

Size-structured planktonic ecosystems: constraints, controls and assembly instructions

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Received April 9, 2009; accepted in principle November 17, 2009; accepted for publication December 16, 2009

Corresponding editor: Roger Harris

Here we present a nutrient–phytoplankton–zooplankton (*NPZ*) model that has arbitrary size-resolution within the phytoplankton- and zooplankton-state variables. The model assumes allometric scaling of biological parameters. This particular version of the model (herbivorous zooplankton only) has analytical solutions that allow efficient exploration of the effects of allometric dependencies of various biological processes on the model's equilibrium solutions. The model shows that there are constraints on the possible combinations of allometric scalings of the biological rates that will allow ecosystems to be structured as we observe (larger organisms added as the total biomass increases). The diversity (number of size classes occupied) of the ecosystem is the result of simultaneous bottom-up and top-down control: resources determine which classes *can* exist; predation determines which classes *do* exist. Thus, the simultaneous actions of bottom-up and top-down controls are essential for maintaining and structuring planktonic ecosystems. One important conclusion from this model is that there are multiple, independent ways of obtaining any given biomass spectrum, and that the spectral slope is not, in and of itself, very informative concerning the underlying dynamics. There is a clear need for improved size-resolved field measurements of biological rates; these will both elucidate biological processes in the field, and allow strong testing of size-structured models of planktonic ecosystems.

KEYWORDS: size-structured planktonic ecosystems; plankton diversity; allometric scaling

INTRODUCTION

Beginning with the seminal work of Sheldon *et al.* (Sheldon *et al.*, 1972), Kerr (Kerr, 1974) and Platt and Denman (Platt and Denman, 1977), we have been trying to derive theoretical explanations for the size structure of planktonic ecosystems. Observations show a relatively stable slope of the normalized biomass spectrum (*sensu* Platt and Denman, 1978) for plankton, varying by less than a factor of 2 over a range of

organism sizes, geographic areas and seasons (e.g. Gaedke, 1992; Gin *et al.*, 1999; Cavender-Bares *et al.*, 2001; Franks and Jaffe, 2008). Furthermore, evidence is accumulating showing that planktonic ecosystems are structured such that, as total biomass increases, organisms are added in increasingly large size classes (e.g. Yentsch and Phinney, 1989; Chisholm, 1992; Ciotti *et al.*, 2002; Li, 2002; Irigoien *et al.*, 2004). These apparent regularities in ecosystem structure may point to

doi:10.1093/plankt/fbp145, available online at www.plankt.oxfordjournals.org. Advance Access publication January 24, 2010

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regularity in the underlying dynamics that structure the ecosystem.

One approach to exploring the dynamics structuring planktonic ecosystems is through size-structured models (e.g. Moloney and Field, 1991; Gin *et al.*, 1998; Armstrong, 1999; Zhou, 2006; Baird and Suthers, 2007). Such models are often based on the assumption that fundamental biological rates vary systematically with organism size: allometric scaling. Typically a variable A that scales allometrically with the size s of the organism will vary as $A(s) = A_0 s^e$, where A_0 is the value of the variable at the smallest size, and e is the exponent specifying how that variable varies with size. One significant advantage of allometric scaling is that it greatly reduces the number of parameters necessary for constructing a model: rather than specifying the parameter separately for each model state variable (different phytoplankton classes, for example), all size classes are parameterized using a single relationship and two parameters.

Even with the reduced number of parameters obtained through allometric scaling, size-structured models of planktonic ecosystems tend to be complex and difficult to solve. Reliance on numerical solutions limits how thoroughly we can explore parameter space, and thus makes it difficult to generalize the model's behavior, or the dynamics that structure the ecosystems.

Here we present a nutrient–phytoplankton–zooplankton (NPZ) model that has arbitrary structure within the phytoplankton- and zooplankton-state variables. The model has analytical solutions that allow efficient exploration of the effects of different parameterizations on the model's equilibrium solutions. For the purposes of this investigation, we formulate a model with size-structured phytoplankton and zooplankton variables that allow for allometric scaling of all the biological parameters. The model demonstrates that there are constraints on the possible combinations of allometric scalings of the biological rates that allow ecosystems to be structured in the manner that we observe them. Furthermore, the zooplankton (more generally, predators) control the diversity of the ecosystem through size-specific grazing. One important conclusion from this model is that there are multiple ways to obtain any given biomass spectrum, and that the spectral slope is not, in and of itself, very informative concerning the underlying dynamics. There is a clear need for improved size-resolved field measurements of biological rates; these will both elucidate biological processes in the field, and allow for more thorough testing of size-structured models of planktonic ecosystems.

THE SIZE-STRUCTURED MODEL: CONTINUOUS FORM

We base our size-structured model on a three-compartment NPZ architecture, similar in form to Franks *et al.* (Franks *et al.*, 1986). However, we allow for different classes of phytoplankton and zooplankton distinguished by their size, s . Size is measured as a linear dimension (e.g. equivalent spherical diameter, etc.). In this continuous model, the state variables are dissolved nutrient N , phytoplankton biomass per unit size \tilde{P} , and zooplankton biomass per unit size \tilde{Z} . The phytoplankton biomass, P in a size class of width ds is $P = \tilde{P} ds$ and the zooplankton biomass, Z in the same size class is, $Z = \tilde{Z} ds$.

The equations governing the rate of change of phytoplankton and zooplankton biomass per unit size, of size s_0 — $\tilde{P}(s_0)$ and $\tilde{Z}(s_0)$ —are

$$\frac{\partial \tilde{P}(s_0)}{\partial t} = \tilde{P}(s_0) \left[\mu(s_0) \frac{N}{N + k(s_0)} - \lambda(s_0) - \int_{s_{\min}}^{s_{\max}} \alpha(s, s_0) g(s) \frac{\tilde{Z}(s)}{F(s) + K(s)} ds \right], \quad (1)$$

$$\frac{\partial \tilde{Z}(s_0)}{\partial t} = \tilde{Z}(s_0) \left[\gamma(s_0) g(s_0) \frac{F(s_0)}{F(s_0) + K(s_0)} - \delta(s_0) \right], \quad (2)$$

$$N_T = N + \int_{s_{\min}}^{s_{\max}} \tilde{P}(s) ds + \int_{s_{\min}}^{s_{\max}} \tilde{Z}(s) ds, \quad (3)$$

$$F(s_0) = \int_{s_{\min}}^{s_{\max}} \alpha(s_0, s) \tilde{P}(s) ds. \quad (4)$$

For generality, we have allowed all the parameters to have size dependence. We have assumed a saturating nutrient uptake function for the phytoplankton similar to the Michaelis–Menten or Monod form, with a maximal uptake (=growth) rate of $\mu(s)$ and a half saturation constant of $k(s)$. Phytoplankton lose biomass through respiration, dissolved organic matter (DOM) release, cell death etc. at rate $\lambda(s)$, while the zooplanktonic rate of loss is $\delta(s)$. Grazing is modeled as a saturating function of the total food available $F(s)$ with maximal grazing rate $g(s)$ and half saturation constant $K(s)$. The grazing kernel $\alpha(s, s_0)$ determines the range of phytoplankton sizes that a given size class of zooplankton grazes on, and how that grazing intensity is distributed over phytoplankton size classes. Zooplankton have an assimilation coefficient $\gamma(s)$. The total amount of nutrient in the system N_T is conserved, and is the sum of the dissolved nutrient N and the integral over all sizes

of the biomasses per unit size of the phytoplankton and zooplankton [equation (3)].

The model equations include phytoplankton growth based on uptake of nutrients, phytoplankton losses to grazing and respiration/DOM release/cell death. Zooplankton growth is determined by the assimilated fraction of their phytoplankton diet, and they have losses due to mortality/respiration/DOM release. Unassimilated food, and biomass lost to respiration/DOM release/mortality is recycled back to the dissolved nutrient pool.

In the particular form of the model we analyze here, we assume the zooplankton to be herbivorous. We are analyzing more complex versions of the model that include both a range of prey sizes, and omnivory of zooplankton feeding, and hope to publish those analyses in the near future. The present model does not include the growth of organisms into new size classes, and is thus most applicable to bacteria and protists, rather than the rarer metazoan zooplankton that have complex life cycles covering a wide range of sizes.

THE SIZE-STRUCTURED MODEL: DISCRETE FORM

To simplify the model, we first put equations (1)–(4) in discrete form, in which the biomass per unit size-class width is \tilde{P}_i and \tilde{Z}_i . The discrete versions of equations (1)–(4) are:

$$\frac{d\tilde{P}_i}{dt} = \tilde{P}_i \left[\mu_i \frac{N}{N + k_i} - \lambda_i - \sum_{j=1}^m \alpha_{ji} g_j \frac{\tilde{Z}_j}{F_j + K_j} \Delta s_j \right], \quad (5)$$

$$\frac{d\tilde{Z}_i}{dt} = \tilde{Z}_i \left[\gamma_i g_i \frac{F_i}{F_i + K_i} - \delta_i \right], \quad (6)$$

$$N_T = N + \sum_{i=1}^n \tilde{P}_i \Delta s_i + \sum_{i=1}^n \tilde{Z}_i \Delta s_i, \quad (7)$$

$$F_i = \sum_{j=1}^m \alpha_{ji} \tilde{P}_j \Delta s_j. \quad (8)$$

Here Δs_i is the width of size-class i . If we solve these equations in their present form, we recover the normalized biomass spectra $\tilde{P}(s)$, $\tilde{Z}(s)$. We choose instead to reformulate the model in terms of P and Z that has units of biomass in a given size class. We obtain these by defining $P = \tilde{P} \Delta s$ and $Z = \tilde{Z} \Delta s$. These variables are more useful since they have the units of the quantities that are measured in experiments. In the particular form of the model we analyze here, each zooplankter Z of size s_o eats only phytoplankton P of size s_o , where

the constant r is the predator–prey size ratio. The predator–prey size ratio can vary from $r = 1$ (predators eat prey their own size) to $r > 1$ (predators eat prey smaller than themselves). We keep r fixed for a given ecosystem, and all predators in an ecosystem have the same r (though this is not a necessity). This assumption changes the grazing kernel α in equations (5) and (8) to a Kronecker delta function so that $F_i = P$. With these changes, equations (5)–(8) become:

$$\begin{aligned} \frac{dP(s_o)}{dt} &= P(s_o) \\ &\times \left[\mu(s_o) \frac{N}{N + k(s_o)} - \lambda(s_o) - g(rs_o) \frac{Z(rs_o)}{P(s_o) + K(rs_o)} \right], \end{aligned} \quad (9)$$

$$\begin{aligned} \frac{dZ(rs_o)}{dt} &= Z(rs_o) \\ &\times \left[\gamma(rs_o) g(rs_o) \frac{P(s_o)}{P(s_o) + K(rs_o)} - \delta(rs_o) \right], \end{aligned} \quad (10)$$

$$N_T = N + \sum_{i=1}^n P(s_i) + \sum_{i=1}^n Z(s_i). \quad (11)$$

In this work, we discretize the size classes so that they vary logarithmically in width (i.e. equally spaced on a log scale). The normalized biomass spectrum is given by $\tilde{P}(s)$ or $\tilde{Z}(s)$ plotted versus s . Here we investigate the properties of the non-normalized biomass spectra $P(s)$ and $Z(s)$ versus s ; the normalized spectra can be obtained from these by dividing by Δs , which—with size classes evenly spaced in log space—will decrease the slope on a log–log plot by -1 .

We now explore this size-structured NPZ model, derive criteria for which size classes of phytoplankton and zooplankton can exist and determine the amounts of biomass in each of the phytoplankton and zooplankton size classes.

CONSTRAINTS

From our simple size-structured NPZ model [equations (9)–(11)], we can immediately derive a criterion for the conditions under which a phytoplankter of size s_o can exist at equilibrium. This criterion is obtained from the equation that governs the rate of change of phytoplankton in the absence of any predators, and is,

$$N_{s_o}^* = \frac{k(s_o)}{\frac{\mu(s_o)}{\lambda(s_o)} - 1}. \quad (12)$$

If $N \ll k(s_o)$ then the uptake of nutrients is almost

linear in \mathcal{N} and the criterion reduces to

$$\mathcal{N}_{s_0}^* = \frac{k(s_0)\lambda(s_0)}{\mu(s_0)}. \tag{13}$$

This criterion states that for a phytoplankter of size s_0 to exist, the dissolved nutrient concentration must be at least $\mathcal{N}_{s_0}^*$. The same criterion was originally identified by Stewart and Levin (Stewart and Levin, 1973) and Tilman (Tilman, 1977), and was also more recently derived by Armstrong (Armstrong, 1999) in his planktonic ecosystem model. The criterion embodies the dynamics of competition for resources—in this case nutrients: the greater the value of $\mathcal{N}_{s_0}^*$, the less competitive the organism, and the more likely it is to be excluded in an equilibrium situation. A novel aspect of our work is to show that this criterion also includes important constraints on the possible allometric scaling relationships of fundamental physiological properties of the phytoplankton.

Numerous studies have suggested that the maximal growth rate of phytoplankton should scale allometrically with size s as

$$\mu = \mu_0 s^{e_\mu}, \tag{14}$$

where μ_0 is the growth rate of the smallest size class, and e_μ is the allometric scaling exponent of the growth rate (dimensionless). Empirical and theoretical studies have suggested that $e_\mu = -0.75$ when s is measured as a linear dimension (e.g. Moloney and Field (1989) and references therein, though see Marañón (2008) for a contradictory analysis based on field data). In our model, equations (9)–(11), we have allowed for the possibility that all the model parameters are size-dependent. If we assume that these parameters vary allometrically with size, our $\mathcal{N}_{s_0}^*$ criterion (13) becomes

$$\mathcal{N}_{s_0}^* = \frac{k_0 s^{e_k} \lambda_0 s^{e_\lambda}}{\mu_0 s^{e_\mu}} = \frac{k_0 \lambda_0}{\mu_0} s^{e_k + e_\lambda - e_\mu}, \tag{15}$$

where the subscript on the exponent e_i indicates the scaling for the particular parameter i .

Field studies have shown that the fraction of the smallest phytoplankton decreases strongly with the total phytoplankton biomass (e.g. Yentsch and Phinney, 1989; Chisholm, 1992; Ciotti *et al.*, 2002; Li, 2002; Irigoien *et al.*, 2004). Thus, as the total phytoplankton biomass increases, biomass is added in the larger size classes, while the biomass of the smaller size classes remain relatively unchanged. This suggests that $\mathcal{N}_{s_0}^*$ should be an increasing function of size s because more nutrients are required to support larger phytoplankton cells.

Therefore, we require

$$e_k + e_\lambda - e_\mu > 0. \tag{16}$$

If $e_\mu = -0.75$, as if often assumed, then

$$e_k + e_\lambda > -0.75. \tag{17}$$

This criterion provides an important constraint on the allowable size-dependencies for k (half saturation constant for nutrient uptake) and λ (rate of respiration, DOM leakage, death, etc.) that is consistent with observations. If one of these characteristics decreased with size (i.e. e_k or e_λ was negative), the other must increase with size to compensate. Tang and Peters (Tang and Peters, 1995) present data that suggest that phytoplankton volume-specific respiration decreases with size with $e_\lambda = -0.6$ (Tang and Peter’s exponents were converted here to account for the fact that their scalings were based on the volume of the organism, and ours are based on linear dimension; see also Han and Straskraba, 1998). As well, Moloney and Field’s (Moloney and Field, 1991) synthesis suggests that k increases with size with $e_k = 1.14$, which satisfies criterion (17). A decrease of k with size would not have allowed Moloney and Field’s (Moloney and Field, 1991) model to reproduce the fundamental property of planktonic ecosystems that biomass tends to be added in increasingly larger size classes as the total biomass increases. Thus, a decrease of phytoplankton growth rate μ with size implies that only one of respiration/DOM release/cell death and the half-saturation constant for nutrient uptake can decrease strongly with size, while the other must increase to ensure that equation (16) is satisfied.

CONTROLS

Criteria (12), (13) and (16) yield constraints on the conditions under which a given size class of phytoplankton *can* exist in a community. However, even when these criteria are satisfied, it does not guarantee that that particular size class *will* necessarily exist. Indeed, without something controlling the biomass of the smallest (most competitive) size class of phytoplankton, it would be the only size class that could exist.

If we look for equilibrium solutions to equation (10), we find that for a zooplankter to exist in equilibrium in the absence of any predators its food supply must be equal to or greater than the following critical value,

$$P_{s_0}^* = \frac{K(rs_0)}{\gamma(rs_0)g(rs_0)/\delta(rs_0) - 1}. \tag{18}$$

If $K(r_{s_0})P \gg P(s_0)$ grazing rate increases linearly with phytoplankton prey, and the above equation is replaced by,

$$P_{s_0}^* = \frac{K(r_{s_0})\delta(r_{s_0})}{\gamma(r_{s_0})g(r_{s_0})}. \quad (19)$$

These criteria (18) and (19) show that, for a zooplankter of size r_{s_0} to exist, there must be a sufficient food supply, namely $P_{s_0}^*$. Interestingly, these criteria also show that the amount of phytoplankton (or in general any prey) of a given size in equilibrium is controlled completely by the properties of the zooplankton (its predator). If these parameters scale allometrically with size, then from (19).

$$P_{s_0}^* = \frac{K_0 s_0^{e_K} \delta_0 s_0^{e_\delta}}{\gamma_0 s_0^{e_\gamma} g_0 s_0^{e_g}} = \frac{K_0 \delta_0}{\gamma_0 g_0} s_0^{e_K + e_\delta - e_\gamma - e_g}. \quad (20)$$

Therefore, the slope b of the phytoplanktonic size spectrum is set by the size-dependencies of the zooplanktonic grazing, assimilation, and respiration/death:

$$b = e_K + e_\delta - e_\gamma - e_g. \quad (21)$$

Moloney and Field (Moloney and Field, 1991) suggest that $e_g = -0.75$, $e_K = 0.24$ and $e_\delta = -0.75$. For a flat phytoplankton spectrum with $b = 0$ (i.e. a normalized biomass spectrum β of slope -1 , Platt and Denman, 1978) this requires that the assimilation $\gamma(s)$ increase with size with a scaling exponent of $e_\gamma = 0.24$. In an analysis of many animal types, Humphreys (Humphreys, 1981) discovered a positive allometric relationship of assimilation to an index composed of the biomass of the organisms (in units of cal m^{-2}) divided by the weight of the organism. While it is difficult to separate the effects of biomass and weight on the regressions, an interpretation of his results is that assimilation does indeed increase with organism size. Hansen *et al.* (Hansen *et al.*, 1997), on the other hand, found $e_g = -0.20$, $e_K = -0.16$ (for non-dinoflagellate protists) and $e_\gamma = 0$. Again, to obtain a flat phytoplankton spectrum, this would require $e_\delta \sim 0$. If dinoflagellates and copepods were added to the regressions, $e_K = 0$, requiring a decrease of metabolic losses with size ($e_\delta = -0.23$) to balance the decrease in maximum ingestion rate with size ($e_g = -0.23$).

Our analyses thus suggest that, although the competition for resources (bottom-up control) regulates the phytoplankton size classes that *can* exist, it is the top-down control (grazing) that regulates whether they *do* exist, and the amounts of biomass of that phytoplankton. Thus, the simultaneous actions of bottom-up and top-down controls are essential for maintaining and structuring planktonic ecosystems.

The slope of the zooplankton spectrum is more complex than the phytoplankton spectrum and depends on both the phytoplankton and zooplankton processes. The criterion for the amount of zooplankton of size r_{s_0} at equilibrium that is obtained from equation (9) is

$$\begin{aligned} \zeta_{r_{s_0}}^* &= \left(\frac{P_{s_0}^* + K(r_{s_0})}{g(r_{s_0})} \right) \\ &\times \left(\mu(s_0) \frac{N_{s_0}^*}{N_{s_0}^* + k(s_0)} - \lambda(s_0) \right). \end{aligned} \quad (22)$$

The biomass of a given size class of zooplankton is thus dependent on the amount of its food ($P_{s_0}^*$), as well as a combination of the zooplankton grazing parameters (g and K) and the net growth rate of its phytoplankton-prey in the absence of grazers.

With allometric scaling of the rates, the zooplankton spectrum can be written

$$\begin{aligned} \zeta_{r_{s_0}}^* &= \left(c_1^{e_K + e_\delta - e_\gamma - 2e_g} + c_2^{e_K - e_g} \right) \\ &\times \left(\frac{c_3^{e_K + e_\lambda}}{c_4^{e_K + e_\lambda - e_\mu} + c_5^{e_K}} - c_6^{e_\lambda} \right). \end{aligned} \quad (23)$$

The functions c_i for $i = 1-6$ are linear functions of size s . The resulting spectral slope for zooplankton is a complicated function of the various biological processes. However, some simple cases can reveal some of the dominant dynamics. Consider, for instance, a system in which only the phytoplankton growth rate is size-dependent. The zooplankton spectrum now has the form

$$\zeta_{r_{s_0}}^* = \left(\frac{c_3}{c_4^{-e_\mu} + c_5} - c_6 \right), \quad (24)$$

which has nearly the same slope as the phytoplankton growth rate, e_μ , when $c_4 \gg c_5$. As we established earlier [criteria (15) and (20)], if only the phytoplankton growth rate is size-dependent, the dissolved nutrients N increase with increasing N_B the spectral slope of phytoplankton is flat (P_s^* is constant), and the zooplankton spectrum follows the size-dependency of the phytoplankton growth rate.

If we further assume the zooplankton grazing rate is size-dependent (e.g. Hansen and Christoffersen, 1995; Hansen *et al.*, 1997), the zooplankton spectrum at equilibrium is approximately

$$\zeta_{r_{s_0}}^* = \left(c_1^{-2e_g} + c_2^{-e_g} \right) \left(\frac{c_3}{c_4^{-e_\mu} + c_5} - c_6 \right). \quad (25)$$

This yields a zooplankton spectral slope close to $e_\mu - e_g$ when $c_4 \gg c_5$, $c_3 \gg c_6$ and $c_2 \gg c_1$. Thus, if the phytoplankton growth and zooplankton grazing rates both

have the same allometric scaling, the zooplankton spectrum should be relatively flat, as the two size dependencies offset each other. Size dependencies of other biological processes will similarly affect the slope and structure of the zooplankton spectrum. In general, we expect the zooplankton spectrum to be relatively linear over the smallest size classes, with a roll-off of the spectrum (by that we mean that the spectral slope rapidly becomes more negative and biomasses decrease rapidly with size) at the larger size classes.

EQUILIBRIUM SOLUTIONS: CONSTRUCTING AN ECOSYSTEM

Our simple size-structured NPZ model has exact analytical solutions to the equilibrium biomasses of the dissolved nutrients and the phytoplankton and zooplankton size classes. These solutions allow us to very easily explore the effects of various parameters on the ecosystem structure.

The analytical solutions build up the ecosystem by sequentially adding nutrients, which allows the introduction of phytoplankton and zooplankton size classes. We have verified that these equilibrium solutions are solutions to the time-dependent model by running a model to steady state for a range of different initial conditions and allometric scalings. Furthermore, we have substituted these solutions into the right hand sides of equations (9) and (10) to verify that the fluxes are zero to within machine precision.

We begin with a system so impoverished in nutrients that no phytoplankton or zooplankton can exist—only dissolved nutrients. As nutrients are added, a two-stage cycle begins. First, all the compartments are held fixed in biomass except for one phytoplankton size class that increases linearly with the total biomass. Second, the phytoplankton biomasses are held fixed as the dissolved nutrients and zooplankton—up to a particular size— increase linearly with total biomass. All the larger size classes are absent.

The general solution for the p^{th} stage of this ecosystem construction is:

Stage 0: Dissolved nutrients increasing, no P or Z .

$$0 < N_T < N_{s_1}^*, \tag{26}$$

$$N = N_T, \tag{27}$$

$$P(s_i) = 0 \quad \text{for } i = 1, \dots, n, \tag{28}$$

$$Z(r_{s_i}) = 0 \quad \text{for } i = 1, \dots, n. \tag{29}$$

Stage $(2p-1)$: Phytoplankton of size $P(s_p)$ increase as nutrients added.

$$\begin{aligned} N_{s_p}^* + \sum_{i=0}^{p-1} (P_{s_i}^* + Z_{rs_i(p-1)}^*) &\leq N_T \\ &\leq N_{s_p}^* + P_{s_p}^* + \sum_{i=0}^{p-1} (P_{s_i}^* + Z_{rs_i(p-1)}^*), \end{aligned} \tag{30}$$

$$N = N_{s_p}^*, \tag{31}$$

$$P(s_i) = \begin{cases} P_{s_i}^* & \text{for } 1 \leq i < p \\ 0 \leq P(s_i) \leq P_{s_i}^* & \text{increases } i = p \\ 0 & \text{for } i > p \end{cases}, \tag{32}$$

$$Z(r_{s_i}) = \begin{cases} Z_{rs_i(p-1)}^* & \text{for } 1 \leq i < p \\ 0 & \text{for } i \geq p \end{cases} \tag{33}$$

Stage $2p$: Zooplankton increases in biomass.

$$\begin{aligned} N_{s_p}^* + P_{s_p}^* + \sum_{i=0}^{p-1} (P_{s_i}^* + Z_{rs_i(p-1)}^*) &\leq N_T \\ &\leq N_{s_p}^* + \sum_{i=0}^p (P_{s_i}^* + Z_{rs_i(p-1)}^*), \end{aligned} \tag{34}$$

$$N = N_{s_p}^* \leq N \leq N_{s_{p+1}}^* \quad \text{increases,} \tag{35}$$

$$P(s_i) = \begin{cases} P_{s_i}^* & \text{for } 1 \leq i \leq p \\ 0 & \text{for } i > p \end{cases}, \tag{36}$$

$$Z(r_{s_i}) = \begin{cases} Z_{rs_i(p-1)}^* \leq Z(r_{s_i}) \leq Z_{rs_i p}^* & \text{increases } i \leq p \\ 0 & \text{for } i \geq p \end{cases} \tag{37}$$

Finally, the amount of zooplankton in the i^{th} size class at the p^{th} stage is

$$Z_{s_i p}^* = \left(\frac{P_{s_i}^* + K(r_{s_i})}{g(r_{s_i})} \right) \left(\mu(s_i) \frac{N_p^*}{N_p^* + k(s_i)} - \lambda(s_i) \right). \tag{38}$$

We now have all the information required to construct size-structured planktonic ecosystems based on our NPZ model dynamics presented in equations (9)–(11).

EQUILIBRIUM ECOSYSTEM SIZE SPECTRA

Our model allows for arbitrary relationships of the model parameters with size—they are not constrained to scale allometrically, or to necessarily vary with size at all. In the interests of reducing model complexity and difficulties in parameterization, we only explore a few effects of allometric parameter size dependencies. These special cases are chosen because reveal the relationships of planktonic size spectra to the underlying biological processes.

We choose an arbitrary size interval of $s(i + 1) = 1.0182s(i)$ that produces a highly resolved biomass spectrum, and will reveal potential nonlinear features in the spectra. Changing the size resolution does not change the normalized spectra $\tilde{P}(s)$, $\tilde{Z}(s)$, but changes the biomass P , Z of a given size interval. For example, with half the size resolution, the biomass in an interval is approximately the sum of the biomasses of the two size categories present in the higher-resolution case, i.e. twice the biomass of the finer-resolution case. The structure of the spectra—the slopes, size ranges and roll-offs—do not change with changing size resolution. The scaling exponents e_i will be specified in the various scenarios. However, the coefficients of the biological processes were generally kept constant with $\mu_o = 5.9 \text{ day}^{-1}$, $k_o = 1.0 \text{ } \mu\text{M N}$, $\lambda = .017 \text{ day}^{-1}$, $g_o = 7.0 \text{ day}^{-1}$, $K_o = 1.0 \text{ } \mu\text{M N}$, $\gamma_o = 0.7$ and $\delta_o = 0.17 \text{ day}^{-1}$. Note that when size dependence is included, the realized values of these parameters are quite different than the multiplicative constants given here. The results presented here do not depend qualitatively on the values of these parameters.

First we consider a system in which the only size-dependent process is phytoplankton growth, which decreases allometrically with size with $e_\mu = -0.75$ (Fig. 1) and none of the zooplankton parameters are size-dependent. From equations (18), (19) and (21), we expect the phytoplankton spectrum to be flat ($b = 0$). Criterion (24) indicates that the zooplankton spectrum should fall off with size with a slope of e_μ due to the size-dependence of phytoplankton growth, $\mu(s)$. Criterion (18) also indicates that as $N_{s_o}^*$ increases, an increasing number of larger phytoplankton can co-exist in the ecosystem. Thus, as the total nutrient N_T of the system increases, both larger phytoplankton and zooplankton can be supported (Fig. 1). In addition, while the phytoplankton in a given size class remains constant with increasing N_T the amount of biomass of zooplankton in a size class increases.

Under these conditions, the total “particle” spectrum $[\log\{P(s_o) + Z(rs_o)\} \text{ versus } \log(s)]$ shows a break in slope

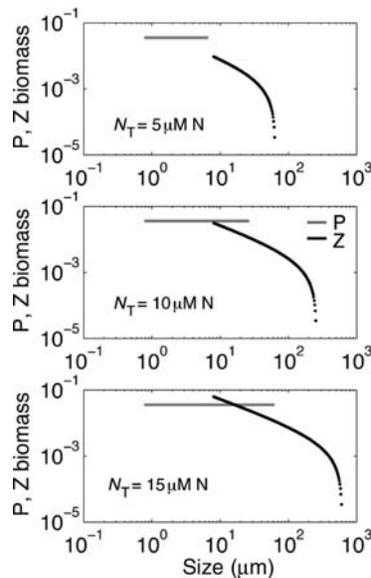


Fig. 1. Phytoplankton (gray) and zooplankton (black) biomass spectra for an ecosystem with $e_\mu = -0.75$, plotted for three different values of the total nutrient, N_T . Based on criteria (20) and (24), we expect the phytoplankton spectrum to have a slope of $b = 0$, and the zooplankton spectrum to have a slope of $b = -0.75$. We can see that this is the case.

between the phytoplankton-dominated (flat) part of the spectrum, and the zooplankton-dominated (downward sloping) part of the spectrum. The overlap of the phytoplankton and zooplankton spectra depends on the predator–prey ratio r ; with $r = 1$ (zooplankton eat phytoplankton their own size), there is complete overlap of the phytoplankton and zooplankton size classes and the structure of the aggregate spectrum depends on the relative abundances of the two types of organisms at a given size (Fig. 2A and D). Because the relative abundances of the phytoplankton and zooplankton are different, as r increases the aggregate spectrum can have considerable structure (Fig. 2). The spectral slope of the aggregate spectrum can be different from both the zooplankton and phytoplankton spectra, and the aggregate spectrum can show lumps where there is a predator–prey offset between the two spectra.

Criterion (25) suggests that including a size-dependent zooplankton grazing rate with a scaling exponent $e_g = -0.75$ in addition to the size-dependent phytoplankton growth rate should produce a flat zooplankton spectrum. Furthermore, criterion (21) suggests that the phytoplankton spectrum should slope upward with $b = 0.75$. The model equilibrium solutions (Fig. 3) show that this is the case with the ecosystem still structured as before: the larger organisms are introduced as more nutrients are added to the system.

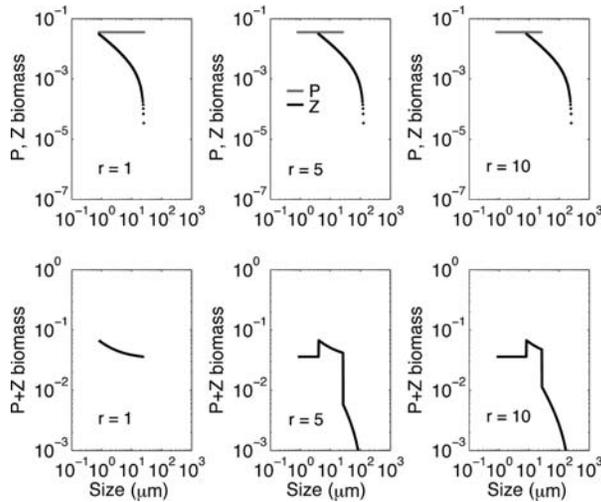


Fig. 2. Ecosystems with $e_\mu = -0.75$ and $N_T = 10 \mu\text{M N}$ plotted for three different values of the predator-prey ratio r . Top panels: phytoplankton (gray) and zooplankton (black) biomass spectra. Bottom panels: aggregate $P + Z$ spectra, such as might be acquired by a particle counter.

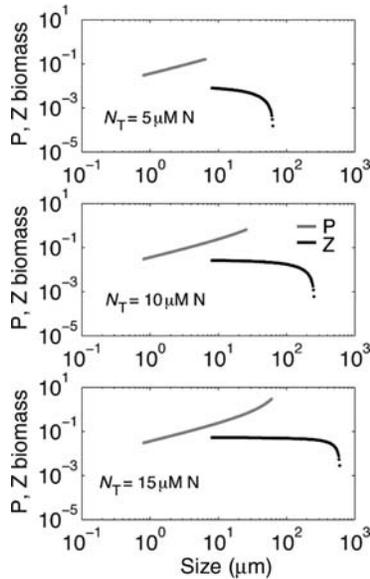


Fig. 3. Phytoplankton (gray) and zooplankton (black) biomass spectra for an ecosystem with $e_\mu = -0.75$ and $e_g = -0.75$, plotted for three different values of the total nutrient, N_T . Criteria (20) and (25) predict a 0.75 slope for the phytoplankton and a zero slope for the zooplankton biomass spectra. The predator-prey size ratio $r = 10$.

Almost any spectral slopes can be obtained by the appropriate selection of allometric scaling exponents. For instance, we can construct an ecosystem with zero slopes of both the phytoplankton and zooplankton by choosing $e_\mu = -0.75$, $e_g = -0.5$, $e_\delta = -0.5$ and $e_k = -0.5$ (Fig. 4). Manipulation of the values of the

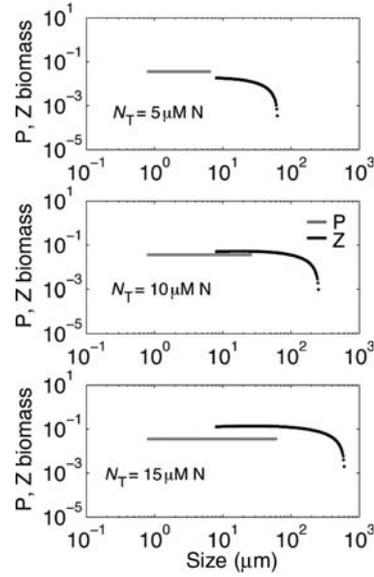


Fig. 4. Phytoplankton (gray) and zooplankton (black) biomass spectra for an ecosystem with $e_\mu = -0.75$, $e_g = -0.5$, $e_\delta = -0.5$ and $e_k = -0.5$, plotted for three different values of the total nutrient, N_T . For this combination of allometric scalings both the phytoplankton and zooplankton are predicted by criteria (20) and (23) to have predominantly zero slope to their biomass size spectra.

rate constants (rather than the exponents) will change the relative biomasses of the phytoplankton and zooplankton, while leaving the spectral slopes unchanged. The spectra still behave as before with increasing N_T : as the total nutrient in the system increases so does the abundance of large plankton.

While the interaction of the various biological processes can lead to complex changes in the planktonic size spectra, it is possible to make some gross generalizations about the effect of changing the size dependence of a given process on the structure of an ecosystem (Table I). The effects of some processes are relatively intuitive and consistent with other models: a decreasing grazing rate with size leads to greater phytoplankton biomass, and a more positive slope to the phytoplankton size spectrum. However, many of the results are less intuitive. For example, a decreasing grazing rate with size leads to a more positive slope of the zooplankton spectrum. That is, if larger zooplankton graze more slowly, their biomass will be higher. The phytoplankton biomass and spectral slope are unaffected by the parameters governing the phytoplankton rates, but are instead controlled by the zooplanktonic processes. Furthermore, a decreasing half-saturation constant for grazing (i.e. more effective grazing by larger zooplankton at low food concentrations) with size leads to more negative phytoplankton and zooplankton size spectra.

Table I: The effect of including a size-dependent process that decreases with size (negative allometric scaling exponent) on the structure of a planktonic ecosystem with $e_{\mu} = -0.75$

Process	Description	Phytoplankton		Zooplankton	
		Biomass	Spectral slope	Biomass	Spectral slope
k	Half-saturation constant for nutrient uptake	No effect	No effect	Decrease	More positive
λ	Phytoplankton respiration/DOM release/cell death	No effect	No effect	Decrease	More negative
g	Zooplankton grazing rate	Increase	More positive	Increase	More positive
γ	Assimilation coefficient	Increase	More positive	No effect	No effect
K	Half-saturation constant for grazing	Decrease	More negative	Decrease	More negative
δ	Zooplankton respiration/DOM release/ death	Decrease	More negative	No effect	No effect

DISCUSSION

We have developed an NPZ ecosystem model that allows arbitrary structure within the phytoplankton and zooplankton variables. For the purposes of this paper, we have explored structure consisting of allometrically scaled biological processes such as growth and grazing rates in an herbivore community. We derived analytical solutions to the model that has allowed us to identify potential constraints on the relationships among size-dependent physiological processes that will allow the assembly of realistic size-structured communities of plankton. Only a restricted set of allometric scalings will allow a given ecosystem structure.

While this model is relatively simple, including just three state variables with arbitrary size structure, it gives some insights into the complexities of the size structure of planktonic communities. The equilibrium solutions of the model reveal several attributes that are consistently seen in field-measured planktonic ecosystems: as nutrients are added to the system, biomass is added in increasingly large size classes of both phytoplankton and zooplankton. The constraint and control criteria that we have identified allow us to determine relationships among size-dependent biological processes that may determine the size spectral slopes observed in the field. Further, the aggregate spectrum—such as might be measured by a particle counter—can have interesting nonlinear lumps and structures as a consequence of the differing biomasses of phytoplankton and zooplankton in a given size class.

The diversity of the model ecosystem (i.e. the number of size classes occupied) is controlled by two processes: the total amount of nutrient in the system N_T and the grazing. As N_T increases, the potential diversity increases as more phytoplankton size classes can be supported. However, this diversity is only realized through the characteristics of the zooplankton. Without grazing, the ecosystem would consist of only the most competitive phytoplankton—the class with the smallest $N_{s_0}^*$. It is

only through the reduction in biomass of this class by the zooplankton that other, less competitive phytoplankton classes can grow. These species support additional zooplankton size classes, increasing the diversity of the system. Thus, the diversity of the ecosystem is the result of simultaneous bottom-up and top-down control: resources determine which classes *can* exist; predation determines which classes *do* exist.

Our model results suggest that there are many degrees of freedom underlying a given size spectrum of plankton. Without additional information, the shape and slope of the spectrum is not very informative about the underlying dynamics, as there are many mutually exclusive ways of generating any given spectrum. To constrain such analyses requires careful measurements of the rate processes of the ecosystem and, in particular, the size-dependencies of those processes.

It is possible that significant increases in our understanding of planktonic ecosystem dynamics can be made through careful, quantitative comparison of field data and size-structured models. However, a fundamental impediment is the lack of routinely gathered size-resolved data—particularly the size-dependence of rates, as opposed to standing stocks, abundances or biomasses. It is clear from our model that measurements of biomass spectral slopes, while presenting additional constraints on model performance, are not strong tests of models. There are too many mutually exclusive ways of achieving a given spectral slope or structure. We thus encourage the development of novel technologies that will help generate size-resolved data of biological rates. In particular, it will be beneficial to resolve the phytoplanktonic and zooplanktonic rates and biomasses separately, as our model suggests that there is no fundamental reason why the zooplankton and phytoplankton should show the same spectral slopes. Gathering such data will have a significant impact on our ability to test, reject and improve our models of planktonic ecosystem dynamics.

FUNDING

P.J.S.F. gratefully acknowledges support from the NSF-NOAA sponsored US GLOBEC program, and the NSF-sponsored CCE-LTER program. This is US GLOBEC contribution number 652. F.J.P. gratefully acknowledges financial support from NSERC.

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