bar{P}} \frac{\alpha P^2 Z_0}{1 + \beta P}, \quad (6)$$

where the local functional response is non-sigmoid (Holling type I for $\beta=0$ and Holling type II for $\beta \neq 0$). The coefficient θ is included in α ; the parameters α, β are considered to be depth-independent; \bar{P} is the space average density of phytoplankton.

The unit of plankton density is chosen to be $\mu\text{g C l}^{-1}$. The maximum phytoplankton growth rate approximately belongs to the range $0.1/\text{d} < r_0 < 4 \text{ 1/d}$ (Edwards and Brindley, 1999). The system's carrying capacity K is rather hard to be estimated. I shall consider $K=100 \mu\text{g C l}^{-1}$, which is consistent with some literature (e.g. Franks, 2001). The coefficients describing local functional response of zooplankton can be estimated as $0.01 \text{ d}/\mu\text{g C l}^{-1} < \alpha < 0.3 \text{ d}/\mu\text{g C l}^{-1}$; $0.005 (\mu\text{g C l}^{-1})^{-1} < \beta < 0.2 (\mu\text{g C l}^{-1})^{-1}$ (Hansen et al., 1990; Saiz and Calbet, 2007). The attenuation constant v is given by

$v=0.005 (\text{m } \mu\text{g C l}^{-1})^{-1}$ (Herman and Platt, 1983; Beckmann and Hense, 2007). I consider the diffusion coefficient to be $D=1 \text{ m}^2/\text{d}$ which is in agreement with the data (Beckmann and Hense, 2007). The density of zooplankton in the column (space average density) is assumed to vary between 1 and $20 \mu\text{g C l}^{-1}$.

3.3. Results of modelling

Analysis of model (6) shows that the shape of the overall zooplankton functional response largely depends on the column's depths H . Thus, I shall consider here separately functional responses in deep and shallow waters.

Fig. 3 shows the overall functional responses (upper row) in a plankton ecosystem with a pronounced depth ($H=100 \text{ m}$) plotted versus integral (column-average) food density. Different responses (bold lines) are obtained by varying the coefficient β in the local response ($1/\beta$ gives the half-saturation density of feeding). The dashed curves (with the same numbers) represent the corresponding local responses that would take place in the case of a well-mixed system. Fig. 3A gives functional responses for large half-saturation densities (including Holling type I local response having $1/\beta = \infty$). Fig. 3B shows functional responses for smaller values of half-saturation density.

One can see from Fig. 3A that for small \bar{P} , all the overall responses are close to linear. This is because distribution of food in the column is close to homogeneous (self-shading is negligible) and the influence of spatial heterogeneity is weak. Further, with an increase of \bar{P} , the overall responses become of Holling type III (concave upwards). This is despite the fact that local functional responses are concave downwards. Increase in β shows (see Fig. 3B) that the range of \bar{P} corresponding to a concave upwards overall functional response is shrinking. In particular, for a supercritical β , there is no alteration of type between local and overall responses.

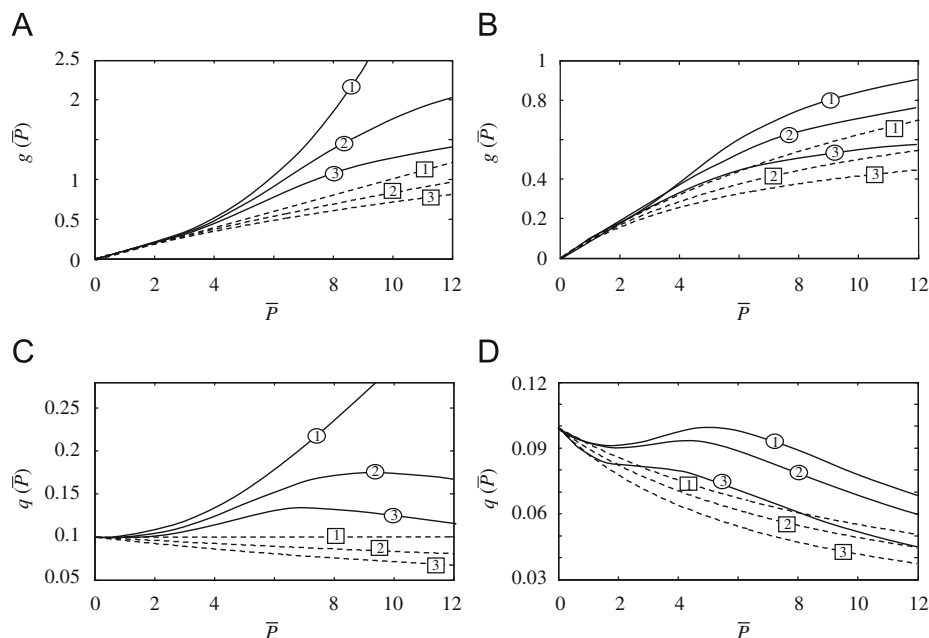


Fig. 3. (A, B) Overall zooplankton functional responses in an ecosystem with a pronounced depth ($H=100 \text{ m}$). The overall responses are represented by bold curves; the dashed curves (with the same numbers) show the corresponding local responses that would take place for homogeneous vertical distribution of plankton (a well-mixed system). Different curves are constructed for different β . (A) Functional responses for large half-saturation densities in the local response; $\beta_1=0, \beta_2=0.02, \beta_3=0.04 (\mu\text{g C l}^{-1})^{-1}$; (B) Functional responses for small half-saturation densities; $\beta_1=0.08, \beta_2=0.1, \beta_3=0.14 (\mu\text{g C l}^{-1})^{-1}$. The other system parameters are $K=100 \mu\text{g C l}^{-1}, \alpha=0.3 \text{ d}/\mu\text{g C l}^{-1}, v=0.005 (\text{m } \mu\text{g C l}^{-1})^{-1}, D=1 \text{ m}^2/\text{d}$ and $Z_0=5 \mu\text{g C l}^{-1}$. (C, D) Overall zooplankton clearance rates (bold curves) obtained for the above constructed overall functional responses. Dashed curves (with the same numbers) show local clearance rates.

The emergence of Holling III type overall response can be seen as well based on the analysis of clearance rates $q(\bar{P})$, obtained by dividing the functional response by food density. Fig. 3C and D shows clearance rates constructed based on responses in Fig. 3A and B, respectively. For small β the overall clearance rates exhibit intervals of increase, i.e. $q'(\bar{P})$. An increase of the clearance rate with \bar{P} can be considered as one of the criteria of the emergence Holling type III response. Note that theoretical studies predict enhancing stability of predator–prey interactions in the case where clearance rate is an increasing function of food density (Oaten and Murdoch, 1975a; Bazykin, 1998).

To understand the mechanism of emergence of Holling type III response in the model, it is convenient to follow the changes in phytoplankton vertical distribution as the total algal biomass increases. Fig. 4 shows profiles of absolute and relative algal densities (Fig. 4A and B, respectively) for different \bar{P} . One can see that the degree of heterogeneity in algal vertical distribution becomes more pronounced when the total amount of phytoplankton increases. Such spatial structuring of phytoplankton in the model occurs due to the process of self-shading. The distribution of active grazers follows that of food (according to (5)) and major grazing is shifted to depths with higher food density. As a result, the overall grazing rate in the column becomes larger compared with the situation where same amount of food is distributed homogeneously.

In Appendix A, the shape of the overall functional response is computed for $K \gg 1$ and $\beta \ll 1$. Considering only two first non-zero terms of (A8) gives

$$g(\bar{P}) \approx \alpha \left(\bar{P} + \bar{P}^3 (vH)^2 \frac{1}{12} \right) \quad (7)$$

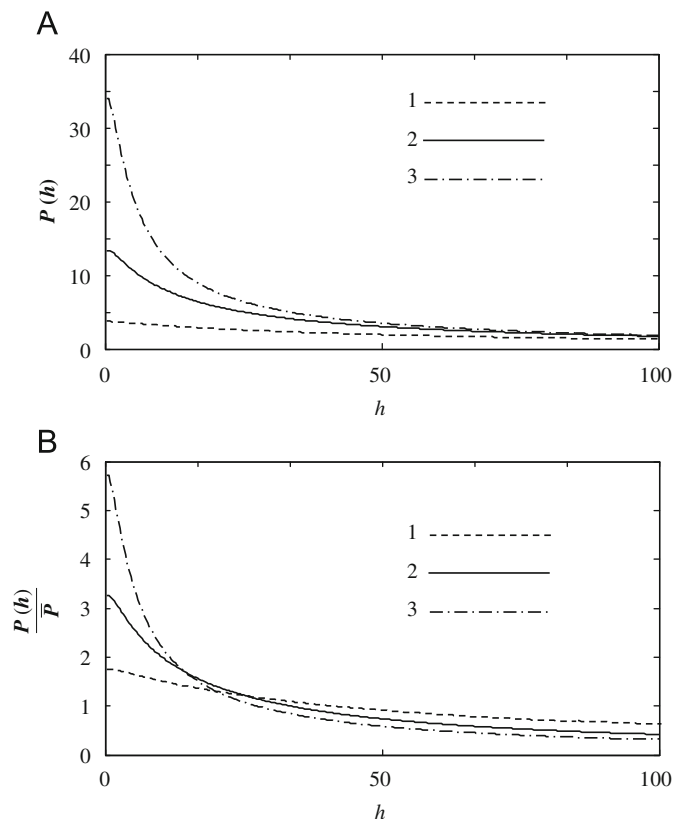


Fig. 4. (A) Variation in vertical profile of phytoplankton in the model with an increase in the total amount of phytoplankton \bar{P} . (B) Corresponding variation in the relative vertical density of phytoplankton P/\bar{P} . The curves in (A, B) are constructed for the following values of \bar{P} : $\bar{P}_1 = 2$, $\bar{P}_2 = 4$, $\bar{P}_3 = 6 \mu\text{g Cl}^{-1}$, $\beta = 0.02 \mu\text{g Cl}^{-1}$. Other system parameters are the same as in Fig. 3.

and for the overall clearance rate

$$q(\bar{P}) \approx \alpha \left(1 + \bar{P}^2 (vH)^2 \frac{1}{12} \right). \quad (8)$$

The stationary vertical profile of phytoplankton is given by (A4). From (7) one can conclude that the increase of the overall functional response for intermediate food densities can be approximately described by a power function. This gives some theoretical background for the implementation of non-linear fitting of the real data in Section 2 in the form $g \approx \alpha \bar{P}^\gamma$.

The functional responses in Fig. 3 have been obtained by varying algal growth rate r_0 for fixed values of Z_0 . Different values of total amount of zooplankton Z_0 change the overall responses. Interestingly enough, such changes turn out to be rather small within the considered parameter range (less than 1–2% of the value of g). This is mostly due to the fact that vertical diffusion ($D = 1 \text{ m}^2/\text{d}$) does not play an important role in shaping vertical profiles of species in the model. Note that in model (6) without diffusion, the overall functional response does not depend on the amount of zooplankton in the system.

The difference between local and overall functional responses becomes less pronounced in plankton ecosystems in shallow waters. Fig. 5 shows the overall functional responses (upper row) in a plankton ecosystem with small depth ($H = 10 \text{ m}$). The corresponding clearance rates are given in the lower row. All the graphs are constructed for the same parameters α and β as in Fig. 3. The corresponding local functional responses are shown by dashed lines. One can see that for the local response of type I ($\beta = 0$), emergence of the overall response of type III (sigmoid response) still takes place. However, the range of β that guarantees alteration of types shrinks substantially compared with the situation in deep waters. For instance, in the considered case, the existence of overall Holling type III becomes impossible already for $\beta > 0.005 (\mu\text{g Cl}^{-1})^{-1}$. Note also that the prediction that the convex behaviour of the overall response becomes less pronounced in shallow waters may also be obtained from expression (7).

Interestingly enough, for supercritical values of β , the overall functional response in shallow waters becomes undetermined for small \bar{P} (see Fig. 5B, D). This is because the system has no stationary states with space average $0 < \bar{P} < P_{cr}$. In this case, a decrease of growth rate r_0 from large values to a certain critical value r_{0cr} would result in a monotonic continuous decrease in \bar{P} up to P_{cr} . A further decrease of r_0 would result in a discontinuous drop of \bar{P} to zero. While varying parameter r_0 in the opposite direction, the whole picture will be different. For small values of r_0 , the only attractor will be a zero stationary state. A further increase in r_0 will not change the picture (even if $r_0 > r_{0cr}$) until the zero state becomes unstable, which happens for $r_0 > \mu$. The loss of stability results in a discontinuous sudden increase of \bar{P} to large values. A further increase in r_0 results in a monotonic increase in \bar{P} . Since $\mu > r_{0cr}$, there is a region of bistability in the parameter space with two stable stationary states, one of the states being the zero state. Note that bistability and hysteresis phenomena in the model occur for small H (shallow waters) and for large β .

Analysis of the influence of the total amount of zooplankton (Z_0) on functional responses in the system shows that in shallow waters such dependence becomes more pronounced compared with the situation in deep waters. In particular, an increase in Z_0 results in an increase of overall functional response. Numerical simulation shows that this is a consequence of a more pronounced vertical gradient in phytoplankton distribution for larger Z_0 . However, the difference between overall responses constructed for $1 < Z_0 < 20$ does not exceed 5% of the value of g .

Finally, I investigated the model's properties in the case where absorption of light by water is taken into account. This can be

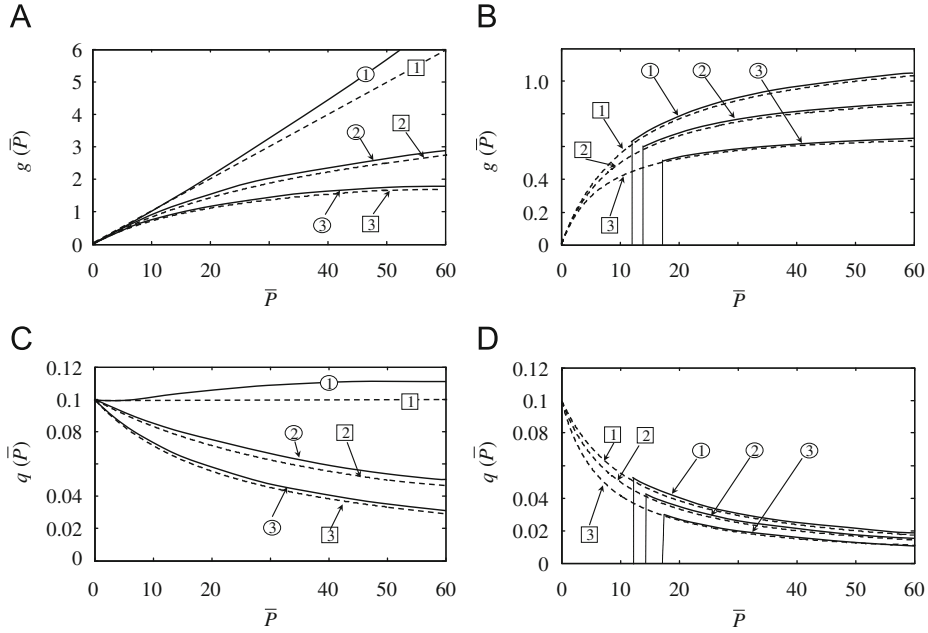


Fig. 5. Overall zooplankton functional responses (A, B) and clearance rates (C, D) in a shallow ecosystem ($H=10\text{ m}$). Overall responses (and the overall clearance rates) are represented by bold curves; dashed curves (with the same numbers) show the corresponding local responses and local clearance rates. Different curves are constructed for different β . (A) Functional responses for large half-saturation densities in the local response; $\beta_1=0$, $\beta_2=0.02$, $\beta_3=0.04\ (\mu\text{g C l}^{-1})^{-1}$. (B) Functional responses for smaller half-saturation densities; $\beta_1=0.08$, $\beta_2=0.1$, $\beta_3=0.14\ (\mu\text{g C l}^{-1})^{-1}$. Note that for large β the overall functional response in shallow waters becomes undetermined for small \bar{P} . For details see the text. The other system's parameters are the same as in Fig. 3.

described via a standard way by multiplying the algal growth rate by $\exp(-\lambda h)$, where λ is the light absorption coefficient (Herman and Platt, 1983). The light absorption coefficient varies within the range $0.01/\text{m} < \gamma < 0.05/\text{m}$ (Herman and Platt, 1983; Vila et al., 1996). The resulting algal growth rate becomes

$$r = r_0 \exp(-\lambda h - v \int_0^h P dx) \left(1 - \frac{P}{K}\right). \quad (9)$$

Numerical simulation shows that inclusion of absorption of light by water does not result in qualitative changes in behaviour of the overall functional response. Moreover, it facilitates emergence of Holling type III overall response; the increase in clearance rate with \bar{P} for $\lambda > 0$ is observed within larger parameter ranges compared with $\lambda = 0$. In particular, Holling type III is found for smaller values of half-saturation density ($1/\beta$) compared with the system with $\lambda = 0$. The corresponding graphs for $g(\bar{P})$ and $q(\bar{P})$ for $\lambda > 0$ are not shown here for the sake of brevity.

An approximate expression for $g(\bar{P})$ in the case where algal growth rate is given by (9) is computed in Appendix A (obtained for $\beta \ll 1$, $K \gg 1$). Considering the first three non-zero terms of (A14) gives

$$g_i(\bar{P}) \approx \alpha \lambda \left(\frac{(1 + \exp(\lambda H)) H v}{2(\exp(\lambda H) - 1)} \bar{P} + \frac{1}{6} H^2 v \bar{P}^2 + \frac{(1 + \exp(\lambda H)) H^3 v^2}{24(\exp(\lambda H) - 1)} \bar{P}^3 \right). \quad (10)$$

The corresponding clearance rate $q\lambda$ can be easily obtained by dividing (10) by \bar{P} . Note that expression (10) transforms itself to (7) when $\lambda \rightarrow 0$. Comparison of the overall responses $g(\bar{P})$ and $g_i(\bar{P})$ reveals that $g_i(\bar{P}) > g(\bar{P})$. Also, the increase in overall clearance rates with \bar{P} (characterized by $q'_i(\bar{P})$) becomes larger for the system with $\lambda > 0$. This can be interpreted as an enhancing of system's stability (Oaten and Murdoch, 1975a). The property that $g_i(\bar{P}) > g(\bar{P})$ can be explained by the fact that gradient in the phytoplankton vertical distribution becomes more pronounced when taking into account absorption by water. Since the active

grazers follow distribution of food, the overall consumption of food in the system with $\lambda > 0$ becomes higher compared with the situation for $\lambda = 0$.

4. Discussion

Dynamics of plankton models is sensitive to the choice of type of functional response of herbivores. Implementation of Holling type III (sigmoid) response enhances the stability of models. There is an opinion in the literature (based on feeding experiments in laboratories) that the use of Holling III type in plankton models is biologically meaningless (DeMott, 1982; Scheffer and De Boer, 1995; Murdoch et al., 1998). In this paper, I challenge this opinion by providing field evidence and theoretical background for the existence of Holling type III zooplankton functional response. I consider the overall functional response of zooplankton in the water column, i.e. the overall intake rate per zooplankton biomass as a function of average food density. Note that it is the overall functional response that is used in all models with implicit vertical space (mean-field models).

My literature search on data on zooplankton feeding *in situ* has revealed that zooplankton populations in the water column (the overall response) often exhibit sigmoid behaviour when local functional responses, observed for the same species in laboratory, are non-sigmoid (i.e. Holling type I or II). Such behaviours have been found in different ecosystems (see Fig. 2). The observed alteration of types between overall and local functional responses was a result of interplay between heterogeneous food distribution in the column and active zooplankton foraging behaviour. As such, it would be preferable to implement type III response in the mean-field plankton models even though non-sigmoid types have been unambiguously reported in laboratories.

I proposed a simple generic model to explain the observed emergence of a sigmoid overall response. The model shows a surprising discrepancy between the behaviour of local response

and that of the overall response. In particular, a Holling type III overall response is observed in the case where local functional response is non-sigmoid. The model predicts the following generic mechanism of emergence of a sigmoid response. The gradient of vertical algal distribution becomes more pronounced with an increase of total amount of phytoplankton in the column (due to self-shading of algae). Grazing of zooplankton becomes shifted to layers with higher food abundance and the total intake rate becomes larger than in the case of a homogeneous distribution with the same amount of food in the column (a well-mixed system). As such, an increase of the total amount of food in the system by the factor $n > 1$ would result in an increase of the intake rate by the factor m ($m > n$). Interestingly, a more detailed analysis of causes of emergence of sigmoid response in real ecosystems (found in references in Fig. 2) indicates that the above mechanism might provide a sound explanation of this phenomenon.

The model predicts emergence of Holling type III response to be facilitated in deep water ecosystems; light attenuation should be also well pronounced (these conclusions can be drawn directly from analysis of expressions (7) and (9) for the overall response). This is related to the fact that in shallow waters the spatial distribution of food becomes more homogeneous and the overall functional response is closer to the local one, which is non-sigmoid. Another important requirement is that half-saturation density in the local response should be sufficiently high. This signifies that the overall response of sigmoid type would arise for large-sized herbivorous, usually characterized by smaller values of β . Interestingly, this conclusion is in good agreement with data on zooplankton feeding *in situ*. For example, the emergence of Holling type III response shown in Section 2 (see Fig. 1), based on data from Bautista and Harris (1992) for large copepod species, is not observed for small-sized species, which exhibit the overall functional response of Holling type II.

Emergence of the overall Holling type III response, shown in this paper, is of vital importance for mathematical modelling of plankton dynamics. In particular, this concerns construction of models without explicit vertical space. Results of the paper suggest that the functional response of the whole zooplankton population in mean-field models might be described by type III response provided the depth of the column is sufficiently large. This would enhance the stability properties of the system (Oaten and Murdoch, 1975a; Scheffer and De Boer, 1995). The choice of concrete parameterization of the overall functional response to be used in mean-field plankton models is a more complicated issue. One can implement expressions (7) and (10) derived analytically, which provide good approximation of $g(\bar{P})$ or small β . However, in case one is interested mostly in qualitative properties of models, the 'classical' parameterization of Holling type III given by $\alpha P^\gamma / (1 + \beta P^\gamma)$ ($\gamma > 1$) might be implemented as well by providing a rough approximation of graphs in Fig. 3. In this case, the half-saturation constant $(1/\beta)^{1/\gamma}$ will have a different meaning from the one measured in laboratory since the parameter β in the overall response would include not only life traits of species but some characteristics of the habitat as well (e.g. depth, light attenuation, vertical diffusion, etc.). On the contrary, in ecosystems with shallow waters the implementation of Holling type II for small \bar{P} in mean-field models becomes more appropriate. In particular, the absence of functional response in models describing shallow waters (see Fig. 5B, D) shows that zooplankton cannot control phytoplankton growth at low algal density. This is exactly what would be predicted by a mean-field model with type II functional response.

In this paper, the overall functional response was considered to be a function of total amount of food in the column, i.e. $g = g(\bar{P})$. However, as follows from (2), different vertical distributions $P(h)$

and $Z(h)$ might correspond to the same average biomasses \bar{P} and \bar{Z} , making computation of grazing rate in terms of the product $g(\bar{P})\bar{Z}$ questionable. However, field observations, especially in nutrient-rich ecosystems, reveal that consumption rate of zooplankton (per unit biomass) in the column can be approximately considered as a function of total amount of food (e.g. Morozov et al., 2008, see also Fig. 1 in this paper), i.e. by $g = g(\bar{P})$. This can be understood from the fact that the profile $P(h)$ is a result of interplay of different biotic and abiotic factors; thus it cannot be arbitrary. In particular, in eutrophic ecosystems there is a strong feedback between vertical distribution of phytoplankton and its total amount \bar{P} in the column (via light attenuation). A typical scenario consists of an increase in gradient of algal spatial distribution when the total amount of phytoplankton is being increased (e.g. Raymont, 1980; Ohman, 1990). Such a property can be seen from a generic model (6) as well (see Fig. 5). I should say, however, that in oligotrophic ecosystems, there is a possibility of alternative density profiles of phytoplankton (i.e. the existence of surface and deep chlorophyll maxima) for the same environmental characteristics (Ryabov et al., 2010). Probably, dynamics of such bi-stable heterogeneous ecosystems can be described adequately only via spatially explicit modelling approach.

The model's predictions are based on an important assumption about the foraging strategy of predators. The distribution of actively feeding zooplankton (i.e. the organisms currently in the active stage of feeding) in the column was considered to be the ideal free distribution. In reality, zooplankton shows more complex food searching behaviour by optimizing its feeding under different constrains (e.g. temperature, presence of high predators, competition among zooplankters of same trophic level, etc.). Incorporation of the mentioned constrains would result in vertical profiles of zooplankton deviating from the ideal free distribution law (e.g. Liu et al., 2003; Lampert, 2005; Leising et al., 2005). However, this should not be considered as a serious restriction for applications of the obtained modelling results. The point is that the overall sigmoid response in model (6) is observed when the ideal free distribution of predators is not really 'ideal'. Simulations show, for small perturbations of the ideal free law (5), an increase of \bar{P} results in a larger than linear increase of functional response, i.e. in a type III response. In particular, this occurs for spatially periodical perturbations having random amplitude and random phase (up to 20–50% of the values of η). Another important issue is that including the mentioned constrains, when modelling the optimal foraging strategy of herbivores, would be ecosystems' specific. On the contrary, positive correlations between vertical location of active feeders and food density in the column have been reported in a large number of plankton ecosystems in different geographic regions (i.e. it is a generic property of most plankton ecosystems). Thus, the free ideal law can be considered as zero-order approximation of vertical distribution of active feeders for implementation in generic plankton models.

Also, I would like to mention that the assumption about the ideal free distribution of active grazers in the column is not crucial to obtain a sigmoid overall functional response. For instance, a sigmoid-shaped overall functional response has been recently found in a model ecosystem (Morozov and Arashkevich, 2008) in the case where rate of active vertical displacement of zooplankton was proportional to the gradient of food concentration. Note that the resultant vertical distribution of zooplankton in the cited paper was not the ideal free distribution. However, the main mechanism of emergence of Holling type III response was similar to the one found in the current paper.

Finally, it is to be emphasized that the mechanism of emergence of Holling type III zooplankton functional response

suggested here is somewhat different from those given earlier in the ecological literature (both in aquatic and terrestrial ecosystems). For instance, the most frequently used explanations of sigmoid-like shape of functional response are: (i) existence of alternative food (Oaten and Murdoch, 1975b; Akre and Johnson, 1979; Gentleman et al., 2003; Elliott 2004), (ii) refuge for prey (Holling, 1966; Taylor, 1984; Poggiale, 1998; Wang et al., 2009) and (iii) learning in food searching by predator (Holling, 1965; Luck et al., 1979; Van Leeuwen et al., 2007). None of them is needed to provide a sigmoid response in model (6).

Sigmoid functional response arising due to heterogeneity of space is less addressed in the literature. Recently, it was shown that prey patchiness and predator aggregation might result in a sigmoid overall functional response when the local response is non-sigmoid (Nachman, 2006). The ecosystem under study was an acarine predator–prey system. In the current paper, a sigmoid-like overall response arises via a close scenario: the ideal free distribution can be considered as aggregation of predators. However, an important difference of plankton ecosystems is the existence of a strong feedback between spatial distribution of prey (algae) and its total amount in the system (via light attenuation). In this sense, nutrient-rich plankton ecosystems are rather unique among other ecosystems. They combine light-mediated aggregation of prey distribution (see Fig. 4) and existence of fast-moving predators capable of regulating grazing load within the whole habitat due to possibility of fast displacement of organisms in the vertical direction. It is quite possible, however, that some other non-plankton ecosystems with similar properties of spatial predator–prey interactions would result in the emergence of an overall Holling type III response according to the reported mechanism.

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Appendix A

Here we derive analytically an expression for the overall functional response in the case $K \ll 1$ and $\beta \ll 1$, i.e. when the local functional response is linear or close to linear.

Let us first consider the situation when attenuation of light is due to self-shading of algae. The model equation is given by (6). To avoid cumbersome formulae, we shall consider the case where the diffusion term in (6) is much smaller compared with growth rate and grazing rate. Neglecting the diffusion term and setting $K \rightarrow \infty$ gives the equation for stationary density of phytoplankton:

$$0 = r_0 \exp\left(-v \int_0^h P dx\right) - \alpha \frac{P}{\bar{P}} Z_0. \tag{A1}$$

It can be easily derived from (A1) that

$$v \int_0^h P(x) dx = -\ln\left(\frac{\alpha P(h) Z_0}{r_0 \bar{P}}\right). \tag{A2}$$

After differentiating both sides of the equation with respect to h we obtain

$$-v P^2(h) = P'(h). \tag{A3}$$

Integration of (A3) gives the stationary profile of phytoplankton:

$$P(h) = \frac{1}{v h + C}, \tag{A4}$$

where C is a constant of integration. Consider the space average of both sides of (A4):

$$\bar{P} = \frac{1}{v H} \ln\left(\frac{v H + C}{C}\right). \tag{A5}$$

The stationary profile of phytoplankton can be re-written as a function of \bar{P} :

$$P = \frac{1}{v\left(h - (H/1 - \exp(\bar{P}vH))\right)}. \tag{A6}$$

The overall functional response is given by

$$g(\bar{P}) = \frac{1}{H} \int_0^H \alpha \frac{P^2(h)}{\bar{P}} dh. \tag{A7}$$

Substituting (A6) into (A7) we obtain after simplification

$$g(\bar{P}) = \frac{\exp(\bar{P}vH) + \exp(-\bar{P}vH) - 2}{(vH)^2 \bar{P}}. \tag{A8}$$

Taylor expansion of (A8) gives the overall functional response in the following form:

$$g(\bar{P}) = \alpha \left(\bar{P} + \bar{P}^3 (vH)^2 \frac{2}{4!} + \bar{P}^5 (vH)^4 \frac{2}{6!} + \bar{P}^7 (vH)^6 \frac{2}{8!} + \dots \right). \tag{A9}$$

Clearance rate can be easily computed by dividing (A9) by \bar{P} :

$$q(\bar{P}) = \alpha \left(1 + \bar{P}^2 (vH)^2 \frac{2}{4!} + \bar{P}^4 (vH)^4 \frac{2}{6!} + \bar{P}^6 (vH)^6 \frac{2}{8!} + \dots \right). \tag{A10}$$

One can see that q is an increasing function of \bar{P} since its first derivative is positive. Numerical simulation shows that expression (A9) provides a satisfactory approximation of the overall response for finite values of carrying capacity K (up to $K=50$) and small values of $\beta > 0$. This approximation can be used even when the vertical diffusion is non-zero ($D > 0$ but small). In particular, it can be used for $D=1$.

Now, let us consider the situation when the absorption of light by water is taken into account. The growth rate of phytoplankton is given by (9). The expression for overall functional response can be derived in a similar way as above. The differential equation for vertical profile of phytoplankton is the following:

$$-\lambda - v P^2(h) = P'(h). \tag{A11}$$

Integration of (A11) gives

$$P(h) = \frac{C \exp(\lambda x)}{v C \exp(\lambda x) - 1}, \tag{A12}$$

where C is a constant of integration. Applying the same technique as before, the vertical profile of phytoplankton can be expressed via space average algal density \bar{P} as

$$P(h) = \frac{\lambda \exp(-\lambda(h-H))(\exp(v\bar{P}H) - 1)}{v(-1 + \exp(H(h + v\bar{P})) + \exp(-\lambda(h-H)) - \exp(-\lambda(h-H) + v\bar{P}H))}. \tag{A13}$$

The overall functional response is given by integration of (A13) over the column. However, the analytical expression for $g_i(\bar{P})$ results in a rather cumbersome analytical formula. The Taylor expansion gives the following expressions for $g_i(\bar{P})$:

$$g_i(\bar{P}) = (a_1 \bar{P} + a_2 \bar{P}^2 + a_3 \bar{P}^3 + \dots), \tag{A14}$$

where

$$a_{2n+1} = \frac{1}{(2n+2)!} \frac{\alpha \lambda (1 + \exp(\lambda H)) H^{2n+1} v^{2n}}{(\exp(\lambda H) - 1)},$$

$$a_{2n} = \frac{\alpha \lambda H^{2n} v^{2n-1}}{(2n+1)!}.$$

Note that (A14) becomes (A9) when $\lambda \rightarrow 0$. Simulations show that the first three terms in (A14) give a good approximation of $g_i(\bar{P})$ in the considered parameter range.

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