Abstract

Two basic features of assemblages of unicellular plankton: (1) their high biodiversity and (2) the power-law structure of their abundance, can be explained by an allometric scaling of cell growth and mortality with respect to cell size. To show this, we describe a numerical study of a size-structured, multispecies, population-dynamic model; the model has a single resource, supporting an arbitrary number of phytoplankton and zooplankton species. If the number of plankton species is large enough, the death rate of prey and cell growth rate of predators have approximate allometric scalings with cell size. Together, these scalings give rise to an equilibrium distribution of abundance near the power law, on which many species can coexist. Scalings of this kind cannot be achieved if the number of species is small. This suggests that the conjunction of species-richness and power-law structures in plankton communities is more than a coincidence. Although the exact allometric scalings used here should not be expected in practice, exclusion of species should be relatively slow if they lie close to the power law. Thus the forces needed to achieve coexistence could be effective, even if they are relatively weak.

1 Introduction

This paper is motivated by two widely observed features of aquatic ecosystems. The first is a great diversity of plankton taxa, in the case of phytoplankton seemingly unconstrained by the small number of resources for which they compete (the paradox of the plankton: [Hutchinson]}
Figure 1: Three basic observed properties of assemblages of unicellular plankton; these motivate the multispecies, population-dynamic model in this paper.

The second feature is a tendency for abundance of aquatic organisms to lie near a special power-law function of body mass. This function corresponds to a biomass density of aquatic assemblages that changes rather little, as body mass (logarithmically scaled) is increased; it is found in the size range of the plankton (Gaedke 1992, Quinones et al. 2003, San Martin et al. 2006), and is thought to apply much more broadly from bacteria to whales (Sheldon et al. 1972). It appears difficult to account for both these features simultaneously: they call both for a mechanism for species coexistence, and also for an emergent assemblage close to the power-law. Although both observations have separately been the subject of much research, and the need to link them is well recognized (Armstrong 1999), a unified dynamical system that generates both features has not been described.

In a phenomenological sense, coexistence of species is a prerequisite for the power law in assemblages of unicellular eukaryotic plankton. These organisms only double in size before cell division, and consequently a power law spanning the size range of unicellular plankton depends on the coexistence of multiple species. The purpose of the work here, and a mathematical paper that underpins it (Cuesta et al. 2017), is to examine the mechanistic link between them. For this we introduce a third ingredient: allometric scalings between ecological rates and cell size. These scalings are important because without them a power-law solution would not be possible. Some of the scalings, such those of metabolism and cell doubling time, are themselves well established empirically in unicellular plankton (Marañón et al. 2013, López-Sandoval et al. 2014). Other scalings are not, namely those of cell growth and death rates that stem from predation: these have to emerge directly from the predator-prey interactions. The core of this paper is to show that predation can generate the allometric scalings needed, leading to results consistent with a triangle of linked observations shown in Fig. 1.

Ecologists do not have a generally accepted mechanism for coexistence of a large number of plankton species (Roy and Chattopadhyay 2007). Hutchinson’s own preferred solution of environmental fluctuations favouring different species (the intermediate disturbance hypothesis) is insufficient in general (Fox 2013). It slows down the rate of loss of species, but this is not equivalent to placing bounds on abundance of species favouring them when they are rare and restricting them when common (Chesson 2000, Fox 2013). One promising idea for bounding population increase in microbial ecology is “killing the winner”, in which
top-down control is strongest on the fastest-increasing prey (Thingstad and Lignell 1997; Winter et al. 2010). This was developed with phage and bacteria in mind, and parallels the idea of predator-mediated coexistence used elsewhere in ecology (Leibold 1996; Vage et al. 2014). Here we extend the idea to predation in plankton assemblages.

Neither do ecologists have a clear-cut model mechanism to generate the observed power-law equilibrium in assemblages of unicellular plankton. Ideas are better-developed in multicellular organisms from the study of so-called size-spectrum models (Silvert and Platt 1978, 1980; Benoit and Rochet 2004; Andersen and Beyer 2006; Capitán and Delius 2010; Datta et al. 2010, 2011; Hartvig et al. 2011; Guiet et al. 2016), where organisms grow, often over orders of magnitude, by feeding on and killing smaller organisms (Datta et al. 2010; Plank and Law 2011). But the power-law structure extends down to unicellular plankton (Gaedke 1992; Quinones et al. 2003; San Martin et al. 2006) where feedbacks are different because organisms do no more than double in body mass. One suggestion is that, although plankton species may individually fluctuate in complicated ways, patterns become more regular after aggregation to the assemblage as a whole (Huisman and Weissing 1999; Scheffer et al. 2003); it remains to be seen whether a power-law pattern after aggregation is likely to emerge from this.

The work here builds on a mathematical theory proposed by Cuesta et al. (2017) for scale-invariant dynamics of a continuum of species with a continuous trait (a characteristic body size) that spans an unlimited range from zero upwards, in addition to a continuous body size within species conventionally used in size-spectrum models. These so-called trait-based models are tractable enough to allow some formal mathematical analysis of multispecies assemblages (Andersen and Beyer 2006; Hartvig et al. 2011). However, they depend on assumptions: (1) that the trait is continuous (the number of species is infinite), and (2) that the trait is unbounded (i.e. the lower bound is zero, and the upper bound tends to infinity). Clearly, real-world assemblages only support a finite number of species, and must have lower and upper bounds to cell size. This calls for a numerical analysis as given in this paper.

To keep a close link to the mathematical theory (Cuesta et al. 2017), we retain its assumptions about allometric scalings of ecological rates with cell mass; only the scalings of cell death and growth are allowed to emerge from the predator-prey interaction. However, it is not our intention to suggest that natural aquatic ecosystems satisfy the scalings exactly—there are many sources of variation that stand in the way of this. Our argument is that approximate scalings of processes with body mass in unicellular organisms bring them closer to ecological balance than has previously been thought. This slows down the rate of exclusion of species, with the consequence that other mechanisms for coexistence (Roy and Chattopadhyay 2007) can be more effective, even if their effects are not big. Note also that the plankton communities here are built on a single limiting resource to show that coexistence near the power law is possible even under the simplest and most exacting conditions; we are not, however, suggesting that there is only one limiting resource in natural plankton assemblages.
2 Theory

We envisage an assemblage of unicellular plankton species, each species having a fixed characteristic cell size, defined as 1/2 of its maximum cell mass. For simplicity, mass is measured relative to that of a notional cell with equivalent spherical diameter (ESD) of 2 \( \mu \text{m} \) and mass \( w_0 \). Throughout, we write \( w \) as the mass expressed on this relative scale, and denote the characteristic cell mass of species \( i \) as \( w_i \) on this relative scale. Lower and upper bounds on cell size are set to span much of the range of unicellular eukaryotic plankton, with ESDs from approximately 2 to 200 \( \mu \text{m} \).

The variables used are as follows. \( N \) is the concentration of nutrients (mass volume\(^{-1}\)), and \( P_i, Z_i \) are the total densities of a species of phytoplankton or zooplankton respectively, with species denoted by index \( i \) (dimensions: volume\(^{-1}\)). However, to allow for allometric scalings in growth of cells, we disaggregate density down to cell mass within species. The state variables are therefore \( p_i(w), z_i(w) \) for the density of phytoplankton and zooplankton respectively at cell mass \( w \) (dimensions also volume\(^{-1}\), because of the relative mass scale chosen above). All these variables are time dependent, but for brevity the time argument is omitted.

The model depends on allometric scalings of cell growth and death with cell mass. We therefore start with these details of cell life histories, and use this as the input into the population dynamics of interacting species. In the population dynamics, phytoplankton species are coupled by competition for a single limiting resource acting on the growth of cells. Zooplankton and phytoplankton species are coupled by predation leading to death of phytoplankton cells and growth of zooplankton cells. Zooplankton species are coupled through predation by larger species on smaller ones.

2.1 A scaling for growth of phytoplankton cells

The von Bertalanffy growth model is a good place to begin, as it is based on allometric scalings with body mass (von Bertalanffy, 1957). It is more often thought of in the context of multicellular organisms, and is used here on the basis that, in unicellular organisms, growth still stems from the balance between (a) resource uptake, and (b) loss through metabolism (Kempes et al., 2012). For cell growth of a phytoplankton species \( i \), we write \( G_i^{(p)}(w) \):

\[
\frac{dw}{dt} = G_i^{(p)}(w) = A_i w^\alpha - B_i w^\beta. \tag{2.1}
\]

Here \( t \) is time, \( \alpha \) and \( \beta \) (\( \alpha < \beta \)) are parameters that scale respectively the gain of mass through resource uptake and the loss of mass through metabolism with body mass \( w \), and \( A_i \) and \( B_i \) are further species-dependent parameters for gain and loss respectively.

It might seem from eq. (2.1) that there are two separate allometric scalings with cell mass. However, it is known that over most of the size range of eukaryotic phytoplankton species there is an approximate scaling of the intrinsic rate of increase (Marañón et al., 2013). This
implies a single scaling of doubling time $T$ with respect to characteristic cell mass that has an exponent say $\xi$, i.e. $T \propto (w_i)^\xi$ (see definition of $w_i$ at start of this section). The scaling of doubling time also implies a scaling on how fast cells from species with different $w_i$s grow: cells that take longer to double, must also have a lower mass-specific growth rate. Terms $A_i$ and $B_i$ in eq. (2.1) carry this dependence on $w_i$ and, with some algebra (Cuesta et al., 2017), eq. (2.1) can be rewritten as:

$$G^{(p)}(w,N) = w^{1-\xi} \left[ \tilde{a}(N) \left( \frac{w}{w_i} \right)^{\alpha+\xi-1} - \tilde{b} \left( \frac{w}{w_i} \right)^{\beta+\xi-1} \right].$$

(2.2)

where $A_i(N) = \tilde{a}(N) \cdot (w_i)^{-(\alpha+\xi-1)}$, $B_i = \tilde{b} \cdot (w_i)^{-(\beta+\xi-1)}$, $\tilde{a}(N)$ and $\tilde{b}$ are independent of $w_i$, and parameters $\alpha$ and $\beta$ are such that $2w_i$ is always less than the asymptotic value of cell size achievable from eq. (2.2). The reason for writing the growth rate in this form is simply to make it clear that all phytoplankton species have the same basic growth function. This takes the form of a power function $w^{1-\xi}$ of cell mass, multiplied by a function of the ratio $w/w_i$. In other words, the growth function scales with cell mass. We have made use of a technical point that allometric scaling can be done with respect to $w$ or $w_i$; see Appendix A.

Note that, in eq. (2.2), we have introduced a dependence of $\tilde{a}$ on the resource concentration $N$; $\tilde{a}$ is a strictly increasing function of $N$, since more resource leads to more gain in mass. This function is important because it has the effect of coupling the dynamics of all phytoplankton species through depletion of the resource.

### 2.2 A scaling for growth of zooplankton cells

We assume that zooplankton cells, like phytoplankton, grow through a balance between resource uptake and metabolism, as in eq. (2.1). However, scaling of resource-uptake needs more attention because these cells grow by consuming other cells, and therefore depend on the abundance of these prey. Thus, if this growth is to have an allometric scaling with cell size, it has to emerge from the predator-prey interactions. Here we introduce three assumptions, justifiable on empirical grounds, that make an allometric scaling possible, although by no means inevitable.

The assumptions are as follows. (a) Zooplankton feeding depends on a volume sensed per unit time that scales with cell mass. This is based on observations of encounters of protists with phytoplankton (DeLong and Vasseur, 2012). (b) Feeding occurs on cells around a fixed ratio of the mass of the consumer. Size-based feeding is well documented in plankton, although the predator-prey size ratios are smaller in larger multicellular consumers (Wirtz, 2012). Within the size range of unicellular organisms, the change in ratio is relatively small, and a fixed ratio is a reasonable approximation (Wirtz, 2012). (c) Predation increases as prey species become abundant more than a simple law of mass action would allow; this acts as a stabilizing force on the population dynamics (Chesson, 2000), and is closely related to the notion of killing-the-winner (Thingstad and Lignell, 1997; Winter et al., 2010). These assumptions retain some elements of the complex food web that operates within plankton.
assemblages, avoiding the reduction to a simple bulk phytoplankton–zooplankton trophic connection (Boyce et al., 2015).

With these assumptions, the rate \( S_{ij}^{(p)}(w, w') \) (respectively \( S_{ij}^{(z)}(w, w') \)) at which a zooplankton cell of species \( i \) and size \( w \) consumes a cell of species \( j \) phytoplankton (respectively zooplankton) of size \( w' \) (\( w > w' \)) is given by

\[
S_{ij}^{(p)}(w, w') = Aw^{\nu} \times s(w/w') \times P_j^\chi, \tag{2.3}
\]

\[
S_{ij}^{(z)}(w, w') = Aw^{\nu} \times (a) \times s(w/w') \times (b) \times Z_j^\chi, \tag{2.4}
\]

where (a), (b) and (c) formalize the three assumptions above. In part (a), \( A \) sets the overall level of encounters, and \( \nu \) is the scaling exponent. The function (b) is a feeding kernel that distributes predation around a fixed ratio of the predator cell mass, assumed for simplicity to be independent of predator species \( i \) and prey species \( j \). A positive value of \( \chi \) in part (c) takes the mortality of prey species \( j \) above the level of the law of mass action and would be expected to help stabilize the assemblage. We used the total density of prey \( j \) (\( P_j, Z_j \)) on the grounds that fine sorting of predation at the level of the size-disaggregated distribution would be unrealistic in organisms that only double in size. This assumption could be changed with little effect on the results.

The growth rate \( G_i^{(z)}(w) \) of a single zooplankton cell of species \( i \) at mass \( w \) now replaces the simple input term (a) in eq. \( (2.1) \) with the information on predation in eqs. \( (2.3), (2.4) \); the metabolic loss is unchanged. This gives

\[
G_i^{(z)}(w) = \epsilon \int \sum_j w' S_{ij}^{(p)}(w, w')p_j(w')dw' \quad \text{(gain from eating phytoplankton)}
\]

\[
+ \quad \epsilon \int \sum_j w' S_{ij}^{(z)}(w, w')z_j(w')dw' \quad \text{(gain from eating zooplankton)}
\]

\[
- \quad w^{1-\xi} \bar{b} \left( \frac{w}{w_i} \right)^{\beta+\xi-1} \quad \text{(loss from metabolism)}, \tag{2.5}
\]

where \( \epsilon \) is the efficiency with which prey mass is turned into predator mass. The gain terms have the form of a feeding rate at size \( w \) on species \( j \) at size \( w' \), multiplied by the density of these prey and their cell mass \( w' \), summed over prey species and integrated over prey cell masses, to get the total rate at which mass is consumed.

A consistent allometric scaling of zooplankton growth requires that it should match the scaling of metabolism, \( w^{1-\xi} \), and hence the scaling of growth in phytoplankton. There is nothing in eq. \( (2.5) \) to ensure this happens. However, the scaling needed does emerge if the population densities lie on a power law, and we will show in Section 3 below that the predator-prey dynamics can generate this structure. Such a power-law solution takes the form

\[
p_j(w) = w_j^{-\gamma}h(w/w_j), \tag{2.6}
\]
where $\gamma$ is the power-law exponent. Showing the statement is true is a matter of algebra, and we provide a proof in Appendix B; see also Cuesta et al. (2017). The emergent scaling is important: it means that there is a set of densities on a power-law of the form given in eq. (2.6) on which the growth rates of zooplankton species in eq. (2.5) have the same allometric scaling of cell mass, $w^{1-\xi}$, as phytoplankton species. This is necessary for the triangle of observations in Fig. 1 to emerge, although this does not preclude other outcomes that lack both the allometric scalings and also the power law (we will show an example in Fig. 3). Note that the power-law exponent $\gamma$, expressed in terms of the other exponents $\nu$, $\xi$, $\chi$, is

$$\gamma = 1 + \frac{\nu + \xi}{1 + \chi}. \quad (2.7)$$

That is all we know so far as growth is concerned; it is quite conceivable for a plankton assemblage neither to be on the power law, nor to relax onto it.

### 2.3 A scaling for death rate

We assume that most cell death comes from predation. With one caveat, this applies as much to zooplankton as to phytoplankton, because predators feed by cell size rather than by cell type. Cell death of prey is tied precisely to cell growth of predators because each consumption event in eqs. (2.3), (2.4) is matched by a corresponding prey death. Reversing the indices so that $i$ is now a prey species of cell mass $w$, we write the rate $S^{(p)}_{ji}(w', w)$ (respectively $S^{(z)}_{ji}(w', w)$) as the rate at which a zooplankton cell of species $j$ and size $w'$ consumes a cell of species $i$ phytoplankton (respectively zooplankton) of size $w$ ($w' > w$). Then the per-capita death rate from predation is part (a) of the following equations:

$$D^{(p)}_i(w) = \int \sum_j S^{(p)}_{ji}(w', w)z_j(w')dw' + d_0w^{-\xi} \quad (2.8)$$

$$D^{(z)}_i(w) = \int \sum_j S^{(z)}_{ji}(w', w)z_j(w')dw' + d_0w^{-\xi}. \quad (2.9)$$

In (a), the terms $S_{ji}^{(z)}$ for consumption by $j$ are multiplied by the density of these predators. The product is then summed over predator species, and integrated over predator cell masses, to get the total per-capita death rate from predation.

The caveat about predation is that, if this was the only cause of death, the largest zooplankton would be free of all mortality; this is because we confine the study to unicellular organisms. Mortality-free dynamics would be unrealistic, and we therefore introduce some background intrinsic mortality with the same scaling in all species, given as part (b) of eqs. (2.8), (2.9). Predation by multicellular organisms would remove the need for this, although some background mortality is to be expected in any event. Thus the total per-capita death rate $D^{(p)}_i(w)$ of a phytoplankton cell (respectively $D^{(z)}_i(w)$ of a zooplankton cell) is given as the sum of (a) and (b) in eqs. (2.8), (2.9).
As in cell growth, there is an allometric scaling of predation with respect to $w$ when the population densities lie on the power law eq. (2.6). This can be shown by the method used for cell growth (Appendix B), and in this case the scaling is $w^{-\xi}$. As noted for growth, the triangle of observations in Fig. II would not be possible without the scaling, although outcomes without this and without the power law would be entirely feasible.

### 2.4 Cell division rate

In addition to cell growth and death, a cell-division process is needed for the dynamics that follow. This is essentially a matter of larger cells splitting into two, but for realism, some variation in the size of daughter cells should be present immediately after cell division. In general, there are two ways of generating this. First, the rate of cell division in species $i$ can be a function $K_i(w)$ that becomes large as cell mass $w$ approaches $2w_i$. Secondly, there can be variation in size of the two daughter cells themselves. For a cell that divides at size $w'$, we define a function $Q(w|w')$ that describes the probability density that the daughters are of size $w$ and $w' - w$, concentrated around $w = w'/2$. The two functions $K_i(w)$ and $Q(w|w')$ ensure that arbitrary features of initial size distributions decay over time in the population dynamics.

### 2.5 A dynamical system for the NPZ assemblage

So far, we have shown that an allometric scaling of cell growth and death with $w$ is present, if population densities lie on a power law of the form in eq. (2.6). However, whether this special set of population densities could actually emerge from the predator-prey interactions is a separate matter, as yet unanswered. This requires a model of multispecies population dynamics that can track the densities of cells over time. The model is built on the cell growth, death and division rates defined above, so that species are coupled through their predator-prey interactions and through their feeding on a common resource. Fig. II sketches the links involved.

The state variables for the model are the resource concentration $N$, the size distributions of an arbitrary number ($m$) of phytoplankton species $p_1(w), \ldots, p_m(w)$, and the size distributions of an arbitrary number ($n$) of zooplankton species $z_1(w), \ldots, z_n(w)$.

The exact form of the resource dynamics is not important, and we use a chemostat function

$$
\frac{dN}{dt} = c \left( 1 - \frac{N}{\hat{N}} \right) - d \sum_{i=1}^{m} \left[ \int_{0}^{\infty} A_i(N,w^\alpha) p_i(w) \, dw \right].
$$

In the absence of phytoplankton, the resource settles to an equilibrium concentration $\hat{N}$. The term for loss of resource to phytoplankton starts with the rate of resource uptake by cells of mass $w$ in species $i$ in eq. (2.1), integrates over all cell masses of species $i$ allowing for their densities, and then sums over phytoplankton species $1, \ldots, m$. The dimensionless parameter
Figure 2: Mass flows in an assemblage of unicellular plankton living on a single resource. Heavy lines are log-scaled size distributions of cells within species $\log p_i(\log w)$, $\log z_i(\log w)$ for phytoplankton and zooplankton species respectively. Continuous arrows denote growth of cells. Dotted arrows show the source of food for cell growth; where growth comes from consuming smaller cells, this is accompanied by death of these cells. Dash-dot arrows denote cell division.
\(d\) takes into account that growth is proportional to resource uptake, but not necessarily equal to it. In this way, loss rate from the nutrient pool in eq. (2.10) matches the total uptake rate of resource, and couples together the dynamics of all phytoplankton species.

For the phytoplankton dynamics we use a form of the size-based McKendrick–von Foerster equation, which is essentially a cell growth-division equation. This has a long history in cell biology (Fredrickson et al., 1967; Bell and Anderson, 1967; Sinko and Streifer, 1971; Diekmann et al., 1983; Heijmans, 1984; Henson, 2003; Giometto et al., 2013), and is an appropriate model for the dynamics of unicellular phytoplankton size distributions, shown here for species \(i\):

\[
\frac{\partial}{\partial t} p_i(w) = - \frac{\partial}{\partial w} \left[ G_i^{(p)}(w, N)p_i(w) \right] + 2 \int_0^\infty Q(w|w')K_i^{(p)}(w')p_i(w')dw' - K_i^{(p)}(w)p_i(w) - D_i^{(p)}(w)p_i(w),
\]

(2.11)

with \(G_i^{(p)}\) from eq. (2.2), and \(D_i^{(p)}\) from eq. (2.8). The first term on the right-hand side is the rate at which cell growth leads to change in density at size \(w\). The second term is the rate at which new cells are generated at size \(w\) from cell division; the probability density \(Q\) concentrates the new cells around \(w'/2\). The third term is the rate at which cells disappear at size \(w\) through cell division, \(K_i^{(p)}\) making this term large near \(2w_i\). The fourth term is the rate of cell loss from mortality. Similarly the zooplankton dynamics for species \(i\) are given by

\[
\frac{\partial}{\partial t} z_i(w) = - \frac{\partial}{\partial w} \left[ G_i^{(z)}(w, N)z_i(w) \right] + 2 \int_0^\infty Q(w|w')K_i^{(z)}(w')z_i(w')dw' - K_i^{(z)}(w)z_i(w) - D_i^{(z)}(w)z_i(w).
\]

(2.12)

with \(G_i^{(z)}\) as in eq. (2.5), and \(D_i^{(z)}\) as in eq. (2.9).

3 Results on the NPZ equilibrium

3.1 Continuum model

The continuum model allows some formal mathematical results to be given about the steady-state behaviour (Cuesta et al., 2017). This model replaces the finite number of species in
a bounded range of body size in eqs. (2.11), (2.12), with a continuum of species that have characteristic cell masses \( w_* \) spanning the range from zero to infinity. Remarkably, it can be proved that this model has a power-law equilibrium. This is an equilibrium on which an infinite number of species coexist, notwithstanding the competition for resource among the phytoplankton and the predator-prey interactions between zooplankton and phytoplankton. The equilibrium has the form given in eq. (2.6), and the abundance of the characteristic masses \( w_* \) scales with \( w_* \) with the exponent given in eq. (2.7). In this case, the equations and the steady-state solution are scale invariant.

The unique power-law equilibrium emerges from the dynamics as a direct consequence of the predator-prey interactions. The power-law structure of the zooplankton holds death rates from predation with a scaling exponent \(-\xi\), consistent with the power law of prey abundance. At the same time, the power-law structure of the prey holds the growth rates of the zooplankton with a scaling exponent \(1 - \xi\), consistent with the power law of predator abundance. Whether this equilibrium could be stable without additional stabilising mechanisms is not known.

### 3.2 Discretized model

For two reasons, it helps to go from the continuum model to a numerical analysis of the discretized, bounded system. First, the number of species is always finite in reality, and secondly there must always be lower and upper bounds on cell size in the plankton. In these circumstances, the perfect power-law equilibrium in the idealised continuum model (Cuesta et al., 2017) can never be achieved exactly, and a numerical analysis can show whether it is a useful guide to more realistic systems. In addition, a numerical stability analysis can show whether the near-power-law equilibrium is an attractor, in other words, whether plankton assemblages should actually be expected to move towards it; this has not been possible in the continuum model. The numerical analysis requires some functions and parameter values to be specified; these are given in Table 1 and Table 2 in Appendix C.

Note first that the NPZ dynamical system eqs. (2.10), (2.11), (2.12) can reach an equilibrium far away from any power law (Fig. 3). This is clear if, for instance, there is a just a single zooplankton species, restricting the size range over which predation takes place; Fig. 3a shows the feeding kernel at the characteristic cell mass of this species. The densities of vulnerable phytoplankton species are driven down to low densities by this localised feeding of the predator, creating a corresponding ‘hole’ in the phytoplankton assemblage (Fig. 3b). This leaves the zooplankton species without enough food, and it tends to zero density (Fig. 3c). As the predator goes to extinction, the phytoplankton assemblage comes to rest at a point where the most vulnerable species have densities close to zero. Put another way, with only one zooplankton species, the predator-prey interaction does not allow the predation-death to settle near an allometric scaling near \(-\xi\). More specialised feeding exacerbates the problem, as can be seen in Fig. 3d,e,f, where there were initially three zooplankton species with narrow feeding kernels. Because the abundances are nowhere near a power law, this behaviour is not consistent with the full triangle of observations in Fig. 1. This is despite the fact that the phytoplankton species do coexist without the predator, and do have an
Figure 3: Absence of a power-law relationship between abundance and cell mass in an assemblage of 20 phytoplankton and a small number of zooplankton species. (a), (b), (c) One zooplankton species with diet breadth $\sigma = 1.0$. (d), (e), (f), Three zooplankton species with diet breadths $\sigma = 0.25$. (a), (d) Feeding kernels for zooplankton cells at characteristic cell sizes $w_i$ of each species. (b), (e) Size spectra for $w_i$ at time 600 of phytoplankton (filled circles), and zooplankton (open circles) species; the initial densities are shown as dots. (c), (f) Time series of the total densities of phytoplankton (continuous) and zooplankton (dashed) species. The time series were obtained from numerical integration of eqs. (2.10), (2.11), (2.12), with $a(N)$, $Q(w|w')$, $K_i^{(1)}(w)$ and $s(w/w')$ as in Table 1 and parameter values as in Table 2 in Appendix C.
allometric scaling of growth and death rates with respect to cell mass. The allometric scaling of death comes from the background mortality that remains in eq. (2.8) in the absence of predation.

The key numerical result of this paper is that a larger number of zooplankton species brings death (and cell growth) from predation approximately to the allometric scaling with cell mass needed for the power law. In effect, more zooplankton species distribute predation mortality better across the range of cell sizes. The outcome is then consistent with the full triangle of observations (Fig. 1), namely: coexistence of species, allometric scalings of ecological rates, and the power-law structure of the assemblage. Moreover, the numerical results show that the equilibrium can be locally asymptotically stable, given a sufficiently positive value of $\chi$. In other words, there is a neighbourhood of the near-power-law equilibrium within which all other initial size distributions return to the equilibrium. The equilibrium is at least a local attractor.

We illustrate this result in Fig. 4, in which we took an assemblage of 20 phytoplankton and 10 zooplankton species with random characteristic cell masses. The second largest zooplankton species tended to zero density, and the 29-species equilibrium (with the second-largest species at zero density) was locally asymptotically stable. Importantly, the equilibrium was quite close to a power law (i.e. close to linear in the double logarithmic plot); this is shown at the characteristic cell masses (Fig. 4a,b), and for the full size distributions of the species (Fig. 4c). It is notable that the two illustrative initial conditions in Fig. 4a,b are far from the equilibrium point, suggesting that the equilibrium has a basin of attraction substantially greater than the range of initial conditions corresponding to a local stability analysis. This ordered structure is generated by the predator-prey interaction. A slope of $2/7$ for the biomass spectrum is predicted from eq. (2.7), and the spectrum that emerged from the numerics is close to this, especially when away from the lower and upper boundaries of cell size (Fig. 4d). The lack of predation on species near the upper boundary would be expected to leave a relatively large footprint near the right-hand boundary, and this is indeed evident in the size distributions and overall densities of these species (Fig. 4c).

4 Discussion

This study shows, for the first time, how predator-prey dynamics can drive unicellular plankton assemblages towards a power-law relationship between cell mass and abundance. With enough species, the near-power-law equilibrium can be an attractor, and the predator-prey interaction can bring the whole assemblage to this state. In this way we obtain a mechanism for coexistence of multiple plankton species near a power-law equilibrium, consistent with the triangle of observations in Fig. 1. The study gives some support to the conclusions of a mathematical analysis of the continuum model, in which an unlimited number of unicellular plankton species can coexist at a power-law equilibrium if cell growth predation and death all scale appropriately with cell mass (Cuesta et al., 2017).

The size-based modelling of predation adopted here improves the resolution of trophic structure in plankton assemblages, as called for by Boyce et al. (2015). It would readily
Figure 4: Convergence to a near-power-law equilibrium of a plankton community of 20 phytoplankton species in presence of predation by 9 zooplankton species. (a), (b) Two contrasting initial conditions lead to the same equilibrium densities of $w_i$ (characteristic cell masses) of phytoplankton (filled circles), and zooplankton (open circles) species; the initial densities are shown as dots. (c) Complete size distributions within phytoplankton (continuous) and zooplankton (dashed) species at equilibrium. (d) Community spectra aggregated over species at equilibrium: size spectrum $p(\log w) = \sum_i p_i(\log w)$ (continuous line), biomass spectrum $b(\log w) = \sum_i w p_i(\log w)$ (dotted line). The dashed reference lines have a slope -1, and the dotted lines have slopes $2/7$ and $-5/7$, corresponding to eq. (2.7) after transforming from $w$ to $\log w$. The set of phytoplankton species and the first three zooplankton species from Fig. 3 were used, together with seven further zooplankton species. Numerical integrations were carried out as in Fig. 3 with parameter values as in Table 2. Integration brought the densities close to equilibrium, after which the equilibrium was obtained by Newton’s method. The Jacobian at equilibrium had a leading eigenvalue with a real part $= -0.0018$, implying local asymptotic stability of the equilibrium.
extend to cover mixotrophic feeding \cite{Flynn2013}. Also, a straightforward extension would be to move the upper bound on body mass to encompass metazoan plankton and fish, and we would expect this to remove some of the roughness at the right-hand side of the plankton spectrum in our computations. Taking this size-based approach through to larger organisms would help to provide a common formal framework for the flow of biomass more broadly through aquatic ecosystems, so-called end-to-end models \cite{Fulton2010}, eliminating the need for closure assumptions at the upper end of the plankton \cite{Edwards2001} and at the lower end of fish assemblages \cite{Datta2010,Hartvig2011}. The extension to more than one limiting resource would not change the qualitative picture we are presenting here.

The caveat about the continuum (mathematical) model \cite{Cuesta2017} is that, although it shows the power-law equilibrium exists, as it stands this equilibrium is not known to be an attractor. However, one further assumption can make the equilibrium stable to small displacements; this is that the dependence of predation on the density of prey is stronger than that given by the standard rule of mass-action. The effect is to make over-abundant species experience disproportionately large mortality. This is closely related to the idea of killing-the-winner in which prey (hosts) are controlled according to how fast they are increasing \cite{Thingstad1997,Winter2010}. With this assumption in place, the exponents in the model are related by

$$\gamma = 1 + (\nu + \xi)/(1 + \chi),$$

and $-\gamma$ emerges as the exponent of the power-law relationship between abundance and characteristic cell mass.

Such predation mortality could come about in various ways, for instance through the ideal-free distribution \cite{Kacelnik1992}, redistribution of predation according to prey species abundance \cite{Armstrong1999}, patchy spatial distributions of prey coupled to predator aggregation \cite{Nachman2006}, and vertical profiles of phytoplankton and zooplankton in the water column \cite{Morozov2010}. A Holling type III functional response \cite{Holling1959} has been suggested as a surrogate for such spatial effects \cite{Nachman2006,Morozov2010}, and was needed to generate plankton blooms in excitable-media models \cite{Truscott1994}. The predation mortality has the effect that predators feed disproportionately on prey species with an excess of biomass, thereby reducing the size of peaks and troughs in the community biomass spectrum. This is not to discount the possible existence of other mechanisms that could stabilize the equilibrium.

An important feature of the near-power-law equilibrium abundance is that it needs enough species to be present to generate allometric scalings for prey death and predator growth. The continuum (mathematical) model shows that the power-law equilibrium becomes exact as the number of species tends to infinity \cite{Cuesta2017}, and this suggests that the allometric scalings become easier to achieve as the number of prey and predator species increases. Broader diets, i.e. feeding over a greater range of prey sizes (coincidentally increasing connectance), would also help in generating the scalings. The coexistence of many species at equilibrium near the power law is not a consequence of more feeding niches with increasing species richness; there is, for instance, no lack of niche space for the few predator species in Fig. 3 at time 0. Neither is there a limiting similarity caused by niche overlap: species can be arbitrarily close together at the power-law equilibrium of the underlying continuum theory \cite{Cuesta2017}. Coexistence of such similar species is consistent with recent molecular
evidence of coexisting cryptic species (e.g. Amato et al., 2007; McManus and Katz, 2009).

These features of the power-law equilibrium are unanticipated in the context of standard ecological theory. This theory does not lead to an expectation that an unlimited number of species could coexist, unconstrained by food-web connectance, and without the need for separate niches. In particular, a great deal of research on random matrices from May (1972) onwards leads to the view that ecological communities are less likely to be stable as species richness and connectance increase. We think it likely that there is structure in assemblages of aquatic plankton that random matrices have yet to take into account. Random matrices would need to generate equilibria that come close to a power-law relationship with cell size, and this probably requires appropriate allometric scalings of ecological rates.

Note that the study of species-poor plankton communities gives no hint that coexistence could be readily achieved in species-rich communities. This invites an obvious and important question as to how a species-rich community close to the power-law abundance could be assembled from its component parts in the first place. That such assemblages exist is not in doubt (Gaedke 1992; Quinones et al. 2003; San Martin et al. 2006). However, it is notable that the biomass spectra of some lake communities have marked peaks and troughs, unlike oligotrophic ocean systems (Sprules et al. 1991; Quinones et al. 2003; Yurista et al. 2014), suggestive of an intermediate state in assembling plankton communities. Assembly is an interesting matter that needs further research.

Clearly, many real-world processes prevent the existence of perfect power-law size spectra and exact allometric scalings of ecological rates. External processes include seasonal fluctuations that leave a strong footprint in community size spectra (Heath 1995). Exploitation of fish stocks causes major changes in size spectra further up the food web (Blanchard et al. 2005), which may be felt lower down through trophic coupling in the ecosystem. Internal processes include species-specific features of plankton life histories that a simple generic model cannot incorporate. For instance, the characteristic cell mass of diatoms decreases as they go through cycles of asexual reproduction; some taxonomic specificity in feeding has been observed (Jezbera et al. 2006) and there is evidence that unicellular taxonomic groups have different preferred predator-prey size ratios (Hansen et al. 1994). The allometric scaling relationships may also change; for instance Marañón et al. (2013) found a positive relationship between intrinsic rate of increase and cell size below cell diameters \( \simeq 5 \mu m \), and there is some change in the scaling of optimal prey size from small to large planktonic predators (Wirtz 2012).

Bearing in mind these caveats, the strongest statement this paper can support is that unicellular plankton species are more balanced in their interactions when close to the power law, than when further away from it. This means that the forces driving exclusion of one species by another are likely to be weaker than has previously been thought. Correspondingly, the forces needed to counteract exclusion and to maintain species-rich plankton assemblages do not have to be so strong to work effectively. A corollary is that this balanced state of coexistence can be disrupted by processes, human or otherwise, that drive aquatic ecosystems further from the power law.
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Appendices

A Allometric scaling and power-law abundances

Allometric scaling of physiological rates with cell size plays an essential role in this paper. There is however a potential for confusion as to whether the allometric scaling depends on the cell size $w$ of an individual or on the characteristic cell size $w_i$ of a species. We clarify this by acknowledging that rates can depend on both $w$ and $w_i$, and that allometric scaling refers to the behaviour of the rate under a rescaling of both $w$ and $w_i$. If $R_i(w) = R(w, w_i)$ denotes some physiological rate for species $i$, then allometric scaling with an exponent $\rho$ means that the rate $R(w, w_i)$ satisfies

$$R(\lambda w, \lambda w_i) = \lambda^\rho R(w, w_i)$$

(A.1)

for any positive scale factor $\lambda$. In other words, $R(w, w_i)$ is a homogeneous function of both arguments. This in turn means that the rate can be written in two alternative scaling forms

$$R_i(w) = w^\rho r(w/w_i) = w^\rho \tilde{r}(w/w_i)$$

(A.2)

where $\tilde{r}(x) = x^{-\rho} r(x)$. Thus it does not matter whether one thinks of allometric scaling in terms of cell size $w$ or in terms of characteristic size $w_i$. The exponent will be the same in either case and only the scaling function of $w/w_i$ will differ.

A similar issue also arises when abundance power laws are discussed: are these power laws in cell size $w$, or in the characteristic cell size of a species $w_i$? Again it helps to view the abundance as a function of both $w$ and $w_i$, as we do in this paper. Saying that the abundance has a power-law form then means that it is a homogeneous function of both arguments and thus can be written equally well in terms of a power of $w$ or a power of $w_i$. For example in the case of the steady state phytoplankton abundance it is equally valid to write $p_i(w) = w_i^{-\gamma-1} f_p(w/w_i)$ as it is to write $p_i(w) = w^{-\gamma-1} \tilde{f}_p(w/w_i)$.

B Allometric scaling of zooplankton growth

Here we show that there is an allometric scaling of zooplankton growth $G_i^{(z)}(w)$ of the form $w^{1-\xi}$ in eq. (2.5), if a multispecies plankton assemblage is at a power-law equilibrium. The argument begins by assuming a power-law equilibrium with densities $p_j(w_j)$ (respectively
The characteristic cell mass \( w_i \) of species \( i \) is defined as half its maximum cell mass. The discrete set of \( w_i \)s replace the continuum of species with characteristic cell mass \( w^* \) in Cuesta et al. (2017). In phytoplankton, values for \( w_i \) were chosen in the range \( 2 \to 30000 \) pg, corresponding to upper limits on cell ESDs of \( \sim 2 \to 40 \) \( \mu m \). Those of zooplankton were chosen in the range \( 200 \to 3 \times 10^6 \) pg, corresponding to upper ESD limits of \( \sim 10 \to 200 \) \( \mu m \). Staggering the cell size ranges in this way ensured that all phytoplankton were vulnerable to predation, and all zooplankton had food to eat.

From a compilation of earlier studies, Tang (1995, Fig. 2) estimated algal cell division rate to scale with an exponent of about \(-0.15\) with respect to cell size. Recently, it has been noted that cell division rates reach a maximum at a cell diameter \( \sim 5 \) \( \mu m \) (Chen and Liu, 2010; Marañón et al., 2013); the change is particularly clear in the transition from bacteria to eukaryotes (Kempes et al., 2012). Marañón et al. (2013) gave an exponent for the rate of increase of cells on the right-hand side of the peak of approximately \(-0.15\), corresponding to a cell doubling time scaling as \( \xi = 0.15 \), the value used here.

Metabolism was assumed to scale isometrically with cell mass \( \beta = 1 \), in keeping with observations on protists in DeLong et al. (2010) and phytoplankton (López-Sandoval et al., 2014). The rate of gain in cell mass was assumed to scale with an exponent \( \alpha = 0.85 \). With the values chosen, the structure of eq. (2.1) is simple, as \( \alpha + \xi - 1 = 0 \). Note that \( \alpha \) must be less than \( \beta \) to ensure that metabolic loss eventually becomes greater than the gain in mass, as cells grow.

We set \( \tilde{a}_\infty \) in the function \( \tilde{a}(N) \) (Table 1) to be substantially greater than \( \tilde{b} \) (2, 0.5 respectively) so that phytoplankton cells would not shrink when the resource level was below its equilibrium level. It was still possible for there to be insufficient resource for phytoplankton cells to grow, in numerical integrations starting at high cell densities. The same could apply to zooplankton cells if the food available was too low. To deal with such cases, negative
Table 1: Explicit functions

| Name       | Eq.   | Function                                      | Comments                                      |
|------------|-------|-----------------------------------------------|-----------------------------------------------|
| $\tilde{a}(N)$ | (2.2) | \( \frac{\tilde{a}_\infty N}{r+N} \)       | functional response for resource uptake       |
| $K_i^{(\cdot)}(w)$ | (2.11), (2.12) | \( G_i^{(\cdot)}(w)\delta(w - 2w_i) \)     | cell division rate set to zero, except at 2\( w_i \) (\( \delta \) is the Dirac \( \delta \)-function) |
| $Q(w|2w_i)$ | (2.11), (2.12) | \( \frac{1}{\sqrt{2\pi\sigma_b w_i}} \exp\left(- \frac{(w/w_i-1)^2}{2\sigma_b^2}\right) \) | distribution of cell masses following division at 2\( w_i \) |
| $s(w/w')$ | (2.3), (2.4) | \( \frac{1}{\sigma\sqrt{2\pi}} \exp\left(- \frac{(\ln(w/w') - \Delta)^2}{2\sigma^2}\right) \) | feeding kernel                                 |

growth rates were replaced by zero, causing cells to stay at the same size, experiencing the level of mortality corresponding to that size. However, at the equilibrium point itself, the growth rate is positive in every species with a positive density. This is intuitive. If it was not so, cells would not get as far as cell division and the species concerned would be decreasing in density, not at equilibrium.

The intrinsic death parameter \( d_0 \) was set at 0.1, so that most mortality would be caused by predation. Some residual mortality is needed for the largest zooplankton species in lieu of larger predators; for comparability, all species were given the same background value.

The parameter \( \sigma_b \) spreads out the size of daughter cells. We investigated the effects of this and chose \( \sigma_b = 0.05 \) as ensuring enough variation for effects of initial size structure within species to attenuate quickly.

Parameter \( A \) describes the overall level of encounters of zooplankton with their prey, and can be used to set the zooplankton abundance relative to the phytoplankton. We chose a value \( A = 0.02 \) as bringing their abundance to within about one order of magnitude. Encounters scale with body mass with an exponent \( \nu \); DeLong and Vasseur (2012) recorded 95% confidence intervals \( \approx 0.7-1.5 \) for the exponent in a meta-analysis of protist-phytoplankton microcosms.

A predator-prey mass ratio was obtained from the relationship between ESD of predators and prey taken from Wirtz (2012). For unicellular plankton this is ESD\(_P = 0.16 \) ESD\(_Z\). Scaling this from diameter to volume and assuming neutral buoyancy gives a rounded value \( \Delta = 5 \). Wirtz (2012) showed non-linearities at large zooplankton size (his Fig 4). Since our work was concerned with unicellular organisms, we worked with the left-hand end where the nonlinearity is small (see eq. 8 Wirtz 2012). Here it is \( \bar{r} \) that matters, estimated as \( \bar{r} = 0.16 \) (Wirtz 2012 page 5). We varied the width of the feeding kernel to tune the connectance.
Table 2: Model parameters and values used in Figs. 3 and 4

| Symbol | Value | Dimensions | Comments |
|--------|-------|------------|----------|
| $\xi$  | 0.15  | –          | exponent scaling doubling time with cell mass |
| $\beta$ | 1     | –          | exponent scaling metabolism with cell mass |
| $\bar{b}$ | 0.5   | $T^{-1}$   | metabolism term |
| $\alpha$ | 0.85  | –          | exponent scaling resource uptake with cell mass |
| $\tilde{a}_\infty$ | 2     | $T^{-1}$   | resource uptake parameter |
| $d_0$  | 0.1   | $T^{-1}$   | intrinsic death rate parameter |
| $\sigma_b$ | 0.05  | –          | size range of daughter cells |
| $c$    | 100   | $M V^{-1} T^{-1}$ | resource growth rate |
| $\dot{N}$ | 100   | $V^{-1}$ | resource equilibrium without plankton |
| $d$    | 1     | –          | proportionality constant for resource uptake to cell growth |
| $r$    | 1     | $V^{-1}$   | type II functional response term |
| $A$    | 0.02  | $V^{-1} T^{-1}$ | encounter parameter |
| $\nu$  | 0.85  | –          | exponent volume sensed |
| $\Delta$ | 5     | –          | log preferred predator prey mass ratio |
| $\sigma$ | 1, 0.25 | –       | diet breadth |
| $\epsilon$ | 0.6   | –          | food conversion efficiency |
| $\chi$ | 0.4   | –          | exponent for density dependence |
| $\delta x$ | 0.025 | –          | size step (logarithmic binning) |
| $\delta t$ | 0.0005 | $T$ | time step |
| $t_{\text{max}}$ | 600   | $T$ | time period for integration |
of the community. The value $\sigma = 1$ used here allows a high degree of connectedness, at the same time as ensuring prey cannot be large enough for cannibalism to take place. A food conversion efficiency $K = 0.6$ was assumed, following [Hartvig et al. (2011)].

The parameter $\chi = 0.4$ describing the form of density-dependent predation was chosen by trial and error, as a small value that was often able to stabilise plankton assemblages.

All computations were carried with log transformed cell mass ($x = \ln w$); this is because of large range of cell masses involved ($\sim 1$ to $10^6$). Computations were started by choosing species $w_i$s from uniformly-distributed random numbers over a range of approximately $\ln2$ to $\ln30000$ for phytoplankton, and $\ln300$ to $\ln(4 \times 10^6)$ for zooplankton. The random $w_i$s were rounded to match the discretization of cell size used in the numerical integration. Eqs. (2.11), (2.12) were discretized into steps of width $\delta x$ as given in Table 2. Integration of the full system was by the standard Euler method, with step sizes as small as computationally feasible. To obtain the equilibrium point, integration was carried out up to time $t_{max}$ to get close to equilibrium. The equilibrium was found by the Newton-Raphson method; this uses the Jacobian matrix from which the leading eigenvalue at the equilibrium point was taken as the measure of local asymptotic stability.

References

Amato, A., Kooistra, W. H. C. F., Ghiron, J. H. L., Mann, D. G., Pröschold, T., and Montresor, M. (2007). Reproductive isolation among sympatric cryptic species in marine diatoms. *Protist*, 158:193–207.

Andersen, K. H. and Beyer, J. E. (2006). Asymptotic size determines species abundance in the marine size spectrum. *American Naturalist*, 168:54–61.

Armstrong, R. A. (1999). Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. *Journal of Plankton Research*, 21:445–464.

Bell, G. I. and Anderson, E. C. (1967). Cell growth and division I. A mathematical model with applications to cell volume distributions in mammalian suspension cultures. *Biophysical Journal*, 7:329–351.

Benoît, E. and Rochet, M.-J. (2004). A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of Theoretical Biology*, 226:9–21.

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A., and Kell, L. T. (2005). Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science*, 62:405–411.

Boyce, D. G., Frank, K. T., and Leggett, W. C. (2015). From mice to elephants: overturning the one size fits all paradigm in marine plankton food chains. *Ecology Letters*, 226:doi: 10.1111/ele.12434.
Capitán, J. A. and Delius, G. W. (2010). Scale-invariant model of marine population dynamics. *Physical Review*, 81:061901.

Chen, H. and Liu, H. (2010). Relationships between phytoplankton growth and cell size in surface oceans: Interactive effects of temperature, nutrients, and grazing. *Limnology and Oceanography*, 55:965–972.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31:343–66.

Cuesta, J. A., Delius, G. W., and Law, R. (2017). A size-disaggregated model for plankton dynamics. *Journal of Mathematical Biology*, (to appear).

Datta, S., Delius, G. W., and Law, R. (2010). A jump-growth model for predator-prey dynamics: derivation and application to marine ecosystems. *Bulletin of Mathematical Biology*, 72:1361–1382.

Datta, S., Delius, G. W., Law, R., and Plank, M. J. (2011). A stability analysis of the power-law steady state of marine size spectra. *Journal of Mathematical Biology*, 63:779–799.

DeLong, J. P., Okie, J. G., Moses, M. E., Sibly, R. M., and Brown, J. H. (2010). Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proceedings of the National Academy of Sciences USA*, 107:12941–12945.

DeLong, J. P. and Vasseur, D. A. (2012). Size-density scaling in protists and the links between consumerresource interaction parameters. *Journal of Animal Ecology*, 81:1193–120.

Diekmann, O., Lauwerier, H. A., Aldenberg, T., and Metz, J. A. J. (1983). Growth, fission and the stable size distribution. *Journal of Mathematical Biology*, 18:135–148.

Edwards, A. M. and Bees, M. A. (2001). Generic dynamics of a simple plankton population model with a non-integer exponent of closure. *Chaos, Solitons and Fractals*, 12:289–300.

Flynn, K. J., Stoeker, D. K., Mitra, A., Raven, J. A., Glibert, P. M., Hansen, P. J., Granéli, E., and Burkholder, J. M. (2013). Misuse of the phytoplankton zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research*, 35:3–11.

Fox, J. W. (2013). The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution*, 28:86–92.

Fredrickson, A. G., Ramakrishna, D., and Tsuchiya, H. M. (1967). Statistics and dynamics of procaryotic cell populations. *Mathematical Biosciences*, 1:327–374.

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, 81:171–183.

Gaedke, U. (1992). The size distribution of plankton biomass in a large lake and its seasonal variability. *Limnology and Oceanography*, 37:1202–1220.
Giometto, A., Altermatt, F., Carrara, F., Maritan, A., and Rinaldo, A. (2013). Scaling body size fluctuations. *Proceedings of the National Academy of Sciences USA*, 110:4646–4650.

Guiet, J., Poggiale, J.-C., and Maury, O. (2016). Modelling the community size-spectrum: recent developments and new directions. *Ecological Modelling*, 337:4–14.

Hansen, B., Bjornsen, P. K., and Hansen, P. J. (1994). The size ratio between planktonic predators and their prey. *Limnology and Oceanography*, 39:395–403.

Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework for size-structured populations. *Journal of Theoretical Biology*, 272:113–122.

Heath, M. R. (1995). Size spectrum dynamics and the planktonic ecosystem of Loch Linnhe. *ICES Journal of Marine Science*, 52:627–642.

Heijmans, H. J. A. M. (1984). On the stable size distribution of populations reproducing by fission into two unequal parts. *Mathematical Biosciences*, 72:19–50.

Henson, M. A. (2003). Dynamic modeling of microbial cell populations. *Current Opinion in Biotechnology*, 14:460–467.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, 91:385–398.

Huisman, J. and Weissing, F. J. (1999). Biodiversity of plankton by species oscillations and chaos. *Nature*, 402:407–410.

Hutchinson, G. E. (1961). The paradox of the plankton. *American Naturalist*, 95:137–145.

Jezbera, J., Horňák, K., and Šimek, K. (2006). Prey selectivity of bacterivorous protists in different size fractions of reservoir water amended with nutrients. *Environmental Microbiology*, 8:1330–1339.

Kacelnik, A., Krebs, J. R., and Bernstein, C. (1992). The ideal free distribution and predator-prey populations. *Trends in Ecology and Evolution*, 7:50–55.

Kempes, C. P., Dutkiewicz, S., and Follows, M. J. (2012). Growth, metabolic partitioning, and the size of microorganisms. *Proceedings of the National Academy of Sciences USA*, 109:495–500.

Leibold, M. A. (1996). Graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist*, 147:784–812.

López-Sandoval, D. C., Rodríguez-Ramos, T., Cermeño, P., Sobrino, C., and Marañón, E. (2014). Photosynthesis and respiration in marine phytoplankton: Relationship with cell size, taxonomic affiliation, and growth phase. *Journal of Experimental Marine Biology and Ecology*, 457:151–159.
Marañón, E., Cervero, P., López-Sandoval, D. C., Rodríguez-Ramos, T., Sobrino, C., Huete-Ortega, M., Blanco, J. M., and Rodríguez, J. (2013). Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use. *Ecology Letters*, 16:371–379.

May, R. M. (1972). Will a large complex system be stable? *Nature*, 238:413–414.

McManus, G. B. and Katz, L. A. (2009). Molecular and morphological methods for identifying plankton: what makes a successful marriage? *Journal of Plankton Research*, 31:1119–1129.

Morozov, A. Y. (2010). Emergence of Holling type III zooplankton functional response: bringing together field evidence and mathematical modelling. *Journal of Theoretical Biology*, 265:45–54.

Nachman, G. (2006). A functional response model of a predator population foraging in a patchy habitat. *Journal of Animal Ecology*, 75:948–958.

Plank, M. J. and Law, R. (2011). Ecological drivers of stability and instability in marine ecosystems. *Theoretical Ecology*, 5:465–480.

Quinones, A., Platt, T., and Rodríguez, J. (2003). Patterns of biomass-size spectra from oligotrophic waters of the Northwest Atlantic. *Progress in Oceanography*, 57:405–427.

Roy, S. and Chattopadhyay, J. (2007). Towards a resolution of the paradox of the plankton: a brief overview of the proposed mechanisms. *Ecological Complexity*, 4:26–33.

San Martin, E., Irigoien, X., Harris, R. P., López-Urrutia, Á., Zubkov, M. Z., and Heywood, J. L. (2006). Variation in the transfer of energy in marine plankton along a productivity gradient in the Atlantic Ocean. *Limnology and Oceanography*, 51:2084–2091.

Scheffer, M., Rinaldi, S., Huisman, J., and Weissing, F. J. (2003). Why plankton communities have no equilibrium: solutions to the paradox. *Hydrobiologia*, 491:9–18.

Sheldon, R., Prakash, A., and Sutcliffe Jr., W. H. (1972). The size distribution of particles in the ocean. *Limnology and Oceanography*, 17:327–340.

Silvert, W. and Platt, T. (1978). Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnology and Oceanography*, 23:813–816.

Silvert, W. and Platt, T. (1980). In Kerfoot, W. C., editor, *Evolution and ecology of zooplankton communities*, chapter Dynamic energy-flow model of the particle size distribution in pelagic ecosystems, pages 754–763. University Press of New England, Hanover, New Hampshire.

Sinko, J. W. and Streifer, W. (1971). A model for populations reproducing by fission. *Ecology*, 52:330–335.

Sprules, W. G., Brandt, S. B., Stewart, D. J., Munawar, M., Jin, E. H., and Love, J. (1991). Biomass size spectrum of the Lake Michigan pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences*, 48:105–115.
Tang, E. P. Y. (1995). The allometry of algal growth rates. *Journal of Plankton Research*, 17:1325–1335.

Thingstad, T. F. and Lignell, R. (1997). Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. *Aquatic Microbial Ecology*, 13:19–27.

Truscott, J. E. and Brindley, J. (1994). Ocean plankton populations as excitable media. *Bulletin of Mathematical Biology*, 56:981–998.

Våge, S., Storesund, J. E., Giske, J., and Thingstad, T. F. (2014). Optimal defense strategies in an idealized microbial food web under trade-off between competition and defense. *PLOS ONE*, 9:e101415.

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Quarterly Review of Biology*, 32:217–231.

Winter, C., Bouvier, T., Weinbaue, M. G., and Thingstad, T. F. (2010). Trade-offs between competition and defense specialists among unicellular planktonic organisms: the “killing the winner” hypothesis revisited. *Microbial and Molecular Biology Reviews*, 74:42–57.

Wirtz, K. W. (2012). Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators and their ideal prey. *Marine Ecology Progress Series*, 445:1–12.

Yurista, P. M., Yule, D. L., Balge, M., VanAlstine, J. D., Thompson, J. A., Gamble, A. E., Hrabik, T. R., Kelly, J. R., Stockwell, J. D., and Vinson, M. R. (2014). A new look at the Lake Superior biomass size spectrum. *Canadian Journal of Fisheries and Aquatic Sciences*, 71:1324–133.