Review

Implementation of the zooplankton functional response in plankton models: State of the art, recent challenges and future directions

Andrew Morozov [a,b,*], Jean-Christophe Poggiale [c], Flora Cordoleani [c]

[a] Department of Mathematics, University of Leicester, UK
[b] Shirshov Institute of Oceanology, Moscow, Russia
[c] Université de la Méditerranée, Marseille, France

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ABSTRACT

The conventional way of describing grazing in plankton models is based on a zooplankton functional response framework, according to which the consumption rate is computed as the product of a certain function of food (the functional response) and the density/biomass of herbivorous zooplankton. A large amount of literature on experimental feeding reports the existence of a zooplankton functional response in microcosms and small mesocosms, which goes a long way towards explaining the popularity of this framework both in mean-field (e.g. NPZD models) and spatially resolved models. On the other hand, the complex foraging behaviour of zooplankton (feeding cycles) as well as spatial heterogeneity of food and grazer distributions (plankton patchiness) across time and space scales raise questions as to the existence of a functional response of herbivores *in vivo*. In the current review, we discuss limitations of the 'classical' zooplankton functional response and consider possible ways to amend this framework to cope with the complexity of real planktonic ecosystems. Our general conclusion is that although the functional response of herbivores often does not exist in real ecosystems (especially in the form observed in the laboratory), this framework can be rather useful in modelling – but it does need some amendment which can be made based on various techniques of model reduction. We also show that the shape of the functional response depends on the spatial resolution ('frame') of the model. We argue that incorporating foraging behaviour and spatial heterogeneity in plankton models would not necessarily require the use of individual based modelling – an approach which is now becoming dominant in the literature. Finally, we list concrete future directions and challenges and emphasize the importance of a closer collaboration between plankton biologists and modellers in order to make further progress towards better descriptions of zooplankton grazing.

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* Corresponding author at: Department of Mathematics, University of Leicester, UK.
  E-mail address: am379@leicester.ac.uk (A. Morozov).

1. Introduction

This paper aims to present a review of the implementation of the functional response framework for modelling the grazing of herbivorous zooplankton. In mathematical ecology, the functional response of a predator is generally defined as the specific rate of consumption of food (per predator biomass per unit of time) as a function of food density (e.g. Solomon, 1949; Holling, 1959; Begon et al., 2005) – the total consumption rate of the whole predator population can thus be computed as the product of its biomass and its functional response. Such an approach has a long history beginning with the famous Lotka-Volterra predator–prey model (May, 1974; Odum and Barrett, 2004; Begon et al., 2005). Most plankton models (either space-resolved or mean-field NPZD models) implement the functional response framework, and the popularity of this approach can be explained in part by a large amount of the experimental work on zooplankton feeding in laboratories. Indeed, numerous experiments have demonstrated that the rate of consumption of food by a zooplankter can be well described as a certain function of food density, which can differ between zooplankton species and food types (see some key-note references in Section 2).

Recently, however, several publications have recognized that the conventional interpretation of feeding experiments in modelling might be too simplistic. In many cases, zooplankters with full guts are found at depths where the food density is well below the feeding threshold, which obviously cannot be observed in laboratories (Leising and Franks, 2000 and references therein). It has been also shown that the parameters describing the zooplankton functional response (maximal consumption rate, saturation constants, etc.) found *in vitro* can largely differ from those found for the same species in real ecosystems (e.g. Rothschild and Osborn, 1988; Saiz and Calbet, 2007). The zooplankton functional response *in vivo* can even have a different shape from the one which is observed in experimental tanks (e.g. Morozov et al., 2008; Morozov, 2010) and this implies alteration of a Holling *type* of functional response. Interestingly, some papers even challenge the very existence of a functional response in real planktonic ecosystems – the rationale for this being that the grazing rate of zooplankton in the ocean/lakes at a given spatial location (e.g. at a given depth) often cannot be described simply as a product of a certain function of food density and the biomass of zooplankton around this location.

Apparent difficulties in the description of zooplankton grazing arise due to the complexity of the active foraging behaviour of zooplankton in the water column (feeding cycles) which takes place on different time and spatial scales (e.g. Leising et al., 2005a and the references therein; see also Tiselius and Jonsson, 1990). Another important issue is that the horizontal distributions of both phytoplankton and zooplankton are highly heterogeneous (patchy) across spatial scales (Mackas and Boyd, 1979; Steele and Henderson, 1992; Abraham, 1998). An important question is how to include the plankton patchiness which takes place on smaller scales (micro- and mesoscales) when describing grazing in models with more coarse horizontal resolution (e.g. the regional scale). In this review, we discuss the limitations of the 'classical' zooplankton functional response approach and consider various ways of amending the existing plankton models based on the functional response framework to cope with recent challenges. Here we mostly consider the grazing of herbivorous zooplankton; however, the same ideas can be successfully applied to the modelling of carnivorous zooplankton as well.

The review is organized as follows. In Section 2, we discuss patterns of zooplankton experimental feeding *in vitro* and define the laboratory functional response. We also consider the effect of intra-population variability on the shape of the functional response. In Section 3, we focus on the existence of a zooplankton functional response in real ecosystems, we suggest two definitions of functional response based on the Lagrangian and the Eulerian frameworks, and we discuss their applicability. In Section 4, we consider two important cases where the functional response framework can be successfully implemented in models operating on large time and spatial scales, where such a response does not exists in a strict sense. In Section 5 we discuss the Lagrangian and the Eulerian approaches to the modelling of zooplankton feeding. Finally, in Section 6, we make some general conclusions about the applicability of the functional response framework in plankton modelling and discuss future perspectives and directions.

2. Zooplankton functional response in laboratories

The popularity of the implementation of the zooplankton functional response paradigm in modelling is closely related to the classical works on experimental feeding in laboratories (e.g. Frost, 1975). There exists a tremendous amount of literature on this topic (see Saiz and Calbet (2007) for a review). In these experiments, it has been shown that for a given sort of food (e.g. fixed size of food particles) the rate of food consumption by a zooplankter can be described as a certain function of food density P, which dependence is referred to as the zooplankton functional response $f(P)$. Thus, the consumption rate of zooplankton with the biomass Z can be computed as $Z f(P)$, an assumption which should hold, at least, for microcosms and small-sized mesocosms. We shall further refer to this functional response as the 'laboratory functional response'. Note that to observe a laboratory functional response, experiments should be carried out under identical setups since other important factors such as feeding history, acclimation time, and small scale turbulence can largely affect the consumption rates, especially, at very low food concentrations (Caparroy and Carlotti, 1996; Carlotti and Poggiale, 2010).

It is well known that different developmental stages of the same species can exhibit different functional responses (Bamstedt et al., 2000; Acuña and Kiefer, 2000) and this should be taken into account in more accurate models. More interestingly, feeders belonging to the same developmental stage often show a large deviation in their individual ingestion rates (e.g. Mullin, 1975; Mackas and Burns, 1986; Mobley, 1987; Saiz et al., 1993; Karaköylü et al., 2009) and there are at least two main reasons for such a deviation. First, this can be due to between individual variations of physiological characteristics (e.g. the presence of more efficient and less efficient feeders), and second, the rate of food consumption of the same individual can show a large variation for the same amount of food. As such, the functional response of an individual zooplankter i can be modelled as $f_i(P) + \varepsilon_i$, where ε_i is a random variable with a zero mean. We should emphasize that by considering the individual response $f_i(P)$ we implicitly average the food intake rate of an organism over a certain time period to take into account feeding rhythms (Karaköylü et al., 2009). As a result, instead of a single functional response, we have a distribution of functional responses, which can be described by a certain probability distribution function both for the quantities $f_i(P)$ and ε_i.

In mathematical models, however, we usually need the rate of food consumption of all feeders of the same cohort (e.g. all organisms of the same developmental stage) or population. This rate is given by the summation feeding rates over the cohort/population:

$$F = \sum_i [f_i(P) + \varepsilon_i] Z_i \approx \sum_i f_i(P) Z_i = Z_0 \sum_i f_i(P) \frac{Z_i}{Z_0}, \qquad (1)$$

where Z_i is the body mass of zooplankter i; Z_0 is the average body biomass. The functional response of N individuals can be defined as the consumption rate per biomass of grazers of the cohort:

$$f(P) = \frac{F}{NZ_0} = \frac{1}{N}\sum_i f_i(P)\frac{Z_i}{Z_0} \approx \frac{1}{N}\sum_i f_i(P), \tag{2}$$

where we assumed for the sake of simplicity that the body mass within the cohort is the same. Thus, the functional response that we use in models should be actually given by averaging the individual functional responses, i.e. by the expectation (the mean value) of $f_i(P)$. Clearly, that the value of $f(P)$ should depend on the distribution function of the individual consumption $f_i(P)$ within the cohort. In reality, we often ignore the shape of $f_i(P)$, as well as the underling probability distribution functions, thus $f(P)$ can be estimated only based on a series of repeated laboratory experiments. Note that in most plankton models the distribution of $f_i(P)$ within cohorts is implicitly considered to be constant, thus $f(P)$ becomes a function of the food density only.

We strongly believe that the main role of the laboratory experiments should consist in providing us with the information about $f(P)$ rather than in revealing the shape of $f_i(P)$. This can be demonstrated from the following example (see Fig. 1). In this figure, we generated $N = 300$ individual functional responses each of which is given by

$$f_i(P) = \begin{cases} aP, & 0 < P < P_1 \\ P_1, & P_1 < P \end{cases} \tag{3}$$

The dependence (3) was suggested theoretically to describe feeding of zooplankton filters (Jeschke et al., 2004). To take into account intra-population variability, we considered that the parameters a and P_1 to be normally distributed random variables. We constructed the functional response $f(P)$ of the cohort by averaging $f_i(P)$ over N individuals (shown by the solid line). We also show $N_1 = 8$ randomly chosen individual functional responses which mimic a laboratory feeding experiment with a small number of individuals (shown by filled circles). To add more realism to our simulations we included random disturbance of each individual functional response, i.e. considering $f_i(P) + \varepsilon$. The filled squares represent averaging over the N_1 'experimental' functional responses, i.e. the experimental estimate of $f(P)$. Finally, the dashed curve represents fitting of the experimental 'data' by curve (3) which we pretend to know *a priori*. One can see that the cohort response $f(P)$ has a rather different shape compared to the best fitted response (3). In particular, $f(P)$ is a concave downward function

which, as it is well known in the theoretical studies, would impede the efficiency of grazing more than the linear functional response (Gentleman and Neuheimer, 2008).

Individual variability in feeding rates causes another difficulty: the choice of the exact analytical formulation for the cohort response $f(P)$ to fit the experimental data. Indeed, we often ignore both the exact shape of individual response and the probability distribution function of those responses within the cohort. In the optimistic case where we know *a priori* the type of the resultant response (say, Holling type II), the conventional approach consists in using 2–3 'universal' fitting functions such as Monod, Ivlev and trigonometric parameterizations and choosing the one giving the highest value of R^2. Usually neither of them describe the exact shape of the functional response $f(P)$ as in illustrated in Fig. 1; however, this fact should not be considered as a major obstacle if the best fitting provides a reasonable approximation of $f(P)$. More serious problems arise in the case where several functions (e.g. Monod, Ivlev, etc.) provide reasonably good fitting for the given data set. This can result in the phenomenon known as structural sensitivity of models: close and statistically indistinguishable zooplankton functional responses may predict rather different model's outcomes (Fussmann and Blasius, 2005; Cordoleani et al., 2011).

Finally, to conclude this section, we would recommended experimentalists to not immediately discard the experimental points with unusually small or large ingestion rates, since those 'outliers' could play an important role in revealing the actual functional response $f(P)$ of the whole cohort/population. This can be seen, for instance, from Fig. 1. In particular, those outliers would allow us to better estimate the consumption rate averaged over the individuals having different life traits as well as a deviation from this average (i.e. estimating the variance of life traits among grazers).

3. Zooplankton functional response in real ecosystems

Does the zooplankton functional response exist in real ecosystems? To answer this fundamental question we first need a proper definition of such a response, since the conventional definition based on laboratory experiments may not necessarily 'work' for real ecosystems. Firstly, the natural environment is characterized by a high spatial variation of food distribution (both in horizontal and vertical directions), which is rather different from the
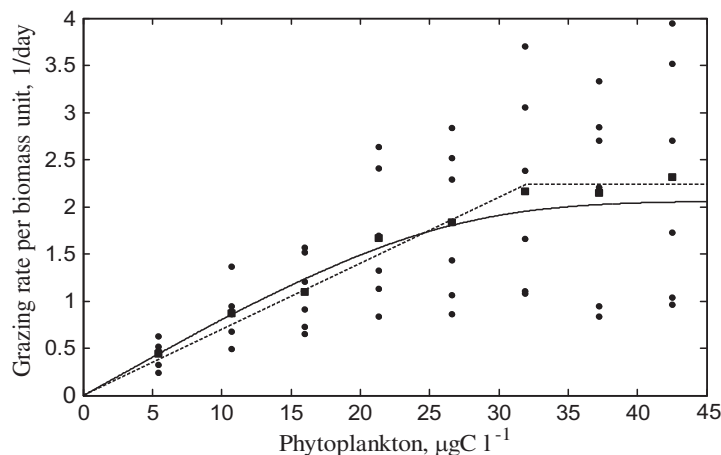

Fig. 1. The role of intra-individual variability in reconstruction of the zooplankton functional response from laboratory experiments. The data (filled circles) simulate the experiments on feeding of $N_1 = 8$ different copepods randomly chosen from a cohort of $N = 300$ individuals. Feeding of each individual is described by the functional response $f_i(P)$ of shape (3), where the parameters a and P_1 are normally distributed ($a \sim (0.1, 0.02)$; $P_1 \sim (30, 10)$). We mimic eventual random deviations from $f_i(P)$ as well as experimental errors by multiplying individual responses by $(1 + \varepsilon)$, where ε is normally distributed random number $\varepsilon \sim (0, 0.05)$. The solid-line curve represents the functional response $f(P)$ of the whole cohort obtained by averaging $f_i(P)$ over N individuals. The filled squares show the reconstructed functional response $f(P)$ based only on the experimental data. The dashed line shows fitting of experimental points based on function (3).

homogenous food supply found in microcosms. Another important issue is the complex foraging behaviour of some herbivores – with feeding cycles taking place on various temporal and spatial scales. The feeding cycle with the largest time and space scales includes regular patterns of diel vertical migration, due to the presence of visual predators, herbivorous zooplankton are forced to leave the euphotic zone in the daytime and limit their grazing to nighttime periods (Bollens and Frost, 1989; Ohman, 1990). Foraging behaviour is also observed at smaller spatial and temporal scales. In particular, on microscales (from several centimetres up to a meter) zooplankters show active foraging behaviour by performing foraging jumps and accumulating in micropatches of high food density (Dodson et al., 1997; Malkiel et al., 2003; Bochdansky and Bollens, 2004). Less studied is the feeding behaviour of zooplankton at intermediate scales (1–3 h and dozens of metres) which can include short-term forages in high density food surface layers and deeper layers, in which organisms digest the consumed food (Leising et al., 2005a and the references therein; Cottier et al., 2006) – as a result, grazing and digestion can be separated in space. Note that even in the case of a simple pattern of movement as a monotonous ascending/descending, the existence of feeding rhythms of the grazer may result in the absence of an apparent correlation between the ambient food distribution and ingestion rate (Simard et al., 1985; Ishii, 1990).

3.1. Lagrangian-based definition of zooplankton functional response

Based on the apparent complexity of foraging behaviour of zooplankton *in vivo* it is natural to suggest a definition of the functional response by following individual grazers along their paths (trajectories) in space instead of fixing the feeding location. This idea appeals to the implementation of the Lagrangian modelling framework (see also Section 5).

For simplicity, we assume that within the habitat there exists only one sort of food and consumers belong to a single species of the same developmental stage. The consumption rate by $N \gg 1$ zooplankters over time period T is given by

$$F = \sum_{i=1}^{N} \langle q_i(t) \rangle_T' = \frac{Z_0 N}{Z_0 N} \sum_{i=1}^{N} \langle q_i(t) \rangle_T' = Z \cdot g_1, \qquad (4)$$

where Z_0 is the body mass of a single individual, Z is the total biomass, $q_i(t)$ is the instantaneous consumption rate by individual i and $\langle \rangle_T'$ denotes averaging over the path of a zooplankter. Thus, the grazing rate of the zooplankton population is given by the product of the biomass Z and a certain quantity g_1. Computation of the feeding rate based on (4) follows the movement of individuals and takes into account complex foraging cycles with periods of active grazing and those of rest. This gives the amount of food consumed by the ensemble of N individuals with biomass Z. The main difficulty in the implementation of (4) arises when one tries to relate g_1 and the ambient food concentration P, since during their foraging cycle, organisms may alternate between food-rich and food poor locations. In the case where the grazing rate of the population can be approximately described as

$$F = Z \cdot g_1(\langle P \rangle_T'), \qquad (5)$$

we define g_1 as the functional response of zooplankton since it relates the grazing rate and the food concentration in the habitat. Here $\langle P \rangle_T'$ denotes the density of food in the layers where the active grazing takes place. The Lagrangian-based response is a function of the food density averaged over the layers where organisms mostly graze. For this reason, the density $\langle P \rangle_T'$ can be higher than the spatial average density of food in the column. In particular, it can be equal to the maximal density of phytoplankton since feeding often takes place at depths with maximal food density (Mullin and Brooks, 1972; Pierson et al., 2009; Morozov and Arashkevich, 2010).

Implementation of (5) in models requires the knowledge of the individual paths and the grazing rates along those paths to obtain the path-averaged density $\langle P \rangle_T'$. Since the current technologies do not allow us to track movement of grazers *in vivo* and simultaneously measure their ingestion rates, questions about the existence of functional responses (5) are still open, but we can use computer simulations to calculate zooplankton foraging paths based on individual-based modelling (IBM) (see Section 5). This could shed some light on the existence of functional response (5). We should say, however, that in the absence of a simple way allowing us to easily compute $\langle P \rangle_T'$, the fact that the Lagrangian-based response exists is not of much importance.

3.2. Eulerian-based definition of zooplankton functional response

In the Eulerian approach, we consider a certain physical part (domain) of an aquatic habitat (this can be the whole habitat) with volume V, i.e. the feeding location is fixed. The organisms can enter, remain or leave the domain during the considered time. Let the overall rate of consumption of food within the domain be $Q(t)$. The rate of food consumption F during time T (per unit volume) will be given by

$$F = \frac{\langle Q(t) \rangle_T}{V} = \frac{\langle Q(t) \rangle_T}{V \langle Z(t) \rangle_{T,V}} \langle Z(t) \rangle_{T,V} = g \cdot \langle Z(t) \rangle_{T,V}, \qquad (6)$$

where $\langle \rangle$ signifies averaging over space (V) and/or time (T) as indicated in the corresponding subscript. We divide and multiply the initial expression by $\langle Z(t) \rangle_{T,V}$, which is the time and space average biomass of those grazers which have been consuming food within the domain V during period T. As such, to describe the consumption of food in V, one needs to multiply the average density of zooplankton in this domain and the quantity g, which is mathematically a *functional* (i.e. a function of functions) since its value depends on the spatial distributions of species.

Our definition of the functional response of zooplankton states that such a response exists if the grazing rate F in the domain V over time T can be computed (up to the necessary degree of accuracy) by

$$F = g(\langle P \rangle_{T,V}) \cdot \langle Z(t) \rangle_{T,V}. \qquad (7)$$

In other words, the definition implies that g needs to be a function of the average food density $\langle P(t) \rangle_{T,V}$ in the given domain. Note that definition (2) is a generalization of the classical functional response of a predator (Solomon, 1949; Holling, 1959; Begon et al., 2005).

The choice of the time T, and the size V of the domain are determined by the spatial/temporal scale as well as the model resolution. For instance, whenever a researcher constructs a mean-field plankton model which does not explicitly consider diel variation of zooplankton distribution (or the heterogeneity of vertical food distribution), the required timescale T should not be less than 1 day and the size of the domain should include the whole euphotic zone. This approach has been implemented in all classical NPZ models (e.g. Wroblewski, 1977; Evans and Parslow, 1985; Edwards and Brindley, 1999; Franks, 2009). In the other extreme case, when $V, T \to 0$, we obtain the 'local' functional response g defined as

$$F(t,x,y,z) = g(P(x,y,z),x,y,z) \cdot Z(t,x,y,z), \qquad (8)$$

where P, Z are the local densities of food and predators, respectively, in the vicinity of (x, y, z). In the case where Eq. (3) holds for any point, the overall grazing can be computed by integration of (3) over the habitat. Note that this is a standard technique implemented in

the modelling literature based on the PDE approach (e.g. Oguz et al., 1999; Gruber et al., 2006).

Surprisingly enough, applying the definition (1) to real planktonic ecosystems shows that such a response is often not observed across time and space scales. Let us first consider small time and space scales (e.g. several centimetres and seconds) implying the implementation of a local functional response determined by (3), which gives the consumption rate in the vicinity of a given point in space. The available field data (based on gut content analysis) often shows no functional relation between the consumption rate of herbivores and the ambient food density in layers where the organisms were caught (Boyd et al., 1980; Tande and Bamstedt, 1985; Dagg and Wyman, 1983; Tseng et al., 2008; Morozov and Arashkevich, 2010). Interestingly, the absence of a dependence of the gut fullness on the ambient food density is not only due to the high level of environmental noise; it is also caused by the fact that individuals caught in layers with lower food density often migrate to those layers to digest food that they have consumed in other layers with a high food abundance (Dagg and Wyman, 1983; Leising et al., 2005a; Morozov and Arashkevich, 2010), and grazing at such a depth cannot be computed by (3) simply because only a relatively small part of Z at this depth is participating in the actual grazing.

On the scale of the whole euphotic zone, the ecosystem's behaviour is described in terms of average over the column species densities $\langle Z \rangle_{T,V}$, $\langle P \rangle_{T,V}$ and the grazing rate is to be computed as $F = \langle Z \rangle_{T,V} g(\langle P \rangle_{T,V})$. Note that ignoring the actual vertical profile of food as well as that of consumers can lead to some unacceptable ambiguity. Indeed, for the same $\langle P \rangle_{T,V}$ there is no way to separately model the beginning of a bloom, when the phytoplankton is mostly located in the upper layers, and the period after the bloom when the chlorophyll maxima progressively descend towards deep layers (Ohman, 1990; Limsakul et al., 2002). Note that the depth of the chlorophyll maximum determines the behaviour of zooplankton feeding and thus, the rate of grazing (e.g. Harris, 1988). Some papers show the existence of multiple possible dynamical regimes in plankton systems which can occur for the same environmental conditions: one regime can be characterized by a deep chlorophyll maxima (Mann and Lazier, 1996) while another one can have a surface chlorophyll maximum (Ryabov et al., 2010 and references therein) and in this case defining the functional response of zooplankton as a function of total amount of food in the column does not make sense.

Finally, we should say that the feeding of microzooplankton in the water column can often be described based on the local functional response concept (8), i.e. by multiplying the ambient zooplankton density by a function of ambient food density (e.g. Edwards et al., 2000). Microzooplankton can be defined as grazers with a size of less than 0.2 mm, and their characteristic growth rate is of the same order as that of phytoplankton, making them efficient grazers (Calbet, 2008). There is a growing body of evidence emphasizing their importance in marine trophic chains (Sherr and Sherr, 2007; Landry, 2002; Calbet and Landry, 2004; Irigoien et al., 2005). Due to their small size, microzooplankton usually do not exhibit feeding behaviour which implies active movement in a vertical direction, but rather they feed in layers where organisms are currently dwelling.

4. Implementation of the zooplankton functional response in models operating on large spatial and temporal scales

In Section 3 we concluded that the Eulerian-based functional response is rarely observed, especially on large temporal and spatial scales. Should we abandon the functional response framework in models operating on large scales (e.g. the scale of the whole euphotic zone)? We would say, not always! In this section we provide two ecologically important examples in which the grazing of zooplankton on large-scale models can be satisfactorily computed using the Eulerian-based overall functional response.

4.1. Zooplankton functional response in models without vertical spatial resolution

There are still a large number of plankton models without explicit vertical spatial resolution. The main goal of these mean-field models is not to provide a precise quantitative description of an ecosystem, rather, they aim to reveal generic properties of ecosystem dynamics: stability (instability) of equilibria, the possibility of sustained oscillations of species density, the key model parameters, etc. Thus, a suitable choice of the zooplankton functional response in such a model should entail the best possible qualitative similarity between the model's behaviour and the ecological patterns observed in real ecosystems. In particular, discrimination between Holling types (e.g. between concave or convex functions) becomes more important than accurately determining the parameters of those functions (Edwards and Brindley, 1999; Gentleman and Neuheimer, 2008).

The most serious shortcoming of models without spatial resolution is that we can lose information about the ecosystem when trying to describe its state via the average over the column density. However, it has been theoretically shown that highly heterogeneous spatial models can be reduced to mean-field models with qualitatively similar dynamics. The aggregation method (Poggiale and Auger, 1996; Michalski et al., 1997; Auger et al., 2000) is a model reduction technique which can be implemented when the spatial displacement of organisms is a faster process than the growth rates of species, which is especially true in the case of mesozooplankton vertical migration. In the resultant mean-field model without spatial resolution, consumption of food by grazers can be described via an overall functional response which is a function of the average food density $\langle P \rangle_{V,T}$ (Poggiale, 1998; Poggiale et al., 2008; Morozov, 2010). Note that the existence of the overall zooplankton functional response in planktonic ecosystems with heterogeneous vertical distribution has some observational background. It was recently found that the column-average ingestion rate of some marine copepods can be approximately described as a function of the total amount of consumable chlorophyll a in the column (Morozov et al., 2008; Morozov, 2010). Interestingly, in the cited works it was possible for an overall functional response to emerge even for highly heterogeneous vertical distributions of species. This was partially due to the fact that the increase in total phytoplankton in the column took place according to a typical scenario of initiation and early development of spring plankton blooms, i.e. the increase of algal density occurred mostly in surface layers (Mann and Lazier, 1996).

Another important issue is the shape of functional response that we need to use in models without explicit vertical resolution. Conventionally, the functional response in mean-field models is taken directly from laboratory experiments, but such an approach might be rather misleading. Indeed, it has been shown in a number of theoretical studies that the overall response in the water column might be substantially different to the local grazing, which we assume to follow the laboratory experiments (e.g. Poggiale, 1998). Surprisingly, the difference between the local and the overall responses might even include a shift between different Holling types (e.g. Poggiale, 1998; Morozov and Arashkevich, 2008; Morozov, 2010). In particular, a sigmoid overall functional response can emerge from local non-sigmoid responses (Poggiale, 1998; Morozov and Arashkevich, 2008; Morozov, 2010). Interestingly, the predicted change of type between the overall and local responses, and the emergence of a sigmoid overall response has

some observational background (Morozov et al., 2008; Morozov, 2010). The emergence of a sigmoid overall functional response is of great importance for the stability properties of the ecosystem, since in this cases theoretical studies predict an enhancement of stabilization of plankton models with a high nutrition load (Oaten and Murdoch, 1975; Truscott and Brindley, 1994, Scheffer and De Boer, 1995). Thus, despite the fact that laboratory experiments support non-sigmoid natured functional responses for most herbivorous zooplankton (DeMott, 1982; Hirst and Bunker, 2003; Jeschke et al., 2004), implementation of a sigmoid response in mean-field NPZD models can be well justified.

4.2. Including the effects of horizontal plankton patchiness on microscales into macroscale models

It is well known that horizontal spatial distribution of plankton exhibits patchiness which varies from several centimeters to several hundreds of kilometers (Mackas and Boyd, 1979; Legendre and Demers, 1984; Steele and Henderson, 1992; Folt et al., 1993; Abraham, 1998; Folt and Burns, 1999). Unlike the rapid movement of individuals in vertical direction, the ability of plankton to actively move in horizontal direction, becomes rather limited by strong horizontal turbulent diffusion, which outweighs the self-motion of organisms.

In plankton models with a coarse horizontal resolution (e.g. the regional ecosystem models), small-scale spatial variability is usually ignored. As a result, models operate with densities averaged over smaller scales and thus ignore the spatial patchiness of plankton on microscales and small mesoscales. However, we can incorporate the effects of small-scale horizontal patchiness in the resultant functional response when operating on a coarser resolution. The conventional method for doing this is the scale transition theory (Chesson, 1998; Chesson et al., 2005; Wallhead et al., 2008). According to this technique, model equations describing dynamics on larger spatial scales should be modified to take into account implicitly local interactions, thus a regional-level model combines local interactions from smaller spatial scales and the spatial variances and covariances of species densities. The mathematical background is based on nonlinear averaging, usually considering the quadratic (second moment) approximation (Chesson, 1998).

Using the scale transition framework, the local grazing rate $f(P)Z$ can be scaled up to compute the global grazing rate F in a model operating on larger scales in the following way (Chesson et al., 2005; Bergstrom et al., 2006; Englund and Leonardsson, 2008):

$$F \approx \langle Z \rangle_V \cdot f(\langle P \rangle_V) + \langle Z \rangle_V \frac{d^2 f(\langle P \rangle_V)}{d\langle P \rangle_V^2} \frac{\sigma_P^2}{2} + \frac{df(\langle P \rangle_V)}{d\langle P \rangle_V} \sigma_{P,Z}. \qquad (9)$$

In other words, to compute the grazing rate in a regional-scale model one can use the local functional response $f(P)$ (e.g. based on laboratory data) and two additional terms taking into account the effects of spatial heterogeneity. These terms are referred to as the 'variance effect' and the 'covariance effect' and combine the local nonlinearities with the spatial variance of food distribution and the covariance between the distributions of food and grazers, respectively. The local functional response of Holling type II (Monod response) is scaled up as (Englund and Leonardsson, 2008)

$$F \approx \langle Z \rangle_V \cdot f(\langle P \rangle_V) - \langle Z \rangle_V \frac{\alpha\beta\langle P \rangle_V}{(1 + \beta\langle P \rangle_V)^3} \sigma_P^2 + \frac{\alpha}{(1 + \beta\langle P \rangle_V)^2} \sigma_{P,Z}. \qquad (10)$$

The variance and covariance terms can be either estimated from an underlying model with high spatial resolution (see example below) or based on direct field observation. It has been shown in several different ecosystems that $\sigma_{P,Z}$ and σ_P^2 are functions of prey and predator density (Taylor et al., 1980; Wallhead et al., 2008; Englund and Leonardsson, 2008), thus they are generally

time-dependent. Finally we should mention that in some cases it is possible to analytically compute $\sigma_{P,Z}$ and σ_P^2 based only on $\langle P \rangle_V$ and $\langle Z \rangle_V$ as solutions as a system of differential equations, i.e. without explicitly modelling species distribution on smaller spatial scales (for details see Wallhead et al., 2008).

In a model operating on a larger spatial scale (macroscale) the densities $\langle P \rangle_V$ and $\langle Z \rangle_V$ averaged over a microscale can themselves be considered as 'local' densities with the local grazing term F given by (10). Note that in general we cannot call the ratio $F/\langle Z \rangle_V$ a 'true' zooplankton functional response since its value usually depends not only on species densities but also on time. Nevertheless, in some cases we can approximate the local feeding in the macroscale model using only the macroscale densities $\langle P \rangle_V$ and $\langle Z \rangle_V$; in this case the ratio $F/\langle Z \rangle_V$ can be considered as a functional response.

To illustrate the implementation of the scale transition technique we can constructing the zooplankton functional response on a large scale ($L \sim 10$ km) using the local response f evaluated on a small scale (several meters). We model horizontal patchiness (in 1-D space) within the habitat of size L using a simple phytoplankton–zooplankton model (for details see Appendix A). The modelling results are shown in Fig. 2. By blue diamond symbols we show the average consumption of food by the whole population Z per zooplankton biomass defined by $g = F/\langle Z \rangle_V$. The quantity g is computed directly from model simulations at equal moments of time ($\Delta T = 5$ days). For the sake of brevity we do not show here the underlying spatial distribution of species, which are highly irregular. The red filled circles represent the approximation of g given by (10), where $\sigma_{P,Z}$ and σ_P^2 are computed directly from the model equations. The black curve in Fig. 2 shows the local functional response f which is supposed to be of Holling type II (A3). In the given model, the horizontal patchiness results in a decrease on average in the consumption rate per zooplankter compared to the situation where the same food densities are distributed homogeneously. Also, one can see that the scale transition method provides a reasonable approximation of the consumption rate per zooplankton biomass given by g.

By plotting the value of g every ΔT time units (ΔT is supposed to be large) we can interpret g as a random variable and we can compute its average $\langle g \rangle$ for each fixed P. In the case where the scattering of points from $\langle g \rangle$ is not very pronounced (small variance of g), we can approximately consider $\langle g \rangle$ as the global functional response of the whole zooplankton population. This signifies that we can assume that $\sigma_{P,Z}/\langle Z \rangle_V$ and σ_P^2 are approximately constant:

$$g \approx \langle g \rangle \approx f(\langle P \rangle_V) - \frac{\alpha\beta\langle P \rangle_V}{(1 + \beta\langle P \rangle_V)^3}\sigma_P^2 + \frac{\alpha}{(1 + \beta\langle P \rangle_V)^2} \frac{\sigma_{P,Z}}{\langle Z \rangle_V} \qquad (11)$$

In Fig. 2 we plotted $\langle g \rangle$ by fitting the parameters $\sigma_{P,Z}/\langle Z \rangle_V$ and σ_P^2 using the nonlinear regression. The fitting curve is shown by the solid blue line. The obtained resultant response $\langle g \rangle$ can be implemented when reducing the initial spatial model (A1), (A2) to a mean-field model (macroscopic system) operating with the average species densities. The same holds true in the case where the characteristic time scale T (time mesh) of the macroscopic system is sufficiently larger than the correlation time ΔT of the oscillations in the underlying microscopic model, i.e. during time T there will a large number of random deviations from $\langle g \rangle$ which will on average cancel each other out.

Field data on horizontal plankton patchiness sometimes show negative correlation between phytoplankton and zooplankton patches, i.e. $\sigma_{P,Z} < 0$. This is usually explained by the effects of phytoplankton depletion due to intensive grazing by herbivores (Riley, 1976; Folt et al., 1993; Abraham, 1998). On the other hand, a number of references report positive values of $\sigma_{P,Z}$, which can be explained as the effects of physical processes (e.g. eddies) which act in a similar way on both zooplankton and phytoplankton, caus-
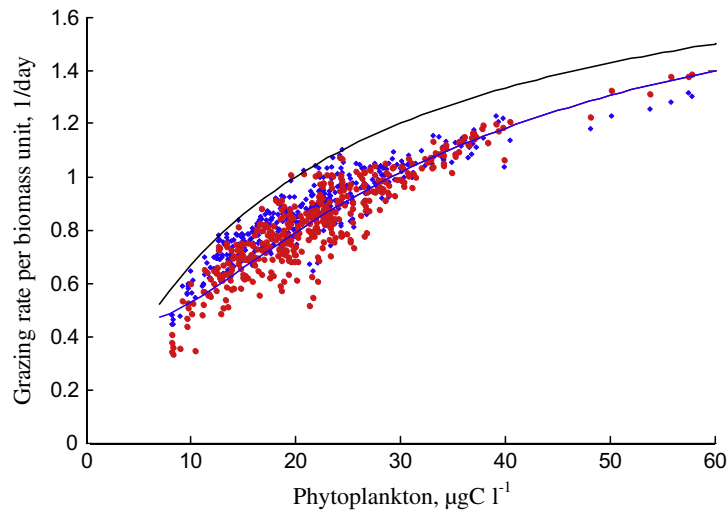
Fig. 2. Influence of horizontal patchiness on zooplankton functional response in a model planktonic ecosystem (see Appendix A for details). The local functional response f is depicted by the black solid curve. The per capita grazing rate g of the whole population of zooplankton in the entire habitat is shown by blue diamond symbols (constructed at equal moments of time $T = 5$ days). Red filled circles represent approximation of the global response based on scale transition method (8) with $\sigma_{P,Z}$ and σ_P^2 computed directly from the model equations. The blue curve gives fitting for $\langle g \rangle$ (the mean value of g), i.e. of the blue symbols obtained based on (10). For the model parameters, see Appendix A. Fitting of $\langle g \rangle$ is based on LSM giving $\sigma_P^2 = 31.26 \pm 3.5$; $\sigma_{P,Z}/\langle Z \rangle_V = 7.2 \pm 1.6$.

ing their patchiness to coincide (Tiselius, 1992; Yen et al., 1998; Folt and Burns, 1999). This will increase the global grazing rate (10). Overall, the effect of patchiness largely depends on the magnitudes of the spatial variance and covariance, since even for a positive covariance the global response can be smaller than the local response due to a high value of the variance, as is the case with the model system shown in Fig. 2.

Finally, when including microscale and mesoscale patchiness in the models operating on larger scales we should mention another method which is close to the scale transition technique: the modified mean-field approach (Pascual et al., 2002). This approach assumes that the spatial variance and covariance of species are functions of species densities. In particular, it has been shown that in the case of a linear local functional response (Holling type I), the global functional response can sometimes be expressed as a product of certain powers of the average species densities, i.e. $g \approx a \langle P \rangle_V^\gamma \langle Z \rangle_V^{\zeta - 1}$. The question remains, however, regarding the type of patchiness for which the modified mean-field approach is applicable (Pascual et al., 2011).

5. The Lagrangian *vs* the Eulerian approach in the modelling of zooplankton grazing

There is a tendency in the current literature on plankton modelling towards implementation of the Lagrangian approach. These models are known as individual-based models (IBMs) in which each zooplankter (or a homogeneous group of individuals) is explicitly modelled as a discrete entity. Each individual is described by a set of variables (gut fullness, size, age, filtration rate, etc.), and its behaviour is governed by prescribed rules. The dynamics of the whole population emerges as a result of interactions among a large number of individuals and their environment (Carlotti and Wolf, 1998; Leising, 2001; Batchelder et al., 2002; Leising et al., 2005a).

Among the major advantages of IBMs is the possibility of a more detailed description of behavioural aspects (e.g. active foraging) of organisms as well as heterogeneity of physiological traits within populations (e.g. difference in filtration rates). The central idea of IBMs is to obtain the population dynamics based on 'first principals', i.e., by describing the life and feeding cycles in all possible

mechanical details. This represents a certain advantage over density-based models since the dynamics of a population of organisms having a distributed life trait (also called a 'physiologically structured population') may be different from a population of identical individuals with the same mean value of this life trait (McCauley et al., 1996; McNair et al., 1998; Claessen et al., 2002; Diekmann et al., 2010). For instance, it has been shown that the functional response of an ensemble of individuals can be close to linear (Holling type I), while the response of each zooplankter is of Holling type II with a threshold (Leising et al., 2003). Note that the use of Holling type I and II responses with a threshold will provide significantly different modelling results. Compared to the Eulerian approach, the Lagrangian approach allows us to include complex movement of animals more easily, especially when the movement of individuals is not synchronized in space and time. An important example of such a situation is the unsynchronized vertical migration of zooplankton characterized by a constant short-term non-synchronous exchange of organisms between the surface and deeper layers, with little change in the vertical profile as a whole (Cottier et al., 2006; Morozov and Arashkevich, 2010).

An instructive example of the implementation of IBMs in modelling the complex active foraging behaviour of copepods in the water column is given in (Leising et al., 2005a). The authors considered the realistic situation in which copepods were feeding in surface food-rich layers and descended to layers with less food abundance for digestion. A typical grazer was considered to follow the so called 'feed and run' strategy: after the gut content is full, a copepod starts sinking into deep layers characterized by less abundance of food, but providing more refuge from visual predators. Numerous observations, indeed, report that large gut contents of copepods are observed at depths with relatively low food density, which are often below the feeding threshold of animals (Boyd et al., 1980; Tande and Bamstedt, 1985; Dagg and Wyman, 1983; Tseng et al., 2008; Morozov and Arashkevich, 2010). The Lagrangian-based framework allows the modelling of such a situation when the grazing of a zooplankter is no more just a function of the ambient food, but is a reflection of the physiological condition of the organism. As a result, in the situation where a functional response based on the Eulerian framework does not exist, implementation of the Lagrangian framework can make sense. Note that in the work of Leising and colleagues, the authors have used a some-

what mixed approach by assuming the active grazing to be of Holling type II which, indeed, is usually observed for copepods in the laboratory (e.g. Frost, 1975). Saturation in the zooplankton functional response for large food densities often arises because of the time that organisms need to digest the food consumed (Jeschke et al., 2002), however, while in the given model digestion was supposed to take place in food-poor spatial locations, i.e. not at the depths of active grazing.

Implementation of IBMs has some disadvantages as well. One of the major problems is that we are not able to describe the behaviour of a zooplankter on the individual level in all detail since this behaviour is still poorly understood. For instance, the feeding patterns of a zooplankter can be completely different in the presence of high level predators (Fossheim and Primicerio, 2008), which is rarely taken into account in models. A typical IBM depends on a large number of un-measurable parameters, and in such a situation, including or omitting some features in feeding strategy on a microscale (individual level) can result in a large error on a macroscale (population level). As a result, the central idea of IBMs – to obtain emergent population dynamics from first principles – becomes seriously undermined. We should also emphasize that the herbivores density in the column is usually rather large ($>10^3$–10^4 inds./m^2) and this would require a large number of variables leading to a large computational cost. The problem becomes practically unsolvable when we are modelling dynamics of a planktonic metapopulation inhabiting an area with a horizontal dimension of dozens of kilometres (or considering the regional scale). In this case, the classical density-based approach can be more natural.

Interestingly, as it has been shown in theoretical ecology, the complex behaviour of animals on an individual level can be included on the population level via density dependant models based on the Fokker–Planck formalism (e.g. Giuggioli et al., 2009; Clerc et al., 2010). In particular, complex patterns of collective behaviour of a large group of individuals – including swarming – can be described via mean-field theory by constructing the so-called moment equations (see Romanczuk and Schimansky-Geier, 2012 and the references therein). There also exist standard techniques for incorporating a non-heterogeneous life trait distribution within a population of grazers, as well as the age structure of the population in density-based models (for example, see the book by Magal and Ruan (Eds.), 2008). Construction of the functional response of predators in continuously structured models is described in (Logan et al., 2009). In particular, complex interactions between *Daphnia spp.* and phytoplankton can be successfully described based on physiologically structured models (Diekmann et al., 2010 and the references therein). Finally, the feeding cycles of zooplankton, including periods of active grazing and digestion, can be incorporated into simple density-based models – for instance, this can be done by partitioning the whole population of grazers into groups (classes) according to their feeding status. Thus, one can separately consider actively grazing and digesting subpopulations and model explicitly the spatial distribution of active grazers. In the simplest case, one can consider that the active grazers follow the ideal free distribution (Morozov and Arashkevich, 2010; Morozov et al., 2011), but such an approach can be extended to more complex vertical distribution patterns of actively grazing zooplankton.

Overall, while comparing the Lagrangian-based and Eulerian-based descriptions of zooplankton feeding it is impossible to say which approach, in general, should provide more accurate grazing rates – such a question would be ill posed (e.g. Woods et al., 2005). In our opinion, both approaches should potentially give *the same* result in the case of a large number of grazers if they are implemented correctly. Indeed, the dynamics of any complex IBM model with a large number of individuals can be approximated as close as is necessary by a certain density-dependent model (for instance,

based on some complex integrodifferential equations with delay): the only problem is how to construct and parameterize such a Eulerian-based model. The IBM approach is currently gaining more popularity since it appeals to a rather tentative idea of modelling population dynamics from first principles. Another important reason is the existing large amount of experimental observations of movement and feeding of individual zooplankters on small scales: it is indeed very tentative to 'extrapolate' the observed experimental feeding patterns on microscale to the scale of the whole ecosystem (e.g. Gergs and Ratte, 2009). In reality, the degree of uncertainty regarding the behaviour of each individual in IBMs in different parts of the habitat (e.g. near the surface and the bottom of the euphotic zone) can be as large as in the case when one constructs complex density-based models.

6. Conclusions and future research directions

An adequate description of zooplankton grazing is of crucial importance for an enhancement of the predictive power of plankton models, since the reproduction and growth of herbivores strongly depends on the amount of food they consume, and conversely, grazing by herbivores largely shapes the phytoplankton dynamics (Anderson et al., 2010). The conventional description of food consumption in models is usually based on the functional responses obtained in the laboratory. We argue that there are at least two major factors which can make such an approach too simplistic. These are: (i) non-homogeneous spatial distribution of food and grazers (plankton patchiness) and (ii) complex foraging behaviour of herbivores across space and time scales. As a result, it may not be possible to accurately describe the grazing of herbivores as simply a product of a certain function of food density (i.e. the functional response) and the density/biomass/population size of grazers. In a large number of cases, the zooplankton functional response *in vivo* might simply not exist at all (e.g. Boyd et al., 1980; Dagg and Wyman, 1983; Tseng et al., 2008; Morozov and Arashkevich, 2010). Finally, the functional response can be dependent on spatial/time scale and on the modelling frame (e.g. changing the space resolution of the model for a fixed size of the habitat).

Our main conclusion regarding the implementation of a zooplankton functional response can be expressed briefly in one phrase: 'The zooplankton functional response is dead ... long live the zooplankton functional response!' It is 'dead' in the sense that the response observed in laboratory can only be used in modelling with great care: for example, in the case where experimental feeding shows a threshold density below which organisms stop consuming food (Leising and Franks, 2000); in real ecosystems organisms can simply avoid patches of low food density and graze at depths with high food density. As a result, intensive feeding can still take place when the average density of food is well below laboratory threshold. Overall, strictly speaking, the functional response based on a classical definition (e.g. Holling, 1959) or on generalization (7), can hardly be found in any real ecosystem at any time/space scale.

The zooplankton functional response, however, is 'alive' in the sense that this framework can be still an excellent modelling tool. Indeed, any plankton model is, of necessity, a simplification of reality and where the required accuracy is achieved we can still implement this framework. In particular, a number of model reduction techniques (e.g. the aggregation approach, the scale transition approach, the modified mean-field approach) allow us to satisfactorily describe the consumption of food by zooplankton on different spatial and temporal scales in terms of mean densities of food and consumers. We argue that the shape of the resultant functional response on larger scales can be *substantially different* from the one obtained for the same species on small scales (e.g.

in laboratory) and, consequently, we need to take this into account when constructing models. In particular, active food seeking behaviour of grazers in the water column can result in the alteration of Holling types, and lead to the emergence of a global sigmoid-shape response from non-sigmoid laboratory responses.

The non-existence of the local functional response for some species has resulted in wide-scale implementation of IBMs in the literature. We agree full-heartedly with the need for development of such models in marine ecology, but we also argue that the implementation of IBMs needs to be justified for herbivorous zooplankton which are characterized by large densities and patchy spatial structure. We also claim that the density-dependant framework can also provide powerful modelling tools capable of efficiently incorporating complex patterns of foraging behaviour and the variability of physiological traits within populations. Overall, a parallel development and comparison of plankton models based on Lagrangian and Eulerian approaches would be profitable for both frameworks, and this should, clearly, be a future direction for research.

To make further progress in modelling zooplankton grazing, more vigorous collaboration between modellers and field biologists is needed, with the main focus on studying processes *in vivo* and not on the feeding of organisms in bottles/tanks (Carlotti and Poggiale, 2010). We also want to emphasize that future field observation should not only focus on revealing patterns across small space and time scales (and the individual level) but should also provide an adequate picture on a macroscale level (e.g. on the scale of the whole euphotic zone) and the population level. For this reason, we need data on grazing on small (e.g. 10–15 m scale in the water column) spatial scales to be collected throughout a given habitat (or a large part of this habitat). In mathematical terms, to estimate the global grazing impact we need to 'integrate' the local grazing impact based on field data collected for a sufficiently large set of points. This would allow us to avoid problems associated with unjustified extrapolation/interpolation of field data on grazing, based sometimes on measurements at a single depth or station. For example, we need information on gut fullness, filtration rate, and physiological states of organisms throughout the *whole* water column, and the same concerns mesoscale horizontal transects. Finally, we need to understand temporal variation of the observed patterns of grazing. The collected data would allow for both the justification of the implementation of models without explicit spatial resolution and for construction of models with a coarse explicit spatial resolution.

Another challenge is the investigation of physiological heterogeneity within populations of consumers (e.g. difference in filtration rate), its potential influence on individual feeding behaviour (e.g. the preferable location in the water column) and its consequences for dynamics emerging on population level. This is particularly important as theoretical models predict different dynamics of structured populations compared to non-structured ones (McNair et al., 1998; Diekmann et al., 2010). In particular, it would be interesting to verify the existence of a potential trade-off between high grazing rates of organisms within the same population and the time which they spend in surface layers with higher predation risks. If such a trade-off exists, the vertical distribution of grazers in a population should also be structured according to the individual grazing behaviour of organisms, which would probably result in enhanced survival and reproduction rates for the whole population.

The next important challenge is to reveal how interference among grazers can affect the consumption of food. Throughout the paper, we considered the simplified situation where the grazing of an individual zooplankter was a function of food only, but there is some experimental and theoretical evidence that consumption of food by a zooplankter can be a function of the surrounding zooplankters (Arditi and Ginzburg, 1989; Arditi and

Saiah, 1992; Poggiale, 1998; Villemereuil and Lopez-Sepulcre, 2011) and that this can occur through a number of mechanisms including intratrophic predation (Pitchford and Brindley, 1998) and direct competition between grazers (e.g. Folt and Goldman, 1981). In particular, it has been shown that the vertical distribution of grazers can be affected by competition among grazers and, consequently, this can influence the total grazing rate of the population (Lampert, 2005). On the other hand, some field data do not show any correlation between the grazing rate by an individual and the surrounding grazers density (Arashkevich, unpublished data). Overall, the question of whether interference among herbivores is a typical pattern and whether we ought to take it into account is an important issue for future research.

Finally, an interesting topic for future investigation is the grazing of zooplankton on multiple food sources, which is a fairly typical situation in nature – for instance, in real ecosystems mesozooplankton often graze simultaneously on phytoplankton and microzooplankton (Batten et al., 2001). The shape of the functional response for zooplankton feeding on multiple sources can be rather complicated (see Gentleman et al., 2003 for a review). Experiments on the parameterization of functional response curves have been carried out in laboratories, where organisms were simultaneously fed on different sort of food (e.g. Ambler, 1986; Stoecker et al., 1986; Strom and Loukos, 1998), but in real ecosystems, however, different sources of food can be separated in space (at different depths) and zooplankton can feed on their preferred food and ignore less profitable items (Leising et al., 2005b). As a result, a laboratory-based multi-food functional response would be erroneous, since experimental organisms have little choice to avoid the food they dislike: for example, it will be hard for filter feeders to discriminate between different types of food when similarly sized particles with different nutrition are well mixed. The question of how multiple food sources affect the foraging behaviour of zooplankton is, clearly, an important challenge.

Peter Franks (2009) in his review of mean-field models, lamented the lack of innovation in the modelling of planktonic ecosystems – in particular the way the grazing of herbivores is being described. Certainly, new plankton models effectively have the same structure of grazing terms as those constructed 30–50 years ago; and those terms are a direct interpretation of laboratory experiments. As we have discussed above, new and powerful techniques of model reduction are now available to incorporate realistic features of grazing and to scale up ecological processes. Those techniques have been successfully implemented in other ecological systems (cf. Bergstrom et al., 2006; Englund and Leonardsson, 2008; Auger et al., 2008; Pascual et al., 2011), and a large number of plankton modellers are probably well aware of the existence of such techniques. Our opinion is that the continuous use of the classical functional response in new plankton models can be explained not only by the mathematical simplicity of this approach, but also by some psychological stereotypes of model builders. The little existing field data for the feeding of zooplankton *in vivo* is partially responsible for this as well. We hope that our review will contribute to the breaking of such stereotypes.

Acknowledgments

Appendix A

The model describing phytoplankton–zooplankton interactions in horizontal 1-D space is given by the following system of differential equations

$$\frac{\partial P(x,t)}{\partial t} = D_1 \Delta P(x,t) + rP(x,t)[1 - P(x,t)/K]$$
$$+ f(P(x,t))Z(x,t), \qquad (A1)$$

$$\frac{\partial Z(x,t)}{\partial t} = D_2 \Delta Z(x,t) + kf(P(x,t))Z(x,t) - m(Z(x,t))Z(x,t), \qquad (A2)$$

where $P(x,t)$ and $Z(x,t)$ are the phytoplankton and zooplankton densities, respectively, at location x at time t; D_i are coefficients of turbulent diffusion (for the sake of simplicity we considered $D_1 = D_2$). The function $f(P)$ describes the local zooplankton functional response (we assume the existence of such a response, alternatively, we can consider this 'local' response to be the overall response of in the entire water column at location x); $m(Z)$ is the zooplankton mortality which we consider to be linear: $m(Z) = m_0 + m_1 Z$. The linear term in the zooplankton mortality describes effects of intraguild predation (Edwards and Yool, 2000). K is the carrying capacity of phytoplankton (which, for the sake of simplicity, we assume to be constant, i.e., nutrient independent); k is the grazing efficiency of zooplankton; r is the maximal growth rate of phytoplankton.

We consider that the local functional response f of zooplankton is given by the simple Monod parameterization (Holling type II)

$$f(P) = \frac{\alpha P}{1 + \beta P}. \qquad (A3)$$

We fulfill numerical simulations for the following set of model parameters which is in agreement with literature (e.g. Edwards and Brindley, 1999; Franks, 2001): $r = 1$ 1/day; $m_0 = 0.05$ 1/day; $m_1 = 0.05$ 1/day; $K = 200$ µg C l^{-1}; $\alpha = 0.1$ 1/day; $\beta = 0.1$ l/µg C, $k = 0.25$, $D_i = 0.1$ m^2/s; the size of the habitat $L = 10$ km.

Numerical simulations of system (A1), (A2) have been carried out based on the classical implicit method (see Thomas, 1995 for details). Our simulation shows that for the given set of parameters the local densities of species oscillate in space, but such oscillations are not periodical; moreover, they are not synchronized in space resulting in complex chaotic patterns (not shown result). The observed patterns of dynamics remain for a relatively large variation of the initial set of model parameters.

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