

Incorporating Complex Foraging of Zooplankton in Models: Role of Micro- and Mesoscale Processes in Macroscale Patterns

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Abstract There is a growing understanding that population models describing trophic interactions should benefit from the increasing knowledge of the complex foraging behavior of individuals constituting those populations. A notable example is the modelling of planktonic food chains where the foraging behavior of herbivorous zooplankton is often complicated and involves active vertical displacement (migration) in the water column with the aim of optimizing the fitness under constantly varying environmental conditions such as distribution of predators, location of food, temperature gradient, oxygen concentration, etc. Vertical migration of zooplankton takes place on different time and space scales ranging from seconds and centimeters to months and the size of the whole euphotic zone. Taking into account active foraging behavior of zooplankton would alter theoretical predictions obtained with earlier plankton models where such behavior has often been ignored—especially in the mean-field models which operate with integrated species biomasses/densities. In this paper, I revisit two important aspects of incorporating patterns of active zooplankton feeding in models, based on recent progress in field observations and experiments. Firstly, I investigate how complex foraging movement of herbivores in the column can alter the shape of the zooplankton functional response on different spatial and temporal scales—in particular, I scale up the local functional response to macroscales (the whole euphotic zone) and show the emergence of a sigmoid functional response (Holling type III) on the macroscale based on a non-sigmoid local response on microscales. Secondly, I theoretically investigate the role of intra-population variability of the feeding behavior of grazers (implying physiological and behavioral structuring of a population) in the persistence of the whole population under predation pressure. I show that structuring

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of the population according to feeding behavior would enhance the population persistence in a eutrophic environment thus preventing species extinction.

1 Introduction

It has been well recognized in ecology that spatial heterogeneity is a crucial factor shaping population dynamics and affecting species persistence ([8, 51, 66, 88]). The growth of a population often takes place in a highly heterogeneous environment characterized by a pronounced variation in the species fitness. In the case organisms have the ability to actively move within a large part of the habitat they can adjust their spatial location to improve their living conditions by acquiring more food, escaping from natural enemies, etc. An important ecological example of such behaviour is the active vertical migration of herbivorous zooplankton in the water column in lakes and the ocean. Although in the horizontal direction the active displacement of plankters is seriously impeded by a pronounced turbulence ([1, 36, 68]), mesozooplankton such as copepods can quickly adjust their vertical location and find the optimal depth within the entire euphotic zone (i.e. the zone where the light intensity is enough to make possible photosynthesis of phytoplankton) depending on the given distribution of predators and food conditions, as well as abiotic factors as temperature, salinity, etc. [10, 37, 53, 60, 65, 90]. Since copepods constitute the main source of food for small pelagic fish (the upper trophic level) and can also control the primary production via intensive grazing, their correct description in models is becoming of crucial importance when simulating the biochemical cycles, sustainable fishery management, toxic plankton blooms, marine biodiversity, etc. Moreover, excluding patterns of active foraging behavior of grazers can be somewhat of a bottleneck in improving the predictive power of plankton models [14, 65].

Active vertical displacement of herbivorous zooplankton in the column takes place on different time and space scales (see Fig. 1). On microscales (seconds and dozens of centimeters, up to 1–2 m) zooplankton show active foraging behaviour by performing small foraging jumps and accumulating in micropatches of high food density [30, 70, 113]. On the intermediate time and space scales (1–3 h and dozens of meters), organisms perform short-term exchanges between surface layers which are rich in food (phytoplankton) and deeper layers, which contain less food but are safer from predators [65, 77, 95]. On a daily time scale zooplankton can show regular diel vertical migration where the organisms ascend to upper (surface) layers for feeding at night and stay in deep layers during the day time. It is believed that this strategy allows herbivores to escape from visual predators [10, 60, 90] and/or because of the energy gain in deeper waters due to low temperature [49, 72]. Finally, zooplankton exhibit variations in movement behavior on a longer time scale (varying from several weeks to months) which is related to the ontogenetic plankton cycles where zooplankters can even leave the limits of the euphotic zone and descend to deeper layers [91, 117].

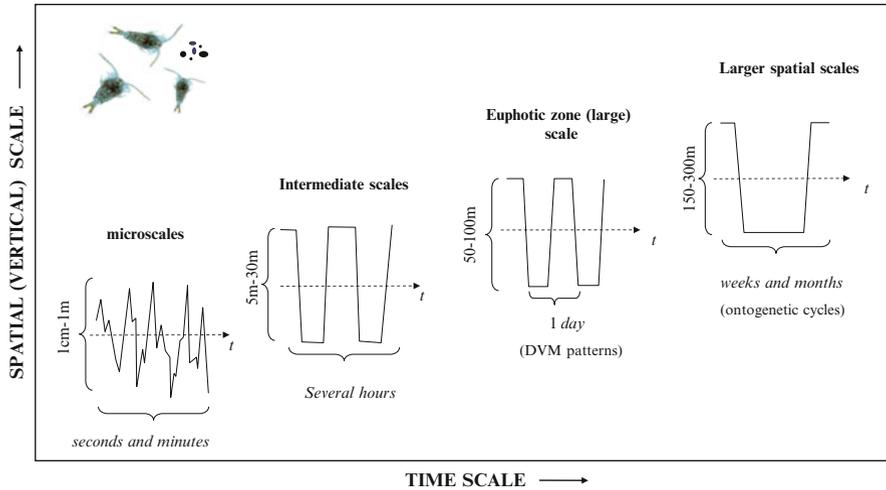


Fig. 1 Active foraging behavior of herbivorous zooplankton in the ocean and deep lakes over different spatial and temporal scales. For details and the literature references see the text

There exist a large number of publications concerning the modelling of active vertical migration of zooplankton. Most of these publications, however, provide models of the regular diel vertical migration (DVMs) taking place on the scale of the whole euphotic zone. In particular, it has been shown that such migrations can be an optimal strategy for the persistence of a population under the threat of predation by visual predators [39, 49, 57, 67, 107]. On the other hand, there also exist a high number of theoretical works on zooplankton movement on microscales ([3, 33, 45, 105, 106, 114]). Such works usually model the movement of zooplankton on microscales as a fractional random walk ([9, 23, 105, 106]) and even as a Levy flight ([3, 120]) and are justified by experimental material on zooplankton movement recorded by cameras [30, 70, 113]. Regrettably though, foraging behavior of zooplankton herbivores on the intermediate time and space scales is studied much less both regarding observation/experimental and modelling works.

An important reason for the lack of studies on intermediate time and space scales is that the active vertical movement of grazers at intermediate scales is often non-synchronized: in other words, exchange of the individuals between the horizontal layers in the column can take places without alteration of the profile of the population as a whole [21, 65, 77]. Such non-synchronized vertical migration is rather hard to investigate *in vivo* since this would require labelling and tracking a large number of small-size organisms in a highly turbulent environment. Another important reason for the mentioned lack of knowledge is rather coarse methods of sampling. As a result, the existence of any fine structure of plankton layers is often overlooked. This concerns, for example, the so-called thin plankton layers with a characteristic vertical width up to few meters but having plankton densities several orders higher than outside the layers [22, 52]. There is an opinion that foraging of zooplankton in these high density food patches can be crucial for the survival of

grazers [13, 64, 82] since the food density outside the patches is often below the feeding threshold of zooplankton (i.e. the minimal concentration of food required below which grazing does not occur). Interestingly, the thin layers of zooplankton and these of algae sometimes do not overlap, resulting in complex foraging jumps of zooplankters into the food layer and back [54, 64, 65].

There is a growing body of evidence that the active foraging of zooplankton on different scales should be incorporated into plankton models (e.g. [14, 65]). However, each ecological model is a simplification of reality and it is impossible for it to encompass all details on the movement of individuals. On the other hand, quite often we simply do not need to describe the individual behavior on a microscale, when, for example, we are interested in the functioning of the whole plankton community. As such, the problem of transition between the modelling scales arises: processes taking place on a finer scale should be implicitly incorporated into a model operating on a larger scale [2, 17, 32, 59]. As a result, the model on a larger scale can be considered as a mean-field model operating with the average characteristics (e.g. the mean species densities, food concentration, etc.). An interesting and practically relevant problem is how to implicitly include active foraging behavior of individual zooplankters on a smaller time and spatial scale (i.e. without using a fine spatial and time resolution as well as a detailed description of interaction between organisms) into a coarse-scale plankton model.

In this paper, I shall address two issues related to including active foraging behavior of zooplankton in models and scaling them up. Firstly, I will consider the zooplankton functional response on different spatial and temporal scales and I will show that the shape of the emerging global functional response of a community can be substantially altered from to the local response of a single individual. Secondly, I shall model the role of intra-population variability in the feeding behavior of grazers in the persistence of the whole population under predation pressure. I find that structuring of the population according to feeding behavior can enhance the population persistence in eutrophic environments (characterized by a high nutrient load) thus preventing species extinction.

The paper is organized as follows. In Sect. 2, I compare the Eulerian and the Lagrangian approaches in the modelling of herbivorous zooplankton. In Sect. 3, I provide two general definitions of the zooplankton functional response based on the Eulerian and the Lagrangian frameworks, and discuss their applicability. Then I demonstrate the emergence of Holling type III (sigmoid) global functional response from a non-sigmoid local response. Section 4 is devoted to the modelling of the role of behavioral structuring on the survival of a population of grazers. Finally, in Sect. 5, I provide a general discussion on the incorporation of foraging behavior in plankton models and consider possible applications of our results for some other (non-planktonic) ecosystems.

2 The Lagrangian vs. the Eulerian Approach in the Modelling of Zooplankton Dynamics

When modelling zooplankton dynamics in the water column, a critical issue is to choose an adequate modelling framework. In ecological modelling there exist the two main approaches: the Eulerian and the Lagrangian frameworks. According to the Eulerian approach, the distribution of organisms in space is regarded as continuous and is described in terms of the population density. The Lagrangian models are known as well as individual-based models (IBMs) where each individual (or a homogeneous group of individuals or super-individual) is explicitly modelled as a discrete entity [46, 47, 104]. Thus each individual/group is described by a set of variables (e.g. age, filtration rate, size, nutrition condition, etc.), and the behavior of an organism/group is governed by a set of prescribed rules. The dynamics at the population level emerges as a result of interactions of a huge number of individuals and their environment [4, 15, 63, 65]. Note that currently there is a tendency in the literature to implement the IBM framework when modelling zooplankton.

Each of the two modelling approaches has its advantages and disadvantages. A general discussion and comparison between the two approaches in theoretical ecology and, in particular, in plankton modelling, should be a matter of separate discussion (e.g. [46, 121]). An advantage of IBMs is the possibility of a more detailed description of the behavioral aspects of organisms as well as heterogeneity of physiological traits within populations. Thus, the central idea is obtaining the population dynamics from the first principals, i.e., by describing the life and feeding cycles in all possible mechanical details. The Lagrangian approach allows us to include complex movement of animals more easily than the Eulerian approach, especially when the movement of each individual is not synchronized in space and time. An important example is the unsynchronized vertical migration of zooplankton characterized by a constant short-term exchange of organisms between the surface and deeper layers, with only little change in the vertical profile of zooplankton as a whole [21, 65, 77]—the Lagrangian-based framework allows us to model the situation when the grazing of a zooplankter is not just a function of the ambient food any more, but is a reflection of the physiological condition of the organism [65].

Implementation of the Lagrangian approach has some disadvantages, however. An important shortcoming of IBMs is that we are not able to describe the behavior of a zooplankter on the individual level in full detail—this behaviour is still poorly understood. 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. It is to be noted that the number of herbivorous zooplankters in the water column is usually rather large ($> 10^3$ – 10^4 inds. per square meter) and this would require a large number of state variables describing all the organisms, incoming a large computational cost.

The problem becomes practically unsolvable when we are interested in modelling the dynamics of a planktonic metapopulation inhabiting an area with a horizontal dimension of dozens of kilometers (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 [18, 40, 44, 119]. Note however, that the resultant equations can differ from the classical reaction-diffusion-advection type equations (e.g. [119]). On the other hand, 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 ([69], see also Sect. 4 of this paper). In particular, complex interactions between *Daphnia* spp. and phytoplankton can be successfully described based on physiologically structured models ([29] 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 ([76, 77]). In this paper, I shall use the density-based (Eulerian) approach when modelling interactions in planktonic communities; however, when suggesting a general definition of the zooplankton functional response (Sect. 3.1), I shall discuss implementation of both the Eulerian-based and the Lagrangian-based frameworks.

3 Modelling and Scaling the Zooplankton Functional Response

In theoretical ecology the functional response of a predator/grazer was initially defined as the specific consumption rate of food by an individual grazer per unit of time [56, 110]. Later on, it was well recognized that such a definition depends on the time and space scales under consideration [20, 32, 75, 99]. In plankton ecology the importance of spatial and temporal scales in feeding is less well recognized, for instance, than in terrestrial ecology. Conventionally, a zooplankton functional response is determined based on experimental feeding of organisms in microcosms. Tremendous amounts of literature exist on this topic showing that the feeding rate of a zooplankton in laboratory settings can be well described by a certain function of food which is referred to as a functional response ([38, 101] for a review). However, the direct interpretation of microcosm plankton experiments in ecosystem models on a larger scale is tricky and not always possible (e.g. [79]). This is mostly related to the two following aspects. Firstly, the environment in which species interactions take place is highly heterogeneous, thus the question of correct averaging arises. Secondly, the foraging cycles of grazers imply periods of active consumption and periods of rest (digestion) and those periods are often characterized by different food densities [21, 65]. As a result, grazing and digestion can be separated in space. Thus, the conventional definition of the functional response, based on the assumption of a homogeneous small-sized (laboratory) environment needs to be refined.

3.1 Defining the Zooplankton Functional Response in Real Ecosystems

The existence of the zooplankton functional response on different temporal and spatial scales is a fundamental issue for modelling and to address this issue one should provide a rigorous definition of such a response. Below I suggest two definitions based on the Eulerian and Lagrangian frameworks.

- (i) The Eulerian-based definition. Consider a certain domain Ψ which is a part of an n -dimensional habitat ($n = 1, 2, 3$). We are interested in the amount of food $E_{T,\Psi}$ that individuals belonging to the given species consumed within this domain during the observation time T . The $E_{T,\Psi}$ quantity can be re-written as

$$E_{T,\Psi} = \langle E(t) \rangle_{T,\Psi} = \frac{\langle E(t) \rangle_{T,\Psi}}{\langle Z \rangle_{T,\Psi}} \langle Z \rangle_{T,\Psi} = F \langle Z \rangle_{T,\Psi} , \tag{1}$$

where $E(t)$ is the instantaneous rate of food consumption and $Z(t)$ is the instantaneous biomass of predators in the domain Ψ . Thus, to compute the total consumption of food in Ψ over time T by the predators one needs to multiply the biomass $\langle Z_{T,\Psi} \rangle$ the predators and the quantity F , which is mathematically a functional (i.e. a function of functions) since its value depends on the spatial distributions of species. The $\langle \rangle$ symbol denotes averaging

We shall define F as a functional response of predators in the case where the consumption of food can be described as

$$E_{T,\Psi} = F (\langle P \rangle_{T,\Psi}, \langle Z \rangle_{T,\Psi}) \langle Z \rangle_{T,\Psi} , \tag{2}$$

up to the necessary degree of accuracy required for a given model. In other words, we require that F should be a function of the total amount of food $\langle P \rangle_{T,\Psi}$, $\langle \rangle$ in the domain. The size of the domain Ψ and the period of time T in the above definitions depend on the modelling purposes. In the limiting case, when the volume of Ψ and T tend to zero, we obtain the “local” functional response $F = F(P(\vec{r}), \vec{r})$, i.e. consumption of grazers in a given space point at a given moment time. The concept of the local functional response is implemented in most PDE-based models in oceanography [48, 89]. In the other limiting case Ψ represents the whole euphotic water column and T is approximately equal to one day and the conventional modelling framework at those scales is the “classical” mean field plankton models ([31, 34]).

- (ii) The Lagrangian-based definition. According to the Lagrangian framework, we do not consider a fixed spatial domain. Instead, we follow the trajectories of the individuals though their paths. Thus, for the consumption rate of N individuals we obtain

$$E_{N,T} = \sum_{i=1}^N \langle e_i(t) \rangle_T = \frac{NB}{NB} \sum_{i=1}^N \langle e_i(t) \rangle_T = F_1 \cdot Z, \quad (3)$$

where B is the average biomass of an individual; Z is the total biomass of N zooplankters; e_i is the instantaneous consumption rate of individual i and the symbol $\langle \rangle$ now denotes averaging of the consumption rate along the path of a zooplankter.

We can define the functional response F_1 in the case the consumption rate of the whole population can be computed (up to the necessary degree of accuracy) as the product between zooplankton biomass and the average food concentration in the habitat, i.e.

$$E_{N,T} = F_1 (\langle P \rangle_T, \langle Z \rangle_T) \cdot Z, \quad (4)$$

Unlike the Eulerian approach, the Lagrangian-based functional response is a function of the food density averaged over the layers where organisms mostly graze. The use of (4) requires the knowledge of individual paths of zooplankters and their grazing rates along those paths. One of the techniques for computing foraging paths uses individual-based modelling (IBM).

The question of applicability of the above definitions (2) and (4) is a matter of much discussion in the literature. For instance, it has been frequently observed that the local Eulerian-based functional response does not exist at all in natural plankton communities. In other words, very often there is no apparent correlation between the ambient food density and the ingestion rate of copepods [11, 25, 77, 112, 116]. This is not only the result of pronounced environmental noise but is due to the fact that the locations of the active food consumption and those of the rest can be different. For instance, a large density of zooplankton in layers with poor nutrition conditions can be explained by the fact that organisms migrate to those layers for digestion or to avoid predators [25, 65].

Note that the Lagrangian-based definition (4) can provide a better fit to the field data than the Euler-based definition, which can be seen from the following illustrative example based on feeding data on *Calanus* spp. in situ (the Central Barents Sea, 2003–2005). All details regarding the collection of material and methods can be found in [79]. Figure 2a shows the local functional response based on the Eulerian framework (the ingestion rates are plotted against the ambient food density), whereas Fig. 2b represents the functional response based on the Lagrangian definition constructed using the same data set.

To construct the Lagrangian-based response, we need to know the exact depths where the organisms are grazing for food before collection. Although we normally ignore those depths, we can try to reconstruct Lagrangian-based response by proceeding in the following way. Zooplankton samples were collected in three separate layers (0–20; 20–50; 50–100m) and at each depth we considered the ingestion rate averaged over all individuals. I used the assumption that the ingestion rate of an individual is an increasing function of food density. Based on this assumption, I compared ingestion rates I_i and I_{i+1} ($i = 1, 2$) in each pair of adjacent layers with the average chlorophyll densities P_i and P_{i+1} , respectively. In the case where $I_i \leq I_{i+1}$, but $P_i \geq P_{i+1}$ I suggested that organisms caught in

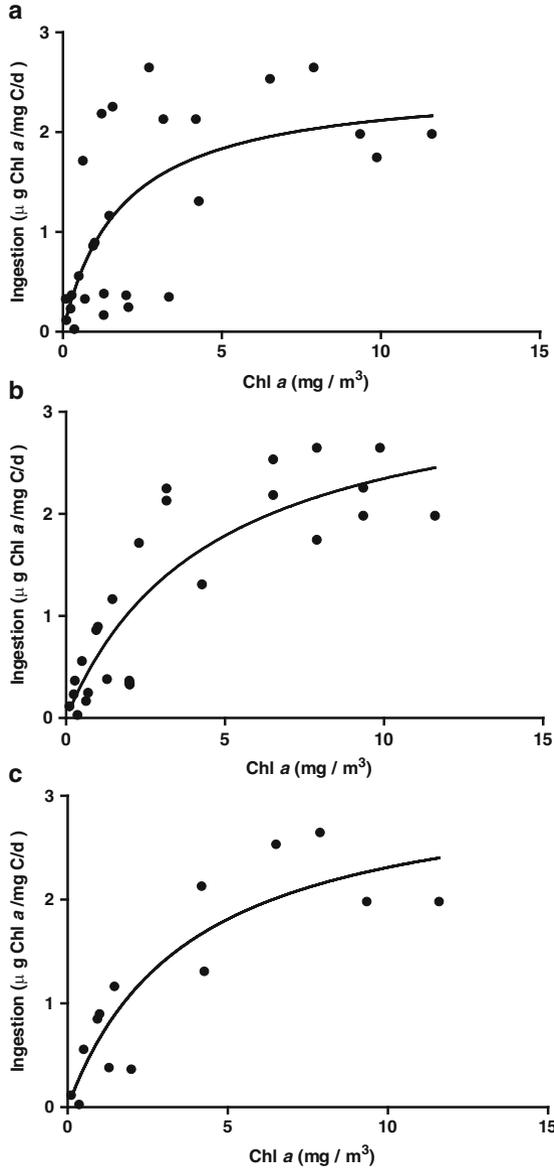


Fig. 2 Functional responses of herbivorous copepods (*Calanus Finmarchicus*, CIV, Central Barents Sea, 2003–2005) measured in situ. **(a)** Local functional response constructed based on the Eulerian framework, i.e. ingestion rates are plotted against the ambient food density. **(b)** Local functional response constructed based on the Lagrangian framework, i.e., ingestion rates are plotted against the food densities, where organisms were feeding the last time before capture. **(c)** Local functional response constructed considering only the actively feeding zooplankton. The fitting curves are obtained based on nonlinear regression (LSM), using the Monod curve as fitting functions. For details on constructing the functional responses see the text

layer $i + 1$, in fact, consumed their food in layer i . In this case, I considered that I_{i+1} corresponds to the density P_i . Alternatively, for $I_i \geq I_{i+1}$, but $P_i \leq P_{i+1}$ I suggested that the actual consumption by organisms caught in layer i was in layer $i + 1$, i.e. that I_i corresponds to P_{i+1} . Moreover, in the case where the ratio I_{i+1}/I_i was close to unity, but P_i was substantially larger than P_{i+1} , I considered that the actual grazing of the organisms caught in layer $i + 1$ took place in layer i . The field observation shows (see [79] for details) that $P_2 > P_3$ for each station and, thus it is easy to prove that the above described algorithm allows to assign I_i to P_j in a unique way. In other words, we assumed that the rate of food consumption was close to linear at low chlorophyll densities (up to $P = 4\text{--}5 \text{ mg/m}^3$ Chl a). The biological justification for the above assumptions is to avoid anomalously large ingestion rates in layers with small food density. Overall, I should emphasize that such a simplified method can give us only estimates of the actual 12 locations (stations) of grazing. We performed the statistical treatment of both functional responses in Fig. 2 based on the least square method (LSM) using the Monod curve as a fitting function, which gives $R^2 = 0.46$ for Fig. 1a and $R^2 = 0.78$ for Fig. 2b. Based on the comparison of R^2 as well on the fact Fig. 2b shows less scattering of points from the fitting curve, one can conclude that the Lagrangian framework would provide a better description of zooplankton functional response than the Euler framework.

Finally, when constructing the zooplankton functional response one can take into account only those consumers which are currently grazing the food and exclude those ones which are digesting food at the moment. I shall refer to those grazing individual as the actively feeding zooplankton. When computing the grazing impact of a zooplankton population, one needs to take into account the contribution of only those feeders. A major problem, however, is that it is almost impossible to distinguish between actively feeding and resting animals when collecting samples [21]. Despite this fact, we can try to reconstruct such a response based on the data set from Fig. 2a. Here I used the hypothesis that in the case where $I_i \leq I_{i+1}$, but $P_i \geq P_{i+1}$ or $I_i \geq I_{i+1}$, but $P_i \leq P_{i+1}$ I ignored those points. In other words, I ignored anomalously large ingestion rates in layers with small food density suggesting that those organisms do not feed in those layers but digest food. The resultant graph is presented in Fig. 2c showing a local functional response of with less scattering of points than Fig. 2a with $R^2 = 0.80$ (the fitting curve was the Monod function). The approach using the functional response based on the actively feeding zooplankton can be considered as a mixture of the Euler-based and the Lagrangian-based approaches and will be used in the next section.

3.2 *Emergence of a Sigmoid (Holling Type III) Overall Zooplankton Functional Response*

A number of plankton models ignore the explicit vertical resolution and consider the species densities averaged over the column. To describe the grazing of herbivorous, one needs to consider an overall/global functional response in the entire euphotic

zone, i.e. to scale up the local/microscale functional response. Interestingly, the overall functional response can be of different Holling classification type compared to the local response and this is a result of the active foraging behavior of zooplankton (I show this below). In particular, an accelerating overall functional response (Holling type III) can emerge from a non-sigmoid (Holling type I or II) local responses.

The overall functional response of zooplankton in the column can be constructed based on the definition (2), where the domain Ψ includes the whole euphotic zone. However, to avoid the situation shown in Fig. 2a, I shall take into account only the actively feeding zooplankton and denote the vertical distribution of such zooplankters by $Z_a(h)$, where h is the depth. Note that the profile of $Z_a(h)$ can be rather different from that of $Z(h)$ which is the total (bulk) zooplankton density since the latter includes also individuals which are currently not feeding (e.g. digesting) [25, 76, 77]. Let us suppose that the instantaneous consumption of the actively feeding zooplankton can be described via the local functional response $f(P)$, where P is the local density of food (phytoplankton). The overall functional response will be defined as

$$F = \frac{1}{Z_0 H} \int_0^H f(P(h), h) Z_a(h) dh , \tag{5}$$

where Z_0 is the total amount of zooplankton, H is the total depth of the euphotic zone where phytoplankton can grow.

The actual distribution of the actively grazing feeders in the column is a matter of much discussion in the literature [11, 25, 77, 116]. In this work, I shall assume that the distribution of the actively feeding zooplankton in the water column is an ideal free distribution. Some field evidence of an ideal free distribution of grazing zooplankton can be found in [43, 61, 80]. In the simplest case, one can suggest that the distribution of feeders follows the distribution of food

$$Z_a(h) = \frac{P(h)}{\langle P \rangle} \cdot Z_0 a , \tag{6}$$

where $\langle P \rangle$ is the spatial mean density of the phytoplankton; $Z_0 a$ gives the total amount of actively foraging animals. Note that one can also take into account possible interference between grazers in the column which can be parameterized by

$$Z_a(h) = \frac{P^\mu(h)}{\langle P^\mu \rangle} \cdot Z_0 a , \tag{7}$$

where μ is a parameter describing the strength of interference of grazers. Some theoretical background for parameterization (7) can be found in [83] (see also [62, 111] for other possible parameterizations). In particular, $\mu > 1$ means a larger degree of interference of predators compared to the “classical” ideal free distribution; the situation with $\mu < 1$ would signify a lesser degree of competition among the foragers in patches with high food density. Note that some field observations and experimental studies in plankton towers show that the ideal free

distribution provides a suitable approximation of real profile patterns of the actively feeding zooplankton [26, 53, 61, 80]. I do not take into account a possible time lag between the changes in profile of chlorophyll and the response of zooplankton to such changes. A large delay in response of zooplankton to changes of chlorophyll profiles would not be realistic in real ecosystems since changing in the vertical profile of phytoplankton takes from some days to a week while the active vertical displacement of zooplankton within a 100 m layer takes 6–10 h [10, 21, 90].

The dynamics of phytoplankton in the water column is described by the following partial differential equation

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial t^2} + r_0 \cdot \exp\left(-\lambda h - \gamma \int_0^h P(h) dh\right) P \left(1 - \frac{P}{K}\right) - Z_a \cdot f(P), \quad (8)$$

where the first term in (8) gives the random vertical displacement of phytoplankton due to turbulent diffusion in the column; the second describes the algal growth and the last term stands for the local grazing. The coefficient r_0 is the maximal per capita algal growth, which depends on the availability of nutrients; the exponential multiplier describes the light attenuation due to absorption by water and because of self-shading; $f(P)$ is the local functional response of herbivores, K is the carrying capacity taking into account mutual interference of algae. To parameterize the local functional response, I use the “classical” hyperbolic (Monod) parametrization [42]

$$f(P) = \frac{aP}{1 + bP}, \quad (9)$$

where a and b are the coefficients with an obvious meaning. Note that this type of response has been found for most herbivorous zooplankton in laboratory experiments ([27, 50, 55, 58] see also Fig. 2b,c). I assume that the total amount of zooplankton in the water column $Z_0 = \text{const}$ on the considered time scale. I also neglect the diel regular vertical migrations which would highly affect the ideal free distributions (6) and (7). I consider (8) with the zero-flux boundary conditions. To obtain a continuous range of $\langle P \rangle$, one needs to vary a control model parameter. I have chosen r_0 as the control parameter. This would allow the modelling of the occurrence of an algal bloom arising as a response to an increase of water temperature, light intensity, etc. [115].

Figure 3 shows the overall functional responses as functions of the average amount of phytoplankton $\langle P \rangle$ calculated for the local response of Holling type II with a large half-saturation constant ($1/b \gg 1$) (a) and with a small half-saturation constant (b). The functional responses are constructed for different intensities of interference of grazers μ . I consider realistic model parameters from the literature [7, 31, 50, 101] giving $0.5 < r < 21/d$; $0.01 < a < 0.3 d/(\mu\text{g Cl}^{-1})$; $0.005 < b < 0.2 \mu\text{g Cl}^{-1}$; $0.005 < \lambda < 0.15 1/\text{m}$; $0.0005 < \gamma < 0.0051/(\text{m} \mu\text{g Cl}^{-1})$; $D = 1\text{m}^2/d$. The local responses are shown by dashed lines. One can clearly see from the graphs the emergence of a sigmoid overall

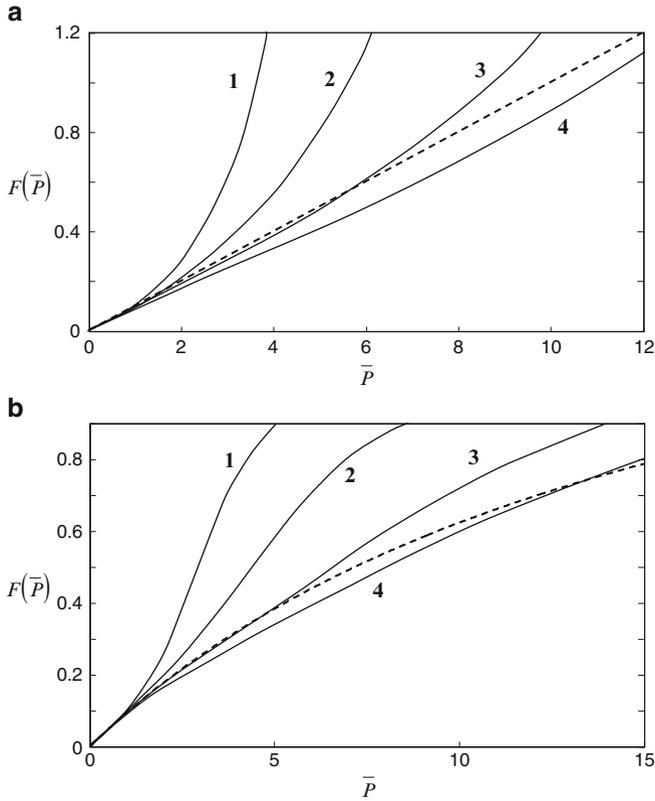


Fig. 3 Overall/global zooplankton functional responses of the zooplankton population in the entire euphotic zone constructed for varying degree of strength μ of grazer interference. The curves 1–4 correspond to $\mu = 0.8$; $\mu = 1$; $\mu = 1.2$; $\mu = 1.35$, respectively. **(a)** Overall functional responses obtained for Holling type I (linear) local response; **(b)** Overall functional responses obtained for Holling type II local response ($b = 0.06$). In both figures the overall response is shown by *bold curves*; local functional responses are depicted by *dashed lines*. The other parameters are $D = 1 \text{ m}^2/d$, $a = 0.1 \text{ d}/\mu\text{g Cl}^{-1}$; $H = 100 \text{ m}$; $Z_{0a} = 1 \mu\text{g Cl}^{-1}$

functional response (Holling type III) from the local non-sigmoid (Holling type II or I) response having a concave downward part. Such an alteration of types of responses requires a small saturation in the grazing rate and a small degree of grazers' interference ($1 \geq \mu$).

The self-accelerating behavior of the overall functional response shown in Fig. 3 can be proven analytically as well. In Appendix A I demonstrate that in the case the diffusion term is small compared to the local growth rate and the grazing term, the overall functional response can be approximated by (21), which, however, results in a rather cumbersome explicit expression (21) is obtained for the a linear local functional response). This expression can be simplified depending on the magnitudes of λ, μ (see Appendix A). In the simplest case (no interference of

grazers, $\mu = 1$) the overall functional response is given by (26)–(28). By taking into account the first three terms in the Taylor expansion for $F(\langle P \rangle)$ and obtain

$$F(\langle P \rangle) \approx \alpha\lambda \left(\frac{1 + \exp(\lambda H)}{2(\exp(\lambda H) - 1)} \langle P \rangle + \frac{\gamma H^2 \langle P \rangle^2}{6} + \frac{1 + \exp(\lambda H)}{24 \exp(\lambda H) - 1} H^3 \gamma^2 \langle P \rangle^3 \right), \quad (10)$$

Based on (10) one can prove that $F'(P) - PF(P) > 0$, which is the stability condition for predator-prey interactions in a eutrophic environment [87].

It is possible to come up with a simple (but not mathematically strict) explanation of the observed emergence of Holling type III functional response. Figure 4a shows the vertical distribution profiles of distribution of actively feeding zooplankton (plotting the ratio $Z_a(h)/Z_{0a}$; the vertical distribution of phytoplankton is the same) constructed, for the sake of simplicity, for $\mu = 1$ (no interference of grazers). An increase in the total amount of phytoplankton $\langle P \rangle$ leads to a sharper gradient of algal distribution (because of algal self-shading). The distribution of grazers $Z_a(h)$ follows that of the food and it results in a larger proportion of zooplankton feeding in food-rich layers, thus increasing the total consumption rate. Note that the emergence of an overall sigmoid functional response due to the above mechanism is possible in the case of a pronounced depth (deep waters), but is impossible for small H since the distribution of plankton becomes more homogeneous and, thus, closer to the local response.

The interference between the grazers (increase in μ) would impede the above alteration between the types of responses. This can be obtained directly from expression (27) for $F(\langle P \rangle)$ found in Appendix A for $\lambda = 0$. Differentiation of those expressions shows that $F'(P) - PF(P) < 0$ for large μ , thus not satisfying the stability condition [87]. However, the impact of interference of the grazers can be better understood directly from Fig. 4b where the distribution of actively feeding grazers (the ratio $Z_a(h)/Z_{0a}$ is shown for the same total amount of phytoplankton in the system ($\langle P \rangle = 4 \mu g C l^{-1}$). One can see that the competition between the grazers results in homogenization of the vertical distribution of active grazers, thus the local functional response is approached. Interestingly, the overall functional response can be even slightly smaller than the local one (see Fig. 3b) despite the fact that a substantial part of the active feeders are located in food-rich surface layers.

It is important to stress here that the emergence of a Holling type III overall response due to active food searching behaviour of grazers has observational background. In particular, it was found that zooplankton species which exhibit non-sigmoid functional response under laboratory conditions show a different overall functional response in real ecosystems [76, 79]. In particular, increasing the total amount of phytoplankton in the system can result in displacement of zooplankton towards surface layers of high food concentration, with feeding taking place mostly in those layers (see [5, 79]).

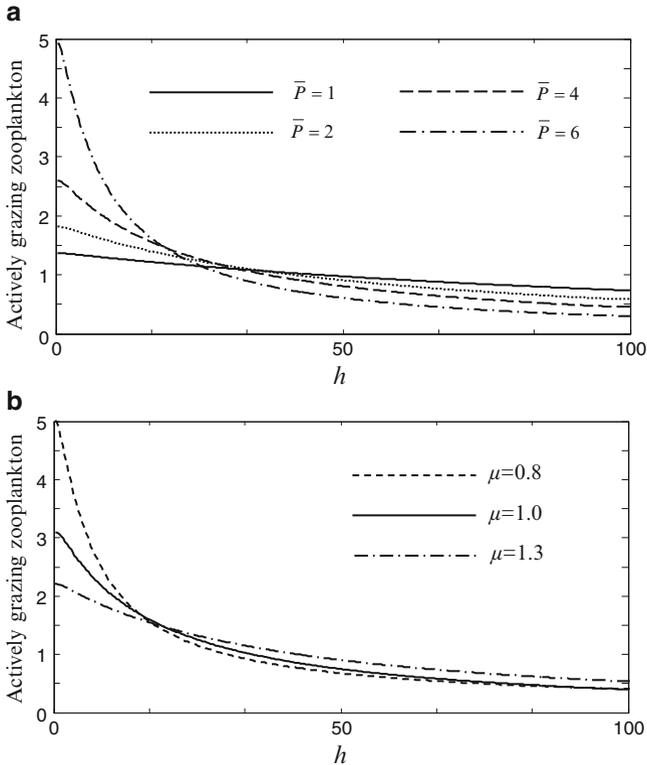


Fig. 4 (a) Mechanism of emergence of a sigmoid zooplankton functional response. Stationary vertical distributions of actively feeding grazers ($Z_a(h)/Z_{0a}$) are shown for different total amounts of food (\bar{P}) ($\mu = 1$, no interference of grazers). An increase in $\langle P \rangle$ results in a sharper gradient of food distribution, the feeders follow the distribution of food and move for feeding to food-rich surface layers. The spatial distribution of phytoplankton is proportional to that of zooplankton and is not shown in the figure. (b) The influence of interference of grazers on the consumption rate. Vertical profiles of actively feeding grazers are shown for the same total amount of phytoplankton ($\langle P \rangle = 4 \mu\text{g Cl}^{-1}$) for different μ . Enhancing the competition of grazing (increasing μ) results in a more pronounced homogeneity in vertical distribution

4 The Role of Intra-population Variability of Zooplankton in Population Persistence

In this section I address another important issue related to the active feeding behavior of zooplankton in the water column: the within-population variability of grazers and its role in the population survival and persistence.

4.1 Describing the Intra-population Variability of Zooplankton Grazers

An important intrinsic property of any real population is that individuals forming this population often differ from each other: organisms have various sizes, different ability to move, and, finally, they can have different personal behaviour (e.g. preference for staying in risky or safe environment, aggressiveness, etc.). There exist a large number of theoretical works considering dynamics of such structured populations ([24, 29, 69, 73, 74, 97, 118]). It has been shown that taking into account intra-population difference would seriously alter modelling outcomes. A proper review on models of structured populations and a comparison with their unstructured analogues should be done elsewhere. In most previous publications, however, the authors have considered population structuring with respect to the age or size of individuals or due to some physiological traits. Less studied are population which are structured according to different behavior of individuals (but see [96]). In this section I shall construct a simple model combining physiological and behavioural structuring of a population of grazers regulated by top predation (carnivorous zooplankton or planktivorous fish).

Zooplankters are known to show a large interindividual variability in their feeding patterns [92, 93, 108]. Figure 5 demonstrates a large variability in the consumption rates of individual zooplankters (*Calanus spp.*) obtained in laboratory (data provided by prof. E. Arashkevich and colleagues). In the figure, the individual consumption rates of copepods are plotted for different temperatures but for the same food density. One can see a large deviation in the consumption rates of the grazers which can be as large as one order of magnitude. Another important observation is that most of the individuals conserve their consumption characteristics/traits for different environmental conditions (various temperatures), i.e. their ability of consuming food at high, intermediate or low rates (see Fig. 5b). Thus, the whole population can be described as physiologically structured. Interestingly, the pronounced difference in food consumption does not seem to be related to the variation in the individual sizes of organisms which were close to each others (not shown result). Note also that zooplankters also show a large interindividual variability in their swimming rates which could result in a large variation in the rate of food consumption [108].

The observed individual differences in the consumption and swimming rates of grazers could eventually result in an intra-population difference in foraging behaviour. Indeed, zooplankton herbivores often migrate to the upper layers with higher food abundance despite the predation risk [10, 65, 90]. Often the grazers implement the eat and run strategy which consists in quickly filling the gut and leaving the risky environment [95]. Since the ability of filling guts can substantially vary from individual to individual, the individuals with high ingestion rate can leave the surface layers faster than the others, thus spending more time outside the risky environment [26, 107]. As such, variation in physiological traits within a zooplankton population can translate itself into different foraging strategies/behaviour and,

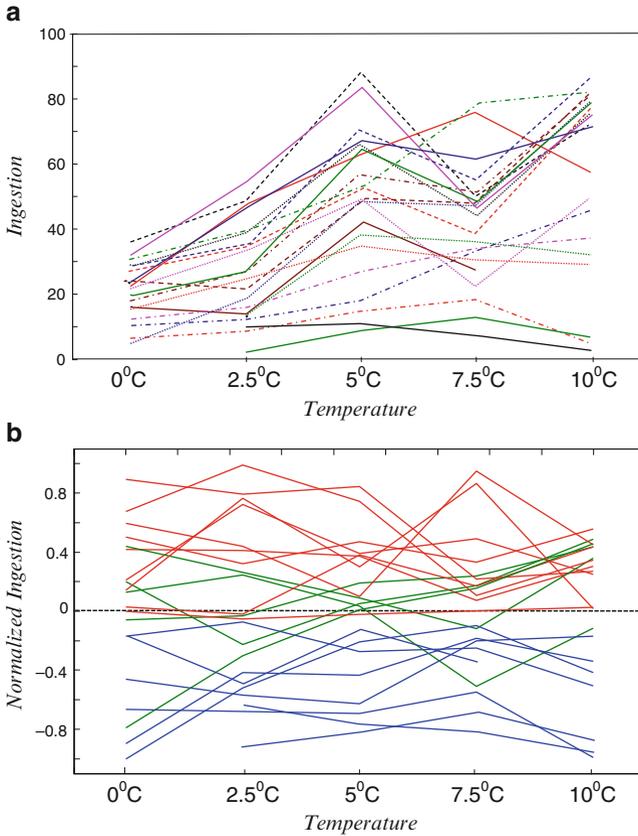


Fig. 5 Individual ingestion rates (mg Chl *a*/ind./day) of copepods *Calanus* spp. measured in the laboratory under different feeding conditions (different temperatures). Each curve describes the ingestion rate of a single individual. (a) The absolute values of ingestion rates. (b) Normalized ingestion rates compared to the mean value for the given temperature. Red and blue curves correspond to individuals with ingestion rates lying, respectively, above and below the population mean value. Green curves describe individuals with highly variable ingestion rates which can be both above and below the mean value. One curve crossing zero is depicted in red since it shows a persistent behavior very close to the mean values. Absence of points for certain individuals can be explained by the fact that the organisms are suggested to be depressed in those experiments and simply did not consume food. The data have been obtained by Prof. E. Arashkevich and colleagues

as a result, into segregation of organisms in space. A similar scenario of segregation of grazers within the same population has been found by Fossheim and Primicerio [37], where different copepodite developmental stages were separated in the column in the presence of top predators (fish). Note that similar differentiation in behaviour due to differences in physiological traits has been found for other non-planktonic species, such as fish [12, 19], octopuses [71] and some mammals [100]. In particular, it was reported in a population of salmon that the interindividual variability in

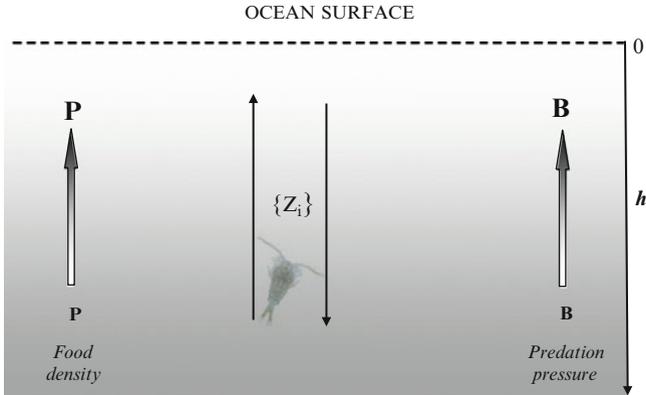


Fig. 6 Schematic diagram explaining construction of physiologically structured model (11)–(12) of trophic interactions between herbivorous zooplankton and their predator (carnivorous zooplankton and/or planktivorous fish). Predation on zooplankton by visual predators takes place mostly in the surface layers (the risky environment) which is also characterized by high food abundance (high density of phytoplankton P). Deeper layers provide a better refuge from the predators but are less abundant in phytoplankton. Zooplankton individuals within a population are divided into cohorts Z_i , which are characterized by different growth rates, location of feeding in the column and the time spent in the risky environment

willingness to take predation risk near the surface could result in structuring of the patterns of vertical migration behaviour in the water column [35].

In this paper, I suggest a generic model showing the potential role of intra-population variability in the life traits and behaviour of the herbivorous zooplankton in persistence and stability. Schematically, the model is depicted in Fig. 6. The food density (phytoplankton) increases in the layers towards the surface. At the same time, the efficiency of visual predators is higher near the surface, thus there is a trade-off between food density and the mortality due to predation risk. In the model, the zooplankton population Z is divided into n cohorts/groups (Z_i) with different behaviour. In particular, cohorts Z_i vary with respect to the amount time spent feeding in surface layers with high predation risk as well as in the depth of feeding. Thus, the mortality rate of zooplankton, which in the model is due to predation, becomes cohort-dependant. I consider that different cohorts can exhibit different growth rates due to the variation of time spent in food-rich layers.

The trophic interactions between the grazers and their predator (carnivorous zooplankton or planktivorous fish) are described via the following differential equations

$$\frac{dZ_i}{dt} = \sum_j w_{ij} R_j Z_j - g_i(Z_i) B, \quad (11)$$

$$\frac{dB}{dt} = B \left(\sum_i \omega g_i(Z_i) - \delta \right), \quad (12)$$

where Z_i and B are biomass of the zooplankton in cohort i ($i = 1, n$) and the predator, respectively. The sum in (11) describes the growth rate of Z_i due to the reproduction of all cohorts; the contribution of cohort j to the growth rate of cohort i is described by the weight w_{ij} . I further call coefficients w_{ij} the demographic factors which I consider to be density independent. I require that the sum of the demographic factors w_{ij} over all cohorts should be equal to unity.

One would expect that $w_{ii} \gg w_{ij}$, i.e. the offspring of each cohort mostly belong to the same cohort. However, I do not formally impose such a restriction by considering as well the possibility of $w_{ii} \approx w_{ij}$. In this paper, I assume that the demographic factors are at genetic equilibrium, i.e. the demographic factors do not change in time (cf. [16]). The coefficient R_j describes the overall per capita growth rate of cohort j . For the sake of simplicity I consider that all R_j are constant, i.e. no intraspecific competition. Such an assumption allows to model plankton dynamics in euphotic environments.

The parameters describing the predators of zooplankton are: the functional response $g_i(Z_i)$, which is different for different cohorts; ω is the food utilization coefficient and Δ is the mortality rate of the predator. For the sake of simplicity, I consider the functional response g_i with saturation of Holling type II given by the Monod parametrization

$$g_i = a_i \frac{Z_i}{1 + b \sum_j \frac{a_j Z_j}{a}}, \tag{13}$$

where b is the coefficient characterizing the saturation of predation at high densities of Z_j . The coefficients a_i , which are proportional to the attack rates, are different for different zooplankton cohorts. I suggest that a_i are larger for those cohorts where the individuals intentionally stay longer in more risky part of the habitat (surface layers) with higher predation pressure. When including the effects of saturation, I take into account the fact that the actual amount of zooplankton which is available for predation in surface layers should be multiplied by certain weights. Those weights would model the relative duration of the zooplankton cohorts stay in the more risky environment, thus they should be a function of the predator attack rate. I suggest that such weights are proportional to the attack rates, since the relative difference in a_i characterizes the relative time spent in surface layers; a denotes in (13) the average values of a_i . I should note that our findings remain qualitatively the same in the case of the ‘classical’ Holling type II response with the same weights, i.e. when removing a_j and a in the denominator of (13).

4.2 Analysis of the Model of the Intra-population Variability of Zooplankton

Model (12)–(13) has been intensively investigated both numerically and partially analytically. In this paper, I focus mostly on the case where there are only two zooplankton cohorts $n = 2$ and only briefly discuss how the patterns obtained for

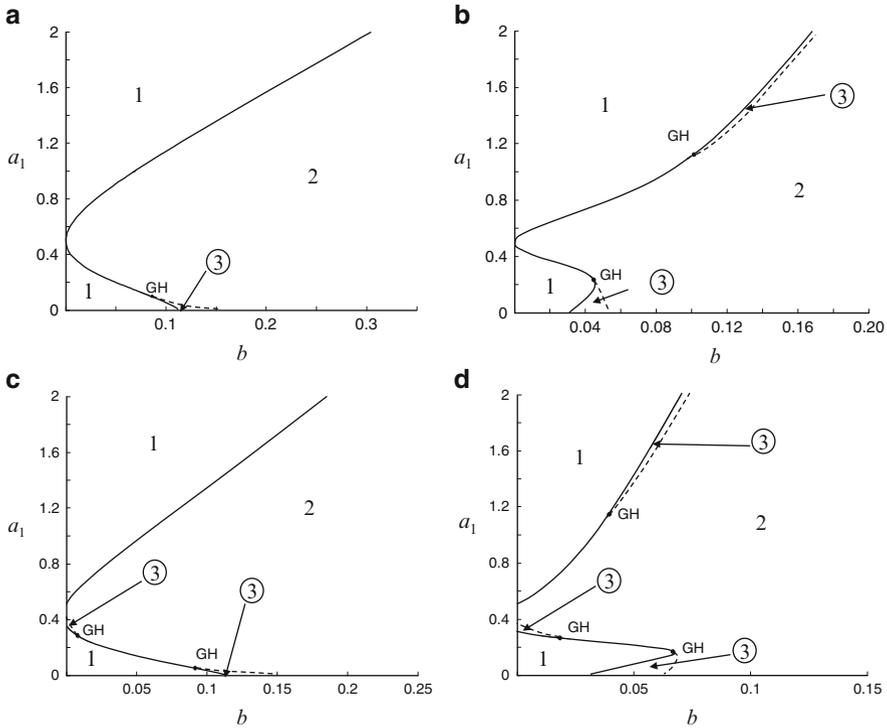


Fig. 7 Bifurcation diagrams in the $a_1 - b$ plane constructed for system (11)–(12) for the number of zooplankton cohorts $n = 2$. Dynamical regimes are described in the text. The system can be regulated in domains 1 and 3 (the solutions are bounded). The *solid curve* is the Hopf bifurcation curve. The *dot-dashed curves* represent limit cycle bifurcation curves. The points GH denote general bifurcation points. (a), (b) Equal per capita growth rates $R_1 = R_2 = 1$; (a) $w_{11} = w_{22} = 0.5$; (b) $w_{11} = w_{22} = 0.8$ (c), (d) Different per capita growth rates $R_1 = 1; R_2 = 2$. (c) $w_{11} = w_{22} = 0.5$; (d) $w_{11} = w_{22} = 0.8$. The other parameters are $a_2 = 0.5, \omega = 0.25, \delta = 0.1$

$n = 2$ will change with an increase in n . The stability of the stationary states of the system for $n = 2$ is addressed in Appendix B (for small b). In particular, I show that the system has a unique nontrivial stationary state which, depending on model parameters, can be either stable or unstable. Note that the system (11)–(12) becomes the classical predator-prey model in the case where all cohorts are equal. This system is always globally unstable for $b > 0$ [6, 87] and is neutrally stable (Lotka-Volterra model) for $b = 0$.

Figure 7 provides an insight into parametric portraits for $n = 2$. The diagrams are obtained with the help of the software MATCONT [28]. The diagrams are constructed in the (a_1, b) plane, the other parameters being fixed. Figure 7a,b describe the scenario when the two cohorts have equal per capita rates $R_1 = R_2$ but different attack rates $a_1 \neq a_2$. Ecologically, it signifies that the larger mortality due

to predation (consequently, a larger time spent in surface layers) has no influence on the reproduction rate. In domain 1 the unique coexistence state (Z_1, Z_2, B) is locally stable, thus small perturbations of the state will eventually vanish. This stationary state, however, is not globally stable. It is surrounded by an unstable limit cycle: for initial species densities located far away from the state, the trajectories would go to infinity and other factors (lack of resources, competition) should limit the population growth. In domain 2 the nontrivial stationary state is globally unstable: all trajectories starting nearby will eventually go to infinity. In the rather narrow domains 3, trajectories unwind from the unstable stationary state to a stable limit cycle. This cycle is enclosed by an unstable outer cycle.

One can see from the Fig. 7a,b that the fact that the attack rates of predators on different cohorts are different can provide the stability of the whole population thus preventing it from extinction. Indeed, for equal attack rates by predators, the population will exhibit oscillations with gradually increasing amplitude, with the minimal species densities approaching zero. Thus producing individuals which are subjected to more predation can be beneficial for the whole population. Interestingly, even in the absence of saturation ($b = 0$), the Lotka-Volterra system can become stable. This fact is analytically proven in Appendix B. Figure 7a is constructed for the equal demographic factors ($w_{ij} = 0.5$). Taking into account a more realistic scenario when $w_{ii} > w_{ij}$ —i.e. the offspring of each cohort mostly belong to the same cohort—results in shrinking of the stability domains 1 (see Fig. 7b, mind the difference between the scales on the b -axis).

I shall now consider a more realistic scenario, where increase/decrease in the attack rate a results into a relative increase/decrease in the growth rate R . This is shown in the diagrams in Fig. 7c,d constructed for $R_2 > R_1$. One can see that compared to the case with $R_2 = R_1$, the size of domains of stabilization (1, 3) have shrunk. Moreover, the diagrams predict that the stabilization will take place when the cohorts with the larger growth rates should have a smaller mortality rate, i.e. for $R_i > R_j$ there should be $a_i < a_j$. This conclusion is analytically justified in Appendix B ($b = 0$). On the contrary, for $R_i > R_j$ and $a_i > a_j$ and a small absolute difference between a_i and a_j the system will be globally unstable. Thus, the existence of a cohort with individuals dwelling more time in food rich (and predation risky) layers and having larger reproduction rates would be destabilizing. Finally, the stability of the system is restored for $R_i > R_j$ and $a_i > a_j$ in the case where the difference between a_i and a_j is sufficiently large. This corresponds to the lower stability domain 1.

It is natural to suggest that the parameters R_i and a_i are not independent but related via a certain trade-off function $a_i = a_i(R_i)$ which has the same functional form $a = a(R)$ for all cohorts. The parameters R and a are potentially related since they both depend on the amount of time spent in food-rich but predator risky environment. For the sake of simplicity consider first that $b = 0$. In the case $a(R)$ is a decreasing function, the coexistence stationary state in the model will always be stable regardless of the shape of this function. On the other hand, an increasing function $a(R)$ may have a destabilizing effect. Interestingly enough, even if $a(R)$ is a decreasing function, the system's stabilization can be still possible provided the rate

of decrease $a(R)$ is sufficiently large. This is related to the fact that for $a_i \rightarrow a_j$ and $R_i \rightarrow R_j$ the size of the instability interval on the a -axis vanishes. This can be seen from the comparison of the upper and the lower figures in Fig. 7 (see also Appendix B). Let us vary the parameter a_1 for a fixed a_2 . I shall decrease R_1 starting from $R_1 = R_2$; it will result in an increase of a_1 . It is shown that (Appendix B) in the case where the gradient of the trade-off function is larger than that of (45), the stability of the stationary state will be guaranteed. Taking into account the saturation in predation $b > 0$ will result in some changes. In particular, the stability of the stationary state will require a larger degree of scattering between a_1 and a_2 (larger absolute values of $a_i \rightarrow a_j$). Thus, even the existence of a fast decreasing trade-off function $a(R)$ will not automatically signify the stabilization of the system (see Fig. 7): a threshold value of ofjiaa should be exceeded in this case.

Note that the stabilization in the structured population of grazers requires that the physiological traits and behavioral patterns within a cohort remain constant. I shall refer to such structuring as the genetic structuring of a population. In contrast, there can be a temporal structuring within a population where the traits of each cohort vary in time due to some stochastic processes. As a result, the splitting of a population into cohorts occurs for a short time period (which is smaller than the individual lifespan time) after which the individuals swap between different cohorts. Model (11)–(12) predicts that stabilization takes place only for a genetically structured population. Figure 8a shows damped oscillations of a genetically structured population of grazers consisting of two cohorts with different attack rates of predator ($a_1 = 1$, $a_2 = 0.6$). The trajectory will tend to a stable stationary state. The situation is different when the population is temporally structured (Fig. 8b). In this case, instantaneously the population still consists of two cohorts with the same vulnerabilities of predation ($a_1 = 1$, $a_2 = 0.6$), however, every Δt time units there is a probability $1/2$ of exchange between the cohorts: individuals swap between the two cohorts. As a result, the oscillations of density become constantly increasing (Fig. 8b) which would result in a population collapse. In this case, the dynamics is equivalent to a non-structured predator-prey system with a Holling type II functional response, which is globally unstable.

Considering a larger number n of cohorts does not qualitatively alter the previous results on stabilization. In particular, bifurcation diagrams constructed for $n = 3, 4$ are qualitatively similar to those from Fig. 7. In general, stability of the coexistence state requires the existence of a trade-off function $a(R)$ with a supercritical slope at $a_i = a_j$ and $R_i = R_j$. Finally, when n is large, the discrete framework (11)–(12) based on the use of a system of ODEs should be replaced by a continuous distribution of the life traits in the population suggesting an infinitely large number of cohorts and the model becomes transformed into a system of two integro-differential equations. In this case, the shape of $a(R)$ will play a critical role in the system stability along with the distribution of the demographic factors w_{ij} . Investigation of such a model will be a part of future research.

One important question concerning this section is which trade-off functions relating the predation risk and the growth rate of zooplankton will be realistic. Although there exists a large amount of literature on this topic, this issue is a matter of

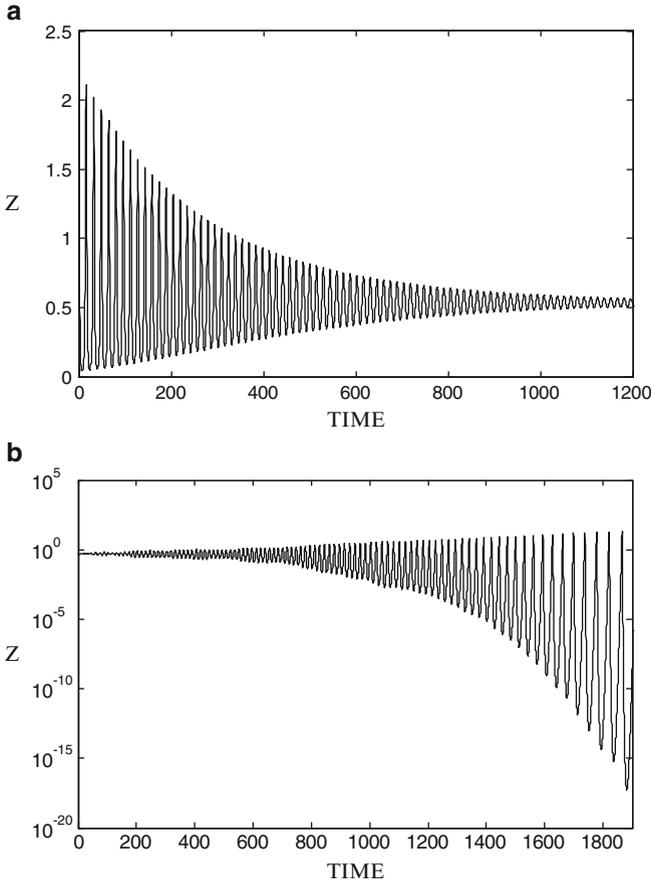


Fig. 8 Explaining the difference between the genetic structuring and the temporal structuring of a population ($n = 2$). **(a)** Genetic structuring: the vulnerability to predation for each subpopulation remain constant $a_1 = 1, a_2 = 0.6$. The total biomass of grazers Z exhibits damped oscillations and the trajectories tend to a stable stationary state. **(b)** Temporal structuring: at each moment of time the values a_i are different and equal to 1 or 0.6; however, every $\Delta = 0.5$ time units there is a probability of 0.5 of swapping between a_i and a_j . The other parameters are $R_1 = R_2 = 1$; $w_{11} = w_{22} = 0.5, a_2 = 0.5, \omega = 0.25, \delta = 0.1; b = 0.02$. The population of grazers will eventually attain very low densities and will collapse

much discussion [10,37,65,67]. Most of the conclusions are derived from modelling results or simply based on common sense (!). For instance, there is an opinion that those zooplankters which spend more time feeding in the risky surface layers should be compensated by an increase in growth rate [41,57,107]. Some grazers which quickly fill their gut in the surface layer and run away to digest the consumed food would need to spend large amounts of energy on vertical migration, thus this energy will not be available for reproduction [65,95]. This would imply that $a(R)$ should

be an increasing function. An important point, however, is that the time spent by zooplankters in the food-rich layer can be a poor indicator of the growth rate. Indeed, individuals who need to stay in surface layers more may simply be poor feeders with low growth rates. The major problem is that there is still a lack of data on the individual variability of zooplankton behavior in situ.

5 Discussion and Conclusions

Taking into account complex foraging behavior of zooplankton in the water column on different spatial and temporal scales is of vital importance for improving plankton models. Very often, however, one needs to incorporate movements of grazers implicitly, especially in models operating on large scales (e.g. the scale of the whole euphotic zone). Scaling up the grazing rate of zooplankters from microscales has its own particular features as compared to some other non-planktonic ecosystems. Firstly, there is a pronounced heterogeneity of the aquatic environment in the vertical direction due to the light attenuation with depth, water stratification in the column resulting in sharp turbulence, temperature, salinity gradients, patchy distribution of predators, etc. Secondly, the zooplankton grazers are usually fast moving organisms, so they are able to cover the whole euphotic zone in a short time period (hours) which is much smaller than the generation time of the population varying from several months to years. Thirdly, the movement of grazers is much faster than the characteristic rate of change of the spatial food distribution (phytoplankton or microzooplankton). Finally, the behavior of grazers depends on the part of the habitat where they are currently dwelling (e.g. between the surface and deep layers). As such, the conventional techniques of theoretical ecology of extrapolation of small-scale dynamics to larger scales (e.g. the aggregation approach, the scale transition approach, the modified mean-field approach) become inappropriate in this case (cf. [2, 17, 32, 94]). For instance, the scale transition framework becomes inefficient in the case where the environmental properties are substantially different [17]. Some other mathematical tools might be needed in this case.

Interpretation of laboratory experiments on zooplankton foraging in modelling can be tricky and should be done with care. For example, it has been nicely demonstrated that in laboratory settings some copepods exhibit swimming behavior which can be described as a fractal random walk (e.g. [105, 106, 108]). The scaling exponent of the motion was estimated [108] which could, in principal, allow us to extrapolate those results to larger scales. However, the characteristic size of the laboratory settings, was rather small (up to 1–2 m) and potential extrapolation of the results even to intermediate scales (10–30 m) looks problematic. In particular, the fractal random walk behavior cannot describe the eat and run strategy of copepods which is observed in reality on intermediate scales [65, 77, 95]. On such scales movement of animals includes persistent ascending and descending of grazers, i.e. a ballistic motion. Our general understanding is that the complex

(multi) fractal food searchery observed on microscales would be only a part of the zooplankton feeding cycle. This goes along with the current understanding of movement in theoretical ecology. Indeed, it is now well recognized that patterns of animal movement can be often considered as a sequence of different phases/modes of movements [81, 86, 109], with each phase corresponding to a different type of activity of the animal, and potentially having different statistical properties. The sequential order of different phases on larger spatiotemporal scales gives the lifetime patch of an individual [86]. Active foraging of zooplankton is a good example of phase-based movement of animals.

In this paper I have considered two examples of the implicit incorporation of active foraging of plankton grazers into models. First, I considered the implementation of the zooplankton functional response on different scales. I demonstrated that scaling up the functional response to the size of the whole euphotic zone can result in alteration of the type of response and, as a result, a sigmoid (Holling type III) overall functional response can emerge from the local non-sigmoid local response. This fact is of importance since investigation of trophic chain models reveals that a Holling type III response usually enhances stability of eutrophic ecosystems [6, 87]. Interestingly, there is a vivid discussion in the literature on the adequacy of implementation of a sigmoid type of response in plankton models [78, 84, 102, 103]. The point is that it has been observed in experimental studies that for most herbivores the functional response is non-sigmoid, i.e. it is either of type I or II ([27, 50, 55, 58]) and, as a result, a rather strong opinion in the literature is that implementation of Holling type III in plankton models is biologically meaningless [27, 84, 103]. The results of Sect. 3 somewhat challenge this opinion and consider this problem from a different angle.

I suggest that the emergence of a sigmoid functional response when scaling up to macroscopic level would be observed for the carnivorous zooplankton as well due to a similar scenario/mechanism. Moreover, a similar alteration of the type of functional response resulting in the emergence of a sigmoid overall response from a local non-sigmoid response due to prey patchiness and predator aggregation has been found in another predator-prey system [85]. The ecosystem under study was an acarine predator-prey system involving the aggregation of predators in food patches. I predict that such a scenario can be found in other non-planktonic systems where there is a strong feedback between the spatial distribution of prey and its total abundance in the system resulting in a sharper gradient of spatial prey distribution (see Fig. 4a).

Another important result we have seen is that the interindividual structuring of grazers according to their behavior can enhance the persistence of the whole population and prevent the species from extinction (Sect. 4). Thus, variation in the behavioral strategy, which translates itself into a variation of time spent in dangerous parts of the environment, would be beneficial for the whole population. Stabilization of the system consisting of grazers and their predators (fish) in an environment with an unlimited carrying capacity requires two major conditions. Firstly, some life traits (in particular, the vulnerability to predation) of individuals should be genetically different, i.e. the mean values for a fixed individual should remain constant.

Secondly, in the case of high variation in the growth rate R among the individuals, there should be a certain trade-off between R and the vulnerability a . Stabilization is guaranteed when a larger growth rate signifies less vulnerability. In the opposite case, the stabilization can be still possible, but requires a supercritical value of slope of the functional dependence $a(R)$. I should admit, however, that the reported mechanism of the enhancement of persistence in plankton communities is still to be tested. The major problem arising here is that the spatial structuring of zooplankton (if it exists in reality) would take place on intermediate spatial scales and it is rather hard or even impossible to follow the trajectory of each zooplankter *in vivo* or in plankton towers. A possible method of experimental justification of the suggested mechanism could be to search for correlation between the vertical location of individual grazers in the column and certain physiological traits of those grazers (e.g. swimming speed, feeding rate, etc.) which can be revealed after sampling.

Note that our results on the stability of the dynamics of structured populations can be applied as well to some other non-planktonic predator-prey systems. Indeed, the key-factor assuring the system stability is the genetic difference in the vulnerability of individuals to predators. As such, in any population where individuals are characterized by a substantially different vulnerability to predation, the above stabilization mechanism could be realized. For instance, such a situation can be possible in the case of the existence of refuges for prey and structuring of the prey population according to the mean time spent in those refuges. Different attack rates on different prey individuals can be due to high genetic variation in physiological characteristics such as mobility, the ability of detecting the predator, etc. Finally, I should note that our result that physiologically and/or behaviorally structured populations are less prone to extinction is in a good agreement with previous theoretical works [96, 98] providing a somewhat different mechanism of stabilization based on intra-population competition.

Among the important challenges for further progress in understanding and modelling patterns of active zooplankton foraging behaviour I would like to highlight the investigation of intermediate scale processes. New studies should include the collection of plankton samples on finer scales. On the other hand, a proper mathematical framework for modelling the movement of plankton on those scales is still lacking. I suggest that such a framework should be based on a density-dependant (Eulerian) approach, but include complex behavioral aspects of the animals. In the absence of such a framework, the current tendency in the literature is the implementation of IBMs, and while I agree full-heartedly with the need for development of such models in marine ecology, I do argue that the need for implementation of IBMs still needs to be justified for herbivorous zooplankton which are characterized by large population numbers and patchy spatial structure. I strongly believe that the density-dependant framework can provide powerful modelling tools capable of efficiently incorporating complex patterns of foraging behavior and the variability of physiological traits within populations.

Appendix 1

Here I derive the expression for the overall functional response of zooplankton. The equation determining the vertical profile of phytoplankton is given by

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial t^2} + r_0 \cdot \exp\left(-\lambda h - \gamma \int_0^h P(h)dh\right) P - \frac{HP^\mu f(P)}{\int_0^H P^\mu(h)dh} Z_0, \quad (14)$$

where D is the diffusion coefficient of vertical turbulence. I consider that the ecosystem is eutrophic, thus $r = const$ and $K \gg 1$. We are interested in computing the stationary vertical profile of zooplankton, which is determined by

$$0 = D \frac{\partial^2 P}{\partial t^2} + r_0 \cdot \exp\left(-\lambda h - \gamma \int_0^h P(h)dh\right) P - \alpha \frac{P}{1 + \beta P} \frac{HP^\mu}{\int_0^H P^\mu(h)dh} Z_0, \quad (15)$$

To be able to provide an explicit analytical expression for the functional response we need to do some simplifications. As such, I neglect the diffusion process which are small terms compared to the local growth rate and the grazing. Also, I neglect saturation in the local functional response. We obtain

$$0 = r_0 \cdot \exp\left(-\lambda h - \gamma \int_0^h P(h)dh\right) P - \alpha \frac{HP^\mu}{\int_0^H P^\mu(h)dh} Z_0, \quad (16)$$

One can simply re-write (16) in the following way

$$\lambda h + \gamma \int_0^h P(h)dh = -\ln \left[\frac{\alpha H}{r_0} \frac{P^\mu}{\int_0^H P^\mu(h)dh} Z_0 \right], \quad (17)$$

After differentiating (17) with respect to h , we obtain the following differential equation

$$\lambda P + \gamma = -\frac{\mu P'}{P}, \quad (18)$$

Integration of (18) which is a Bernoulli equation gives the stationary profile of phytoplankton:

$$P(h) = \frac{\lambda}{C \exp(\lambda h/\mu) - \gamma}, \quad (19)$$

where C is an integration constant. By integrating (19) over the whole water column, we can express C as a function of the spatial average phytoplankton density $\langle P \rangle$.

$$C = \gamma \frac{\exp\left(\frac{\lambda H + \gamma H \langle P \rangle}{\mu} - 1\right)}{\exp\left(\frac{\lambda H}{\mu}\right) \left(\exp\left(\frac{\gamma H \langle P \rangle}{\mu}\right) - 1\right)}, \quad (20)$$

Thus the vertical profile of phytoplankton becomes a function of $\langle P \rangle$, i.e. $P = P(h, \langle P \rangle)$. The overall functional response of zooplankton in the water column is obtained from (5), which gives

$$F(\langle P \rangle) = \frac{\alpha H \int_0^H P^{\mu+1}(h) dh}{\int_0^H P^\mu(h) dh}, \quad (21)$$

with $P = P(h, \langle P \rangle)$ is given by (19) and (20). Note that by integrating (21) one can obtain the explicit expression for the functional response which is rather cumbersome. However, one can obtain tractable analytical expressions for F for some limiting cases.

- (i) $\mu = 1, \lambda = 0$. This signifies that there zooplankton is distributed according to the simplest ideal free distribution law and absorption of the light by water is small compared to the self-shading. Integration and simplification of (21) gives following the functional response

$$F(\langle P \rangle) = \frac{\exp(\gamma H \langle P \rangle) + \exp(-\gamma H \langle P \rangle) - 2}{(\gamma H)^2 \langle P \rangle}, \quad (22)$$

It is easy to prove that the overall functional response (22) is of Holling type III since the stability condition $F'(\langle P \rangle) - \langle P \rangle F''(\langle P \rangle) < 0$ [87] is always satisfied for $\langle P \rangle > 0$. One can easily expand (22) into Taylor series:

$$F(\langle P \rangle) = \alpha \sum_{n=0}^{\infty} \frac{(\gamma H)^{2n} \langle P \rangle^{2n+1}}{(2n+2)!}, \quad (23)$$

One can use few first terms of expansion when modelling consumption rates at small and intermediate amounts of food.

- (ii) $\mu = 1, \lambda \neq 0$. This signifies that there is no interference between the grazers; however there is absorption of light by water along with algal self-shading. Integration of (21) after some simplification gives the following Taylor expansion

$$F(\langle P \rangle) = \alpha \sum_{n=0}^{\infty} c_n \langle P \rangle^n, \quad (24)$$

where the coefficients c_n are determined from

$$c_{2n+1} = \frac{\alpha\lambda}{(2n+2)!} \frac{(1 + \exp(\lambda H)) H^{2n+1} \gamma^{2n}}{\exp(\lambda H) - 1}, \quad (25)$$

$$c_{2n} = \frac{\alpha\lambda H^{2n} \gamma^{2n-1}}{(2n+2)!}, \quad (26)$$

(iii) $\mu \neq 1$, $\lambda = 0$. This signifies that there is some interference between the grazers and the absorption of the light by water is still small compared to the self-shading. Integrating of (21) gives the following explicit expression for the functional response

$$F(\langle P \rangle) = \frac{(\mu - 1) (\exp(\langle P \rangle \gamma H / \mu) - 1) (\exp(\langle P \rangle \gamma H) - 1)}{H \gamma (\exp(\langle P \rangle \gamma H / \mu) - \exp(\langle P \rangle \gamma H))}, \quad (27)$$

By considering the Taylor expansion of (27) we obtain

$$F(\langle P \rangle) = \alpha \sum_{n=0}^{\infty} s_n \langle P \rangle^{2n+1}, \quad (28)$$

It is impossible to obtain simple expressions for the coefficients s_n . However, the first three coefficients can be easily computed:

$$c_1 = 1; c_2 = \frac{(\gamma H)^2}{12\mu}; c_3 = \frac{(\gamma H)^4 (\mu^2 - 4\mu + 1)}{720\mu^3}, \quad (29)$$

Note that for the most general case ($\mu \neq 1$, $\lambda \neq 0$), the expression for the overall functional response becomes rather untractable and only numerical methods can be used to reveal the shape of $F(\langle P \rangle)$.

An important question is about the stability of the profiles obtained. Numerical methods show that those profiles are stable; however, stability for an infinite carrying capacity $K \rightarrow \infty$ requires a certain threshold value of $\gamma > 0$.

Appendix 2

Here I analytically address the stability property of the system (11)–(12) in the case where there are two different zooplankton cohorts showing different behavior. For the sake of simplicity I shall also consider that the functional response of the predator is of Holling type I ($b = 0$). It is easy to prove the existence of a trivial stationary state (0,0,0) as well as semitrivial stationary states where the density of one of species is zero. Simple analysis shows that all those states are unstable. The nontrivial stationary states are determined from

$$0 = w_{11} R_1 Z_1 + w_{12} R_2 Z_2 - a_1 Z_1 B, \quad (30)$$

$$0 = w_{21}R_1Z_1 + w_{22}R_2Z_2 - a_2Z_2B, \quad (31)$$

$$0 = a_1Z_1 + a_2Z_2 - \delta/\omega, \quad (32)$$

From (30)–(32) one can easily find the stationary density B from the evident condition:

$$\Delta = \begin{vmatrix} w_{11}R_1 - a_1B & w_{12}R_2 \\ w_{21}R_1 & w_{22}R_2 - a_2B \end{vmatrix} = 0. \quad (33)$$

This gives the following “characteristic” equation for B

$$a_1a_2B^2 - (w_{11}R_1a_2 + w_{22}R_2a_1)B + (w_{11}w_{22} - w_{12}w_{21})R_1R_2 = 0, \quad (34)$$

Note that a similar characteristic equation will provide the stationary B for in the case the number of zooplankton cohorts is n . Formally, (34) may have up to two positive solutions which are the roots of the quadratic equation. However, a rigorous analysis (resulting into rather cumbersome expressions) shows that in the case of two positive roots of (34), one of the roots always gives a negative stationary density Z_i . Thus, the nontrivial stationary state of (11)–(12) is unique provided it exists. The stability of the nontrivial stationary state is determined by the Jacobian matrix given by

$$J = \begin{pmatrix} R_1w_{11} - a_1B & R_2w_{12} & -\delta a_1Z_1 \\ R_1w_{21} & R_2w_{22} - a_2B & -\delta a_2Z_2 \\ \omega\delta a_1B & \omega\delta a_2B & 0 \end{pmatrix}. \quad (35)$$

However, a direct substitution of explicit expressions for the stationary states results in an analytically intractable formula. To have an analytical insight into the model properties, I shall consider the particular case, where the coefficients are related by $w_{11}w_{22} = w_{12}w_{21}$, which is equivalent to $w_{11} + w_{22} = 1$. This happens, for example, when each cohort produces equal percentage of offspring belonging to it and to the other cohort $w_{11} = w_{22} = 0.5$. Under the above condition the stationary density of species are given by

$$Z_1 = \frac{\delta w_{11}}{\omega a_1(w_{21} + w_{11})}; \quad Z_2 = \frac{\delta w_{21}}{\omega a_2(w_{21} + w_{11})}; \quad B = \frac{w_{11}R_1a_2 + w_{22}R_2a_1}{a_1a_2}, \quad (36)$$

The Jacobian matrix (35) computed at the point (36) becomes

$$J = \begin{pmatrix} -R_2 \frac{a_1}{a_2} \frac{w_{21}w_{12}}{w_{11}} & R_2w_{12} & -\delta \frac{w_{11}}{\omega(w_{21} + w_{11})} \\ R_1w_{21} & -R_1 \frac{a_2}{a_1} w_{11} & -\delta \frac{w_{21}}{\omega(w_{21} + w_{11})} \\ \omega \frac{R_1w_{11}^2a_2 + w_{12}w_{21}R_2a_1}{a_2w_{11}} & \omega \frac{R_1w_{11}^2a_2 + w_{12}w_{21}R_2a_1}{a_2w_{11}} & 0 \end{pmatrix}. \quad (37)$$

The characteristic equation for the eigenvalues of (35) is given by

$$\sigma^3 + \Omega_1\sigma^2 + \Omega_2\sigma + \Omega_3 = 0, \tag{38}$$

where the coefficients Ω_i are determined by

$$\Omega_1 = Sp(J) = \frac{a_2^2 w_{11}^2 R_1 + a_1^2 w_{12} w_{21} R_2}{w_{11} a_1 a_2}, \tag{39}$$

$$\Omega_2 = \frac{\delta}{w_{11}} \frac{w_{11}^3 R_1 a_1 a_2 + w_{21}^2 w_{12} R_2 a_1 a_2 + w_{11}^2 w_{21} R_1 a_2^2 + w_{11} w_{21} w_{12} R_2 a_1^2}{a_1 a_2 (w_{11} + w_{22})}, \tag{40}$$

$$\Omega_3 = det(J) = \delta \frac{(w_{11}^2 R_1 a_2 + w_{12} w_{21} R_2 a_1)^2}{a_2 a_1 w_{11}^2}, \tag{41}$$

The Routh-Hurwitz stability criterion requires that $\Omega_i > 0, i = 1, 3$ and $\Omega_1 \Omega_2 - \Omega_3 > 0$, which can be rewritten in the following way

$$(a_2 - a_1) \left(a_2 + a_1 \sqrt{\frac{R_2 w_{12}}{R_1 w_{11}}} \right) \left(a_2 - a_1 \sqrt{\frac{R_2 w_{12}}{R_1 w_{11}}} \right) > 0, \tag{42}$$

which is equivalent to the following conditions ($w_{12} = 1 - w_{22} = w_{11}$)

$$a_1 \in \left(0, a_2 \sqrt{\frac{R_1}{R_2}} \right) \cup (a_2, +\infty). \tag{43}$$

Here, for the sake of simplicity, I consider that $R_1 < R_2$ since one can easily derive the stability conditions for the opposite sign of this inequality. The stability would occur when the cohort of zooplankton having a larger per capita growth rate R_i has a smaller per capita mortality rate a_i due to predation i.e. for $R_2 > R_1$ we should have $a_2 < a_1$. On the contrary, for a_2 slightly smaller than a_1 (and $R_2 > R_1$) the stability conditions are not satisfied resulting in destabilization of the equilibrium. However, even in this case the stability can be still possible when the difference between a_i is supercritical, i.e. for $a_1 < a_2 \sqrt{R_1/R_2}$.

Suppose that the coefficients a and R are not independent and related via a trade-off function, i.e. $a = a(R)$. In the case where such a function is a decreasing function of R , the stability conditions are satisfied (43) for any shape of $a = a(R)$. In the opposite case $a'(R) > 0$, one can easily derive a criterion which guarantees that the stability conditions are satisfied. One can fix a_2 and vary the value of a_1 starting from $a_1 = a_2$ (corresponding to $R_1 = R_2$). The stability condition (43) requires that

$$a_1(R_1) < a_2 \sqrt{\frac{R_1}{R_2}}. \tag{44}$$

One can re-write (44) in terms of the difference between R_1 and R_2 , i.e. $\Delta R = R_2 - R_1$

$$\Delta a = a_2 - a_1 < a_2 \left(1 - \sqrt{1 - \frac{\Delta R}{R_2}} \right). \quad (45)$$

For a small ΔR we have the condition

$$\Delta a < a_2 \left(1 - \sqrt{1 - \frac{\Delta R}{R_2}} \right) \approx a_2 \frac{\Delta R}{2R_2} = A \Delta R. \quad (46)$$

Thus, in the case the slope of the trade-off relation $a = a(R)$ exceeds a certain constant A , the stationary state (36) will be always locally stable provided it exists. Note that one can analytically prove the same property for a more general case, where w_{ii} are arbitrary values ($i = 1, 2$). In other words, the unique non-trivial stationary state of the system is (locally) stable at least in the parametric region near $a_1 = a_2$ and $R_2 = R_1$ in the case the parameters a and R are related by a trade-off function which can be a linear function. Finally, since the system with $b = 0$ (no saturation in the functional response) is structurally stable, adding small saturation $b \ll 1$ will not violate the previously obtained results.

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References

1. E.R. Abraham, The generation of plankton patchiness by turbulent stirring. *Nature* **391**, 577–580 (1998)
2. P. Auger, S. Charles, M. Viala, J.C. Poggiale, Aggregation and emergence in ecological modelling: integration of ecological levels. *Ecol. Model.* **127**, 11–20 (2000)
3. F. Bartumeus, F. Peters, S. Pueyo, C. Marrassé, J. Catalan, Helical Lévy Walks: adjusting searching statistics to resource availability in microzooplankton. *Proc. Natl Acad. Sci.* **100**(22), 12771–12775 (2003)
4. H.P. Batchelder, C.A. Edwards, T.M. Powell, Individual-based models of zooplankton populations in coastal upwelling regions: implications of diel vertical migration on demographic success and near shore retention. *Progr. Oceanogr.* **53**, 307–333 (2002)
5. B. Bautista, R.P. Harris, Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Mar. Ecol. Prog. Ser.* **82**, 41–50 (1992)
6. A.D. Bazykin, *Nonlinear Dynamics of Interacting Populations* (World Scientific, Singapore, 1998)
7. A. Beckmann, I. Hense, Beneath the surface: characteristics of oceanic ecosystems under weak mixing conditions - a theoretical investigation. *Progr. Oceanogr.* **75**, 771–796 (2007)
8. M. Begon, C.R. Townsend, J.L. Harper, *Ecology: From Individuals to Ecosystems*, 4th edn. (Blackwell Publishing, Oxford, 2005), p. 738
9. D.E. Boakes, E.A. Codling, G.J. Thorn, M. Steinke, Analysis and modelling of swimming behaviour in *Oxyrrhis marina*. *J. Plankton Res.* **33**, 641–649 (2011)

10. S.M. Bollens, B.W. Frost, Predator induced diel vertical migration in a marine planktonic copepod. *J. Plankton Res.* **11**, 1047–1065 (1989)
11. C.M. Boyd, S.M. Smith, T. Cowles, Grazing patterns of copepods in the upwelling system off Peru. *Limnol. Oceanogr.* **25**, 583–596 (1980)
12. S.V. Budaev, ‘Personality’ in the guppy (*Poecilia reticulata*): a correlation study of exploratory behavior and social tendency. *J. Compar. Psychol.* **111**, 399–411 (1997)
13. M.H. Daro, Migratory and grazing behavior of copepods and vertical distributions of phytoplankton. *Bull. Mar. Sci.* **43**, 710–729 (1988)
14. F. Carlotti, J.-C. Poggiale, Towards methodological approaches to implement the zooplankton component in “end to end” food-web models. *Progr. Oceanogr.* **84**, 20–38 (2010)
15. F. Carlotti, K.U. Wolf, A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model. *Fisher. Oceanogr.* **7**, 191–204 (1998)
16. B. Charlesworth, Selection in populations with overlapping generations. III. Conditions for genetic equilibrium. *Theor. Popul. Biol.* **3**, 377–395 (1972)
17. P. Chesson, M.J. Donahue, B.A. Melbourne, A.L. Sears, Scale transition theory for understanding mechanisms in metacommunities, in *Metacommunities: Spatial Dynamics and Ecological Communities*, ed. by M. Holyoak, A. Leibold, R.D. Holt (University of Chicago Press, Chicago, 2005), p. 513
18. M.G. Clerc, D. Escaff, V.M. Kenkre, Analytical studies of fronts, colonies, and patterns: combination of the Allee effect and nonlocal competition interactions. *Phys. Rev. E* **82**, 036210 (2010)
19. K. Coleman, D.S. Wilson, Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* **56**, 927–936 (1998)
20. C. Cosner, D.L. DeAngelis, J.S. Ault, D.B. Olson, Effects of spatial grouping on the functional response of predators. *Theor. Popul. Biol.* **56**, 65–75 (1999)
21. F.R. Cottier, G.A. Tarling, A. Wold, S. Falk-Petersen, Unsynchronised and synchronised vertical migration of zooplankton in a high Arctic fjord. *Limnol. Oceanogr.* **51**, 2586–2599 (2006)
22. T.J. Cowles, R.A. Desiderio, M.E. Carr, Small-scale planktonic structure: persistence and trophic consequences. *Oceanography* **11**, 4–9 (1998)
23. H.C. Crenshaw, L. Edelstein-Keshet, Orientation by helical motion. II. Changing the direction of the axis of motion. *J. Math. Biol.* **55**, 213–230 (1993)
24. J.M. Cushing, *An Introduction to Structured Population Dynamics* (SIAM, Philadelphia, 1998), p. 195
25. M.J. Dagg, K.D. Wyman, Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. *Mar. Ecol. Prog. Ser.* **13**, 37–46 (1983)
26. M.J. Dagg, B.W. Frost, J.A. Newton, Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, US. *Limnol. Oceanogr.* **42**, 974–980 (1997)
27. W.R. DeMott, Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnol. Oceanogr.* **27**, 518–527 (1982)
28. A. Dhooge, W. Govaerts, Y. Kuznetsov, Matcont: a matlab package for numerical bifurcation analysis of ODEs. *ACM TOMS* **29**, 141–164 (2003). <http://sourceforge.net/projects/matcont/>
29. O. Diekmann, M. Gyllenberg, J.A. Metz, S. Nakaoka, A.M. de Roos, *Daphnia* revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example. *J. Math. Biol.* **61**, 277–318 (2010)
30. S.I. Dodson, S. Ryan, R. Tollrian, W. Lampert, Individual swimming behavior of *Daphnia*: effects of food, light and container size in four clones. *J. Plankton Res.* **19**, 1537–1552 (1997)
31. A.M. Edwards, J. Brindley, Zooplankton mortality and the dynamical behavior of plankton population models. *Bull. Math. Biol.* **61**, 202–339 (1999)
32. G. Englund, K. Leonardsson, Scaling up the functional response for spatially heterogeneous systems. *Ecol. Lett.* **11**, 440–449 (2008)
33. G.T. Evans, The encounter speed of moving predator and prey. *J. Plankton Res.* **11**, 415–417 (1989)

34. G.T. Evans, J.S. Parslow, A model of annual plankton cycles. *Biol. Oceanogr.* **3**, 327–347 (1985)
35. A. Ferno, I. Huse, J.-E. Juell, A. Bjordal, Vertical distribution of Atlantic salmon (*Salmo salar* L.) in net pens: trade-off between surface light avoidance and food attraction. *Aquaculture* **132**, 285–296 (1995)
36. C.L. Folt, C.W. Burns, Biological drivers of zooplankton patchiness. *TREE* **14**, 300–305 (1999)
37. M. Fossheim, R. Primicerio, Habitat choice by marine zooplankton in a high-latitude ecosystem. *Mar. Ecol. Prog. Ser.* **364**, 47–56 (2008)
38. B.W. Frost, A threshold feeding behavior in *Calanus pacificus*. *Limnology and Oceanography* **20**, 263–266 (1975)
39. W. Gabriel, B. Thomas, Vertical migration of zooplankton as an evolutionarily stable strategy. *Am. Nat.* **132**, 199–216 (1988)
40. C. Gardiner, *Stochastic Methods*, 4th edn. (Springer, Berlin, 2009)
41. W. Geller, Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): a starvation avoidance mechanism? *Archiv. Hydrobiol.* **74**, 1–60 (1986)
42. W. Gentleman, A. Leising, B. Frost, S. Storm, J. Murray, Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep Sea Res. II* **50**, 2847–2875 (2003)
43. J. Giske, R. Rosland, J. Berntsen, O. Fiksen, Ideal free distribution of copepods under predation risk. *Ecol. Model.* **95**, 45–59 (1997)
44. L. Giuggioli, F.J. Sevilla, V.M. Kenkre, A generalized master equation approach to modelling anomalous transport in animal movement. *J. Phys. A* **42**, 1–16 (2009)
45. T.C. Granata, T.D. Dickey, The fluid mechanics of copepod feeding in a turbulent flow: a theoretical approach. *Progr. Oceanogr.* **26**, 243–261 (1991)
46. V. Grimm, Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* **115**, 129–148 (1999)
47. V. Grimm, S.F. Railsback, Agent-based models in ecology: patterns and alternative theories of adaptive behaviour, in *Agent-Based Computational Modelling: Contributions to Economics*, ed. by F.C. Billari, T. Fent, A. Prskawetz, J. Scheffran (Physica-Verlag, Heidelberg, 2006), pp. 139–152
48. N. Gruber, H. Frenzel, S.C. Doney, P. Marchesiello, J.C. McWilliams, J.R. Moisan, J. Oram, G.-K. Plattner, K.D. Stolzenbach, Eddy resolving simulation of plankton ecosystem dynamics in the California current system. *Deep Sea Res. I* **53**, 1483–1516 (2006)
49. B.P. Han, M. Straskraba, Modeling patterns of zooplankton diel vertical migration. *J. Plankton Res.* **20**, 1463–1487 (1998)
50. B. Hansen, K.S. Tande, U.C. Berggreen, On the trophic fate of *Phaeocystis pouchetii* (Hariot). III. Functional responses in grazing demonstrated on juvenile stages of *Calanus finmarchicus* (Copepoda) fed diatoms and *Phaeocystis*. *J. Plankton Res.* **12**, 1173–1187 (1990)
51. M.P. Hassell, R.M. May, Aggregation in predators and insect parasites and its effect on stability. *J. Anim. Ecol.* **43**, 567–594 (1974)
52. L.R. Haury, J.A. McGowan, P.H. Wiebe, Patterns and processes in the time- space scales of plankton distributions, in *Spatial Pattern in Plankton Communities*, ed. by J.H. Steele (Plenum Press, New York 1978), pp. 277–327
53. A.W. Herman, T. Platt, Numerical modelling of diel carbon production and zooplankton grazing on the scotian shelf based on observational data. *Ecol. Model.* **18**, 55–72 (1983)
54. A.W. Herman, Vertical patterns of copepods, chlorophyll, and production in Northeastern Baffin Bay. *Limnol. Oceanogr.* **28**, 709–719 (1983)
55. A.G. Hirst, A.J. Bunker, Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol. Oceanogr.* **48**, 1988–2010 (2003)
56. C.S. Holling, The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 293–320 (1959)

57. Y. Iwasa, Vertical migration of zooplankton: a game between predator and prey. *Am. Nat.* **120**, 171–180 (1982)
58. J.M. Jeschke, M. Kopp, R. Tollrian, Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biol. Rev.* **79**, 337–349 (2004)
59. P. Kareiva, Population dynamics in spatially complex environments: theory and data. *Phil. Trans. R. Soc. B* **330**, 175–190 (1990)
60. W. Lampert, Zooplankton vertical migrations: implications for phytoplankton-zooplankton interactions. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **35**, 69–78 (1992)
61. W. Lampert, Vertical distribution of zooplankton: density dependence and evidence for an ideal free distribution with costs. *BMC Biol.* **3**, 10 (electronic) (2005)
62. J. Latto, M.P. Hassell, Generalist predators and the importance of spatial density dependence. *Oecologia* **77**, 375–377 (1988)
63. A.W. Leising, Copepod foraging in patchy habitats and thin layers using a 2-D individual based model. *Mar. Ecol. Prog. Ser.* **216**, 167–179 (2001)
64. A.W. Leising, P.J.S. Franks, Copepod vertical distribution within a spatially variable food source: a foraging strategy model. *J. Plankton Res.* **22**, 999–1024 (2000)
65. A.W. Leising, J.J. Pierson, S. Cary, B.W. Frost, Copepod foraging and predation risk within the surface layer during night-time feeding forays. *J. Plankton Res.* **27**, 987–1001 (2005)
66. S.A. Levin, The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* **73**, 1943–1967 (1992)
67. S.H. Liu, S. Sun, B.P. Han, Diel vertical migration of zooplankton following optimal food intake under predation. *J. Plankton Res.* **25**, 1069–1077 (2003)
68. D.L. Mackas, C.M. Boyd, Spectral analysis of zooplankton spatial heterogeneity. *Science* **204**, 62–64 (1979)
69. P.S. Magal, S. Ruan (eds.), in *Structured Population Models in Biology and Epidemiology*. Lecture Notes in Mathematics, vol. 1936, Mathematical Biosciences Subseries (Springer, Berlin, 2008), p. 345
70. E. Malkiel, J. Sheng, J. Katz, J.R. Strickler, The three-dimensional flow field generated by a feeding calanoid copepod measured using digital holography. *J. Exp. Biol.* **206**, 3657–3666 (2003)
71. J.A. Mather, R.C. Anderson, Personalities of octopuses (*Octopus rubescans*). *J. Compar. Psychol.* **107**, 336–340 (1993)
72. J.A. McLaren, Effect of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Board Can.* **20**, 685–727 (1963)
73. J.N. McNair, M.E. Boraas, D.B. Seale, Size-structure dynamics of the rotifer chemostat: a simple physiologically structured model. *Hydrobiologia* **387**, 469–476 (1998)
74. J.A.J. Metz, O. Diekmann, *The Dynamics of Physiologically Structured Populations* (Springer, Berlin, 1986), p. 511
75. J. Michalski, J.-C. Poggiale, R. Arditi, P. Auger, Macroscopic dynamic effects of migrations in patchy predator-prey systems. *J. Theor. Biol.* **185**, 459–474 (1997)
76. A.Y. Morozov, Emergence of Holling type III zooplankton functional response: bringing together field evidence and mathematical modelling. *J. Theor. Biol.* **265**, 45–54 (2010)
77. A.Y. Morozov, A.G. Arashkevich, Towards a correct description of zooplankton feeding in models: Taking into account food-mediated unsynchronized vertical migration. *J. Theor. Biol.* **262**, 346–360 (2010)
78. A.Y. Morozov, E. Arashkevich, Patterns of zooplankton functional response in communities with vertical heterogeneity: a model study. *Math. Mod. Nat. Phen.* **3**, 131–148 (2008)
79. A.Y. Morozov, E. Arashkevich, M. Reigstad, S. Falk-Petersen, Influence of spatial heterogeneity on the type of zooplankton functional response: a study based on field observations. *Deep Sea Res. II* **55**, 2285–2291 (2008)
80. A.Yu. Morozov, E.G. Arashkevich, A. Nikishina, K. Solovyev, Nutrient-rich plankton communities stabilized via predator-prey interactions: revisiting the role of vertical heterogeneity. *Math. Med. Biol.* **28**, 185–215 (2011)

81. J.M. Morales, P.R. Moorcroft, J. Matthiopoulos, J.L. Frair, J.G. Kie, R.A. Powell, E.H. Merrill, D.T. Haydon, Building the bridge between animal movement and population dynamics. *Phil. Trans. R. Soc. B* **365**, 2289–2301 (2010)
82. M.M. Mullin, E.R. Brooks, Some consequences of distributional heterogeneity of phytoplankton and zooplankton. *Limnol. Oceanogr.* **21**, 784–796 (1976)
83. W.W. Murdoch, C.J. Briggs, R.M. Nisbet, W.S.C. Gurney, A. Stewart-Oaten, Aggregation and stability in metapopulation models. *Am. Nat.* **140**, 41–58 (1992)
84. W.W. Murdoch, R.M. Nisbet, E. McCauley, A.M. Roos, W.S.C. De Gurney, Plankton abundance and dynamics across nutrient levels: tests of hypotheses. *Ecology* **79**, 1339–1356 (1998)
85. G. Nachman, A functional response model of a predator population foraging in a patchy habitat. *J. Anim. Ecol.* **75**, 948–958 (2006)
86. R. Nathan, W.M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, P.E. Smouse, A movement ecology paradigm for unifying organismal movement research. *Proc. Nat. Acad. Sci.* **105**, 19052–19059 (2008)
87. A. Oaten, W.W. Murdoch, Functional response and stability in predator-prey systems. *Am. Nat.* **109**, 289–298 (1975)
88. E. Odum, G.W. Barrett, *Fundamentals of Ecology* (Thomson Brooks/Cole, Belmont, 2004), p. 598
89. T. Oguz, H. Ducklow, P. Malanotte-Rizzoli, J. Murray, E. Shushkina, V. Vedernikov, U. Unluata, A physical-biochemical model of plankton productivity and nitrogen cycling in the Black Sea. *Deep Sea Res.* **46**, 597–636 (1999)
90. M.D. Ohman, The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* **60**, 257–281 (1990)
91. K.E. Osgood, D.M. Checkley, Seasonal variations in a deep aggregation of *Calanus pacificus* in the Santa Barbara Basin. *Mar. Ecol. Prog. Ser.* **148**, 59–69 (1997)
92. G.A. Paffenhöfer, Variability due to feeding activity of individual copepods. *J. Plankton Res.* **16**, 617–626 (1994)
93. G.A. Paffenhöfer, J.R. Strickler, K.D. Lewis, S. Richman, Motion behavior of nauplii and early copepodid stages of marine planktonic copepods. *J. Plankton Res.* **18**, 1699–1715 (1996)
94. M. Pascual, Computational ecology: From the complex to the simple and back. *PLoS Comput. Biol.* **1**, 2 (electronic) (2005)
95. S.J. Pearre, Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.* **78**, 1–79 (2003)
96. S.V. Petrovskii, R. Blackshaw, Behaviourally structured populations persist longer under harsh environmental conditions. *Ecol. Lett.* **6**, 455–462 (2003)
97. S.V. Petrovskii, A.Y. Morozov, Dispersal in a statistically structured population: Fat tails revisited. *Am. Nat.* **173**, 278–289 (2010)
98. S.V. Petrovskii, R.P. Blackshaw, B.-L. Li, Persistence of structured populations with and without the Allee effect under adverse environmental conditions. *Bull. Math. Biol.* **70**, 412–437 (2008)
99. J.C. Poggiale, Predator-prey models in heterogeneous environment: emergence of functional response. *Math. Comput. Model.* **27**, 63–71 (1998)
100. D. Reale, B.Y. Gallant, M. Leblanc, M. Festa-Bianchet, Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* **60**, 589–597 (2000)
101. E. Saiz, A. Calbet, Scaling of feeding in marine calanoid copepods. *Limnol. Oceanogr.* **52**, 668–675 (2007)
102. O. Sarnelle, A.E. Wilson, Type III functional response in *Daphnia*. *Ecology* **89**, 1723–1732 (2008)
103. M. Scheffer, R.J. De Boer, Implications of spatial heterogeneity for the paradox of enrichment. *Ecology* **76**, 2270–2277 (1995)
104. M. Scheffer, J.M. Baveco, D.L. DeAngelis, K.A. Rose, E.H. Van Nes, Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol. Model.* **80**, 161–170 (1995)

105. F. Schmitt, L. Seuront, J.-S. Hwang, S. Souissi, L.C. Tseng, Scaling of swimming sequences in copepod behavior: data analysis and simulation. *Physica A* **364**, 287–296 (2006)
106. F.G. Schmitt, L. Seuront, Multifractal random walk in copepod behavior. *Physica A* **301**, 375–396 (2001)
107. T. Sekino, N. Yamamura, Diel vertical migration of zooplankton: optimum migrating schedule based on energy accumulation. *Evol. Ecol.* **13**, 267–282 (1999)
108. L. Seuront, J.-S. Hwang, L.-C. Tseng, F. Schmitt, S. Souissi, C.-K. Wong, Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta* (Copepoda: Poecilostomatoida). *Mar. Ecol. Prog. Ser.* **283**, 199–217 (2004)
109. P.E. Smouse, S. Focardi, P.R. Moorcroft, J.G. Kie, J.D. Forester, J.M. Morales, Stochastic modelling of animal movement. *Phil. Trans. R. Soc. B* **365**, 2201–2211 (2010)
110. M.E. Solomon, The natural control of animal populations. *J. Anim. Ecol.* **18**, 1–35 (1949)
111. W.J. Sutherland, Aggregation and the “ideal free” distribution. *J. Anim. Ecol.* **52**, 821–828 (1983)
112. K.S. Tande, U. Bamstedt, Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea. *Mar. Biol.* **87**, 251–258 (1985)
113. P. Tiselius, P.R. Jonsson, Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis. *Mar. Ecol. Prog. Ser.* **66**, 23–33 (1990)
114. P. Tiselius, P.R. Jonsson, P.G. Verity, A model evaluation of the impact of food patchiness on foraging strategy and predation risk in zooplankton. *Bull. Mar. Sci.* **53**, 247–264 (1993)
115. J.E. Truscott, J. Brindley, Ocean plankton populations as excitable media. *Bull. Math. Biol.* **56**, 981–998 (1994)
116. L.-C. Tseng, R. Kumar, H.-U. Dahms, Q.-C. Chen, J.-S. Hwang, Copepod gut contents, ingestion rates, and feeding impacts in relation to their size structure in the southeastern Taiwan Strait. *Zool. Stud.* **47**, 402–416 (2008)
117. A. Tsuda, H. Saito, H. Kasai, Annual variation of occurrence and growth in relation with life cycles of *Neocalanus flemingeri* and *N. plumchrus* (Calanoida, Copepoda) in the western subarctic Pacific. *Mar. Biol.* **135**, 533–544 (1999)
118. S. Tuljapurkar, H. Caswell, *Structured Population Models in Marine, Terrestrial, and Freshwater Systems* (Chapman and Hall, London, 1997), p. 656
119. A. Visser, Lagrangian modelling of plankton motion: from deceptively simple random walks to Fokker–Planck and back again. *J. Mar. Syst.* **70**, 287–299 (2008)
120. G.M. Viswanathan, V. Afanasyev, S.V. Buldyrev, S. Havlin, M.G.E. da Luz, E.P. Raposo, H.E. Stanley, Lévy flights search patterns of biological organisms. *Physica A* **295**, 85–88 (2001)
121. J. Woods, A. Perilli, W. Barkmann, Stability and predictability of a virtual plankton ecosystem created with an individual-based model. *Progr. Oceanogr.* **67**, 43–83 (2005)