**PARAMETERISING COMPETING ZOOPLANKTON FOR SURVIVAL IN
PLANKTON FUNCTIONAL TYPE MODELS**

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32 **ABSTRACT**

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34 Marine plankton ecosystems are an important component of biogeochemical cycling in the oceans.
35 Operational plankton functional type (PFT) models, that group plankton according to their
36 biogeochemical properties, are currently being developed to resolve biogenic gas exchange between
37 the ocean and atmosphere, and to model the lowest trophic levels in fisheries models. A
38 fundamental problem with these models is that PFTs often go extinct in computer simulations,
39 effectively removing the biogeochemical processes from the models. Cropp and Norbury (Journal
40 of Plankton Research, 31: 939-963) demonstrated that parameter combinations that allowed all
41 PFTs to stay extant for all time in stable, homogeneous environments were rare in a PFT model
42 with two competing phytoplankton and one zooplankton (NP_1P_2Z). In this paper, we examine the
43 dynamical properties of a generic predator-predator-prey PFT model, and apply the analysis
44 techniques developed by Cropp and Norbury to a simple example PFT model with one
45 phytoplankton and two zooplankton (NPZ_1Z_2) in order to explore its properties and parameter
46 space. We find that the properties of predator-predator-prey PFT systems are fundamentally
47 different from those of predator-prey-prey PFT systems. The likelihood of parameter combinations
48 for which all PFTs stay extant for all time in predator-prey-prey PFT systems depends critically on
49 the process formulations used, while the properties of co-existing zooplankton (as defined by their
50 parameter values) are quite different to those of co-existing phytoplankton.

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53 **INTRODUCTION**

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55 Plankton may have a significant influence on climate by drawing down carbon dioxide from the
56 atmosphere and sequestering it in the deep ocean, and by producing dimethylsulphide and other
57 volatile compounds that may affect cloud formation over the oceans. Plankton models that include
58 several plankton functional types (PFTs) are needed to resolve the role of plankton in
59 biogeochemical cycling, as different plankton utilise different elements in different ways (Le Quéré
60 et al. 2005). However, there has been significant debate over whether plankton ecosystems are
61 sufficiently well understood to place any reliance on the results of models that include multiple
62 PFTs (Anderson 2005, Le Quéré 2006).

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64 A particular problem with PFT models is that when the model is solved numerically (as all but the
 65 very simplest PFT models must be) it is common for PFTs to go extinct in the model simulations
 66 (Cropp and Norbury 2009a). This is an undesirable outcome, as each PFT in the model is there to
 67 facilitate a specific biogeochemical process, so it is a common practice to include computational
 68 ‘fixes’ in PFT computer models to prevent PFTs from going extinct. However, such practices mean
 69 that the PFT model that is solved on the computer is different from the PFT model that is described
 70 by the equations. Cropp and Norbury (2009a) observed that this disparity meant that the computed
 71 model solutions were not *bona fide* solutions of the model equations (see Terminology section
 72 below for the definition of our usage). They investigated the nature and ubiquity of the parameter
 73 sets required to ensure that the numerical solution of a model accurately reflected the model
 74 equations rather than a model with fewer PFTs. They considered the parameterisation of a model
 75 that resulted in all PFTs remaining extant for all time to be *bona fide*, and investigated the ubiquity
 76 of this behaviour in a simple PFT model. They observed that over 99% of parameter sets for a
 77 simple PFT model resulted in numerical solutions in which at least one PFT went extinct, and that
 78 consequently *bona fide* parameter sets were rare in the parameter space of these models. They
 79 subsequently developed some heuristics for the construction and parameterisation of simple PFT
 80 models with competing phytoplankton (pPFTs) to ensure *bona fide* properties. We reiterate that a
 81 *bona fide* PFT model is merely one for which the computed solution of a model, as defined by its
 82 equations and parameterisation, maintains all PFTs extant and is therefore a faithful representation
 83 of the model. The terminology does not imply that *bona fide* PFT models are better representations
 84 of real ecosystems.

85

86 The problem of maintaining PFTs extant in computer simulations is consistent with much
 87 ecological theory. The paradox of the plankton (Hutchinson 1961) articulates exactly this problem,
 88 that models of plankton systems typically only allow one functional type to exist per resource in
 89 constant homogeneous environments. Many solutions to the paradox have been proposed, and
 90 include internal chaotic dynamics (Huisman and Weissing 1999), external forcing (Ebenhoh 1988),
 91 spatiotemporal effects (Petrovskii et al. 2003) or interaction effects such as prey-switching by
 92 predators (Krivan 2003). These solutions have proved of little use in practice, as they often rely on
 93 quite special conditions (Schipperers et al. 2001). Similarly, the addition of internal processes such as
 94 intra-guild predation can lead to the presence of alternative stable states (Polis and Holt 1992,
 95 Mylius et al. 2001) that can facilitate competitive exclusion. This raises interesting questions of the

nexus between model formulations that allow multiple stable states, and the ubiquity of parameter sets that realise them as feasible states of the system.

The difficulty of maintaining competing PFTs extant in computer simulations, when the ecosystem models are coupled to physical models of the ocean that vary in space and time, suggests that much of the theory that has been developed for coexistence in variable environments provides little practical benefit in simulations of life in the oceans. We shall demonstrate, however, that some of the basic concepts that underpin processes such as invasion in varying environments are both relevant and able to be explicitly articulated in our analyses. In particular, the concept of the ‘long-term low-density growth rate’ that has been shown to be central to coexistence in a variety of deterministic and stochastic ecosystem models (Ellner 1984, Chesson 1994, Law and Morton 1996, Chesson 2000). This conceptual metric determines whether a species can successfully invade an established ecosystem and is analogous to the crucial eigenvalues that we shall show are readily and reliably obtained in analytic form for the systems we consider.

A tenet of invasion theory based on terrestrial plant communities is that positive long-term low-density growth rates are only ensured by stabilising mechanisms, and that these stabilising mechanisms are always based on the partitioning of a resource (Barot and Gignoux 2004). In terrestrial communities, the partitioning of a resource appears to be considered synonymous with variation in space and/or time (Barot and Gignoux 2004), and that the partitioning of space and time supersedes all other resources (Tilman and Pacala 1993, Chesson 2000). The applicability of these concepts to coexistence among plankton communities is moot, as these organisms live in environments that are relatively homogeneous over the relevant short space and time scales, and have limited ability to move through their environment. We shall therefore focus attention in this work on alternative ways in which organisms may have positive long-term low-density growth rates.

In this paper, we build on the results reported in Cropp and Norbury (2009a), hereafter referred to as CN09, and consider a model with multiple zooplankton functional types (zPFTs) that is a three-dimensional Kolmogorov system in a stable, homogeneous environment. Three-dimensional Kolmogorov systems include a very broad class of ecosystem models, and are merely any system that can be written in the following form

$$\begin{aligned}
 \mathcal{R}_1 &= f_1(u_1, u_2, u_3)u_1 \\
 \mathcal{R}_2 &= f_2(u_1, u_2, u_3)u_2 \cdot \\
 \mathcal{R}_3 &= f_3(u_1, u_2, u_3)u_3
 \end{aligned}
 \tag{1}$$

In the cases we will consider u_1 will represent a phytoplankton and u_2 and u_3 will represent zooplankton. It is debatable whether NPZ_1Z_2 systems are common in the real oceans; however, we observe that understanding the properties of subsystems can provide useful insights into the properties of more complex systems (Cropp and Norbury 2009b). They may also have direct application in so-called ‘end-to-end’ fisheries models, where multiple zPFTs (typically differentiated by size) are required to couple primary production to higher trophic levels in fisheries models (Rose et al. in press).

We will show that the functional forms used to represent mortality, and whether the zooplankton interaction includes omnivory or not, are crucial to the existence of an interior critical point, and also affect the ubiquity of parameter sets that produce *bona fide* PFT systems. We note heuristics that allow predator-predator-prey PFT models to be constructed that are *bona fide* PFT systems for all valid parameter sets; that are never *bona fide* PFT systems for any valid parameter sets; or have varying probability of being *bona fide* PFT systems.

METHOD

We choose the model and its parameters to ensure ecological realism under the conditions derived by Kolmogorov (1936) and explicated by May (1973) and others. We restrict our analysis to f_i that comply with Kolmogorov’s (1936) conditions as many ecosystem models in the contemporary literature have these properties (Huang and Zhu 2005). A more detailed discussion of three-dimensional Kolmogorov systems is provided in CN09.

As in CN09 we look at the particular case of a model that conserves the mass of limiting nutrient as many models applied in biological oceanography also have this property (Spitz et al. 2001, Franks 2002, Vallina et al. 2008). Conservation of mass implies that the total mass of inorganic nutrient (N) present at any time is given by:

$$N = N_T - u_1 - u_2 - u_3 \quad \Leftrightarrow \quad \dot{N} = -\dot{u}_1 - \dot{u}_2 - \dot{u}_3, \quad (2)$$

where N_T is a constant that gives the total effective nutrient in the system and the u_i are the concentrations of the PFTs measured in this currency. We note that conservation of mass is required for many biogeochemical models to be written as Kolmogorov systems, as the nutrient equation in these models typically cannot be written in Kolmogorov form. Conservation of mass causes N to become a ‘virtual’ variable; as shown in equation (2), it allows the $\dot{N}$ equation to be inferred from the other equations that are in Kolmogorov form.

We scale each state variable with respect to the total nutrient (i.e. u_i/N_T), which allows us to define an ecologically feasible ‘state space’ where $0 \leq u_1, u_2, u_3 \leq 1$. We consider the critical (equilibrium) points of this system, denoted by $\{u_1^*, u_2^*, u_3^*\}$ where $\dot{u}_i = f_i(u_i) = 0$ for all i . Implicit in the rationale for constructing plankton models with more than one functional type is the assumption that, in the absence of environmental factors, an interior critical point, with $u_1^*, u_2^*, u_3^* \neq 0$, both exists and is an important determinant of the dynamics of the system. Analogously to CN09, we enquire into the nature of these interior (predator-predator-prey) critical points in systems with one autotroph and two grazers, and how this might inform the development and calibration of more complex PFT models.

We first consider the dynamical properties of a generic three state variable Kolmogorov system (equation (1)) where the u_1 represents an autotroph (pPFT) upon which u_2 and u_3 (zPFTs) graze. The analysis of this generic system provides general results that apply to all such three variable Kolmogorov systems, irrespective of the process formulations (f_i) chosen to represent the interactions between the state variables, and independent of the parameter values used in the model.

We consider the critical points of the system, defined by $\dot{u}_i = 0$ for all i . In Kolmogorov systems, critical points may be obtained from the isoclines in two ways for each equation, when $f_i = 0$ or when $u_i = 0$. Each critical point in a three state variable system has three eigenvalues and three associated eigenvectors. These eigenvalues and eigenvectors describe the local (Lyapunov) stability of the system in the region of each of the critical points, and together form ‘signposts’ that control the dynamics of the system. Example isoclines, critical points and eigenvectors for a predator-

predator-prey system are shown in Fig. 1. Some eigenvectors have been omitted for clarity; none are shown for point D but these can be inferred from those shown for B and C. Eigenvectors that always have positive eigenvalues are shown pointing away from the critical point, those that always have negative eigenvalues are shown pointing towards the critical point, and the others have double-ended arrows. Fig. 1 shows the three-dimensional state space $(\mathbf{x} = f_i(u_1, u_2, u_3)u_i, i = 1, 2, 3)$ in which the isoclines are surfaces; where parts of the isoclines are hidden behind other isoclines they are shown by dotted lines. The dashed lines indicate the conservation of mass conditions for each face.

The NPZ_1Z_2 Model

We then consider a specific example of an NPZ_1Z_2 Kolmogorov system in order to examine the parameterisations of the system that result in *bona fide* PFT dynamics. The study system has conventional phytoplankton (P) growth on inorganic nutrient (N) balanced by zooplankton (Z_1, Z_2) grazing and linear or nonlinear mortality. The zPFTs may also include omnivory in which Z_2 predaes on Z_1 .

We note that there is little consensus over the appropriate forms of the process representations in PFT models (Flynn 2003, Mitra 2009). In this paper, we choose ‘simple’ f_i that are commonly used to allow, as far as possible, for closed form analytic expressions to be found for the critical points and their eigenvalues. Even in this simple model, explicit analytic evaluation is not always possible, and we are forced to develop numerical solutions for one interior value. Analytic expressions for the key properties of PFT systems allow us to understand and predict PFT dynamics rather than merely observe them. We shall present the results of the analysis of the NPZ_1Z_2 model, equivalent to our analysis of the generic Kolmogorov system, and use these results to explore the parameter space and associated dynamical properties of this simple system.

The example NPZ_1Z_2 system is written in a currency of inorganic nutrient, with all state variables expressed as concentrations of nutrient, as described by equations (3) - (5):

$$217 \quad \dot{P} = f_P P = \left[\frac{\mu N}{N + \kappa} - \frac{\varphi_1 Z_1}{1 + \varepsilon_1 P} - \frac{\varphi_2 Z_2}{1 + \varepsilon_2 P} - \sigma P^\alpha \right] P, \quad (3)$$

$$218 \quad \dot{Z}_1 = f_{Z_1} Z_1 = \left[\frac{\varphi_1 (1 - \psi_1) P}{1 + \varepsilon_1 P} - \frac{\phi Z_2}{1 + \varepsilon Z_1} - \sigma_1 Z_1^\gamma \right] Z_1, \quad (4)$$

$$219 \quad \dot{Z}_2 = f_{Z_2} Z_2 = \left[\frac{\varphi_2 (1 - \psi_2) P}{1 + \varepsilon_2 P} + \frac{\phi (1 - \psi) Z_1}{1 + \varepsilon Z_1} - \sigma_2 Z_2^\delta \right] Z_2. \quad (5)$$

220 We check our conservation of mass criterion as per equation (2) and see that

$$221 \quad \dot{N} = \left[\sigma_1 Z_1^\gamma + \frac{\varphi_1 \psi_1 P}{1 + \varepsilon_1 P} \right] Z_1 + \left[\sigma_2 Z_2^\delta + \frac{\varphi_2 \psi_2 P}{1 + \varepsilon_2 P} + \frac{\phi \psi Z_1}{1 + \varepsilon Z_1} \right] Z_2 - \left[\frac{\mu N}{N + \kappa} - \sigma P^\alpha \right] P. \quad (6)$$

222

223 We have chosen the forms of the f_i to allow for several functional forms of grazing, omnivory and
 224 mortality to be easily considered. Phytoplankton uptake of inorganic nutrient is fixed at the
 225 Michaelis-Menten functional form, but zooplankton grazing may take two forms. Setting $\varepsilon_1, \varepsilon_2, \phi = 0$
 226 in the zooplankton grazing terms allows us to represent Lotka-Volterra grazing, while Holling Type
 227 II grazing can be represented by setting $\varepsilon_1, \varepsilon_2, \phi \approx 1$. We allow $\varepsilon_1, \varepsilon_2, \phi$ to vary continuously to
 228 allow a graduation of forms, rather than switching between only two values. Omnivory of Z_2 on Z_1
 229 is allowed if $\phi \neq 0$, and is switched off if $\phi = 0$. Each of the PFT may have linear or nonlinear
 230 mortality; $\alpha, \gamma, \delta = 0$ imposes linear mortality on P, Z_1 and Z_2 respectively, while $\alpha, \gamma, \delta = 1$
 231 imposes nonlinear mortality.

232

233 There have been many functional forms proposed for nonlinear zooplankton mortality, and the
 234 impact of various forms on the dynamics of ecosystem models has been documented by several
 235 authors (Steele and Henderson 1992, Edwards and Yool 2000, Mitra 2009). We shall not
 236 investigate the effects of different nonlinear forms in this work, but shall instead demonstrate a
 237 fundamental difference in the importance of linear and nonlinear zooplankton mortality terms for
 238 the stability properties at the boundary critical points. Importantly, linear mortality terms appear as
 239 a constant in their f_i , while nonlinear mortality terms appear in their f_i as a function of Z such that

mortality term in the f_i goes to zero as Z goes to zero. We note that the latter is the case for all the nonlinear zooplankton mortality terms investigated by Mitra (2009), and we therefore observe that our use of quadratic zooplankton mortality, the simplest nonlinear function available, provides quite general insights.

Different model formulations were defined by the values of $\bar{\phi}$, α , γ and δ . We shall use codes such as [0101] to denote each of these formulations, where the values are ordered $[\bar{\phi}, \alpha, \gamma, \delta]$. These codes represent the actual values used in the model except for $\bar{\phi} = 1$ which indicates that $\bar{\phi} \neq 0$ but may take other values defined by the parameter space.

Parameter Space Search

The parameter space used in CN09 was adopted as the basis for the NPZ_1Z_2 model analysis and was modified slightly to reflect that this analysis considers competing grazers rather than competing autotrophs (Table 1). The values used in CN09 were derived from typical measured values (Fenchel 1982, Moloney et al. 1986, Slagstad and Stole-Hansen 1991, Hansen et al. 1996, Muller-Niklas and Herndl 1996, Gabric et al. 1999, Gabric et al. 2001) and were non-dimensionalised prior to use by scaling time by the maximum growth rate of P (μ) and concentrations by the total nutrient (N_T). As we will be considering the effect of varying parameter values on the model dynamics, it is essential that we scale the parameters so that the influence of each parameter is revealed unequivocally. As we will evaluate each parameter set sampled for validity (see Terminology section below for the definition of our usage) we have allowed the parameter space we search to be somewhat larger than usual; this will allow for differences in the magnitude of parameter values for different process formulations.

The parameter space was searched for each model formulation using a Monte Carlo method based on uniform parameter distributions from which 10^6 randomly selected parameter sets were sampled and evaluated for validity (see definition in Terminology). Each valid parameter set was then tested for the existence and stability of an internal predator-predator-prey critical point. The same criteria used to define validity and existence/stability in CN09 are applied to this model; a parameter set is valid if all boundary critical points are ecologically realistic, Lyapunov stability criteria are used to

determine the stability of critical points. Analytic expressions describing these criteria for this model are given in Table 2. The general derivation of these conditions is presented in the Results, and the explicit derivation related to the model described by equations (3) - (5) is presented in the Appendix. Finally, we examined the frequency distributions of the competition and omnivory parameters of the sets that resulted in *bona fide* PFT.

We note here that the results of the parameter search will be specific to the parameter space we have defined and to the explicit model formulations that we use. Although these are quite generic examples, in that they examine both saturating and non-saturating process functions, the results will change if the parameter space is changed or the process formulations are changed. The results of the parameter space search should therefore be considered as generic examples rather than canonical systems.

Terminology

We will be concerned with several properties of the parameter sets that we examine. We will use the same terminology as CN09 to discuss these properties, and now define the terminology that we shall use. We shall initially classify parameter sets according to:

- their validity, that is, whether all the critical points that Kolmogorov (1936) showed must exist in the feasible region of the state space for the system to be realistic do exist, and
- we further classify valid parameter sets according to the three classes of PFT systems that they define:
 - *Bona fide* PFT systems, in which all PFT stay extant for all time. These systems have an internal critical point that has a negative real eigenvalue, and a complex conjugate pair of eigenvalues that may have positive or negative real parts;
 - Pseudo-PFT systems, in which one or the other of the competing zooplankton goes extinct depending on the initial values used. These systems have an internal critical point that has a positive real eigenvalue, and a complex conjugate pair of eigenvalues that may have positive or negative real parts;
 - Non-PFT systems, in which one or the other of the competing zooplankton goes extinct irrespective of the initial values used, that is the same zooplankton always goes extinct for each parameter set. These systems do not have an interior critical point.

We use the term *bona fide* quite deliberately to describe models for which the computed simulation results are *bona fide* solutions of the model described by the equations; pseudo- and non-PFT systems have computed solutions that are solutions of models with one fewer PFTs than the model described by the equations. To ensure the best available computed solutions we used an adaptive step-size 4-5th order Runge-Kutta integration scheme with absolute and relative tolerances set to machine epsilon (10^{-14}) in all our integrations. *Bona fide* does not therefore equate to realistic, and in fact we will consider both realistic and unrealistic *bona fide* models in this work and discuss the distinction between them.

RESULTS

We initially present the results of the analysis of the generic Kolmogorov system: (equation (1)) where we define u_1 to be an autotroph and u_2 and u_3 to be its grazers. We present analytic expressions for the critical points and eigenvalues where possible, and present the generic properties of the state space described by the critical points, eigenvalues and eigenvectors graphically (Figure 1). We have labelled the critical points in Figure 1 and shall use these labels to identify the critical points and their eigenvalues in the following analysis. The values of the state variables at the critical points are denoted by the asterisk superscripts, and the critical points distinguished by their subscripts. The signs of the eigenvalues are shown where these are defined by the ecological properties of the system and always hold.

The results of this analysis are similar in many respects to the analysis of the Kolmogorov system in which u_1 and u_2 were autotrophs and u_3 was their grazer reported in CN09. The reader is therefore referred to CN09 for much of the detail, and only the differences will receive detailed treatment in this paper.

Origin Critical Point (O):

Every Kolmogorov system has a critical point at the origin (O in Fig. 1) where $u_i^* = 0$ (i.e. no life) and (usually) $f_i \neq 0$ for all i . The eigenvalues at the origin are:

$$\lambda_{0-1} = f_1|_O > 0, \quad (7)$$

$$\lambda_{0-2} = f_2|_O < 0, \quad (8)$$

$$\lambda_{0-3} = f_3|_O < 0, \quad (9)$$

where $f_i|_O$ means that the expression f_i is evaluated at the critical point O (i.e. using the values of the state variables at the critical point). The origin represents the state of the system where only inorganic nutrient exists. Near this point, autotrophs always grow and predators always die, and the point will therefore always be a saddle point. The unstable direction of the saddle (λ_{0-1}) is a result of the autotroph growing by consuming nutrient in isolation along its axis, while the stable directions (λ_{0-2} and λ_{0-3}) are those of the predators dying in the absence of prey along their axes.

Prey-only Critical Point (A):

Every model that complies with Kolmogorov's (1936) criteria will have an prey-only (autotroph) critical point in each of the predator-prey subsystems. In this case with one autotroph, the sole point, which is involved in both predator-prey subsystems, is defined by $u_1^* \neq 0, u_2^* = 0, u_3^* = 0$ (A) and is located where the $f_1 = 0$ isocline intersects the u_1 axis. The eigenvalues of this point are given by:

$$\lambda_{A-1} = \frac{\partial f_1}{\partial u_1} u_1|_A < 0, \quad (10)$$

$$\lambda_{A-2} = f_2|_A > 0, \quad (11)$$

$$\lambda_{A-3} = f_3|_A > 0. \quad (12)$$

The stable eigenvalue (λ_{A-1}) is given by the response of the blooming autotroph to increases in its own biomass ($\frac{\partial f_1}{\partial u_1}$) and is always negative, as autotroph growth rate reduces as nutrient becomes

less available. The other eigenvalues are obtained by evaluating the growth functions (f_i) of the zPFTs at the critical point. These reflect the grazing pressures applied by the predators (λ_{A-2} and λ_{A-3}). Systems that comply with Kolomogorov's criteria will always have λ_{A-2} and λ_{A-3} positive (destabilising) at this point. The directions of these eigenvalues will vary according to the nature of the f_i , but will always point into the interior of, and lie in the plane of, the (u_1, u_2) plane for λ_{A-2} or the (u_1, u_3) plane for λ_{A-3} .

Predator-Prey Critical Points (B, C):

Every sub-system that complies with Kolmogorov's criteria will have a predator-prey critical point. In the system defined by equation (1) these are defined by $u_1^* \neq 0, u_2^* \neq 0, u_3^* = 0$ for B and $u_1^* \neq 0, u_2^* = 0, u_3^* \neq 0$ for C, and are located where the $f_1 = 0$ isocline intersects the $f_2 = 0$ isocline in the (u_1, u_2) plane and where the $f_1 = 0$ isocline intersects the $f_3 = 0$ isocline in the (u_1, u_3) plane respectively. The eigenvalues of these critical points are given by:

$$2\lambda_{B-1,2} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_2}{\partial u_2} u_2 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 - \frac{\partial f_2}{\partial u_2} u_2 \right)^2 + 2 \frac{\partial f_1}{\partial u_2} \frac{\partial f_2}{\partial u_1} u_1 u_2} \Big|_B, \quad (13)$$

$$\lambda_{B-3} = f_3 \Big|_B, \quad (14)$$

for B, and by:

$$2\lambda_{C-1,3} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_3}{\partial u_3} u_3 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 - \frac{\partial f_3}{\partial u_3} u_3 \right)^2 + 2 \frac{\partial f_1}{\partial u_3} \frac{\partial f_3}{\partial u_1} u_1 u_3} \Big|_C, \quad (15)$$

$$\lambda_{C-2} = f_2 \Big|_C, \quad (16)$$

for C. Kolmogorov showed that in almost all cases $\lambda_{B-1,2}$ and $\lambda_{C-1,3}$ will be complex numbers, with positive or negative real parts, indicating that trajectories will either spiral into or away from the critical point. The exceptions to this general case occur if parameter values are varied so that the predator-prey critical point approaches the critical points at the extremes of the prey axis, the origin

and the prey-only critical points. These points are both saddles, and as the predator-prey point closes on them, just prior to colliding with them and undergoing a transcritical bifurcation it must lose its complex eigenvalues and acquire real eigenvalues of opposite sign, so that at the point of collision the eigenvalues of both points are identical.

Spiral curves then lie in the (u_1, u_2) or (u_1, u_3) planes and start or end at B or C. $\lambda_{B-1,2}$ and $\lambda_{C-1,3}$ therefore control the dynamics in the (u_1, u_2) and (u_1, u_3) planes respectively. The dynamics of the system in the direction orthogonal to these planes is controlled by the eigenvalues λ_{B-3} and λ_{C-2} . These eigenvalues are of critical importance to PFT modellers as they determine whether a system will maintain all PFTs extant during simulations. These eigenvalues are associated with eigenvectors that are orthogonal to the (u_1, u_2) and (u_1, u_3) planes respectively, with magnitudes given by the f_i of the competing grazer evaluated at the critical point. These eigenvalues are always real numbers, their direction is known, and analytic expressions for them are easily obtained from inspection of the model equations. The signs of these eigenvalues determine whether an interior predator-predator-prey critical point (D), fundamental to the construction of a *bona fide* PFT model, exists and is stable.

Predator-Predator-Prey Critical Point (D):

As noted above, the system may have a critical point D defined by $u_1^* \neq 0, u_2^* \neq 0, u_3^* \neq 0$ located where the $f_1 = 0$, $f_2 = 0$ and $f_3 = 0$ isoclines all intersect in the (u_1, u_2, u_3) volume. In this case the isoclines are surfaces; typical isocline surfaces are shown in Fig. 1. The existence of this point is not assured by Kolmogorov's criteria as it is a predator-predator-prey system rather than a predator-prey system. However, systems that have critical points at B and C will for some parameter sets have a predator-predator-prey critical point D that lies in the interior of the state space.

The eigenvalues of the critical point D are generally intricate in analytic form, and difficult to interpret, as they involve the roots of a cubic equation derived from the community matrix, and hence it is usually more efficacious to obtain them numerically. Generally, the spiral dynamics enforced on the (u_1, u_2) and (u_1, u_3) planes by the Kolmogorov criteria are observed throughout the

interior of the state space. We therefore expect that the critical point D will have one pair of complex conjugate eigenvalues that control its spiral behaviour in the $(P, \xi_1 Z_1 + \xi_2 Z_2)$ ‘plane’, where ξ_1 and ξ_2 are constants defining a ray on the (Z_1, Z_2) face. The third eigenvalue must be a real number, and its sign will control the outcome of the competition between the two grazers. The real eigenvalue will therefore either repel trajectories away from D toward the predator-prey critical points on the faces (if positive) or attract them away from the faces toward the interior predator-predator-prey critical point D (if negative). This eigenvalue is therefore analogous to the long-term low-density growth rate for each competing species that is a central tenet of invasion theory in terrestrial plant communities.

The global dynamics of the state space must be consistent with the above local information. Therefore, if both predator-prey boundary critical points have positive real eigenvalues, consistency of the vector field requires the existence of an interior critical point with negative real eigenvalues. This will be a stable coexistence point, as the dynamics in the orthogonal direction, determined by the sign of the real parts of the complex conjugate eigenvalue pair of this point, is irrelevant, as shown in CN09. The relevant stability properties of the boundary points are the instability due to positive real eigenvalues pointing to the interior of the state space. Instability in the predator-prey plane (i.e. whether they have stable spirals or limit cycles in the absence of the other predator) does not affect coexistence.

Similar arguments apply for predator-prey boundary critical points that both have negative real eigenvalues, and for those points that have real eigenvalues of opposite sign. If the critical points on the faces B and C both have negative real eigenvalues associated with the eigenvectors that are orthogonal to the faces, the interior critical point D must have positive real eigenvalues, and consequently not be a coexistence point. In the case where B and C have real eigenvalues of opposite signs, D cannot exist in the interior of the state space. In this circumstance, the point is located exterior to the ecologically feasible state space, and it and its eigenvalues do not influence the dynamics of the system.

Ubiquity of valid parameter sets

The results of the parameter searches for each of the functional forms are summarised in Table 3 and reveal several interesting properties of the NPZ_1Z_2 system. The first is that including quadratic

forms for mortality for both zooplankton and phytoplankton generally increases the number of valid parameter sets found. The NPZ_1Z_2 system with quadratic mortality for both zooplankton and the phytoplankton functional types had 83% of randomly selected parameter sets that were valid, whereas only 61% of parameter sets were valid in the equivalent systems with all linear mortality terms. The percentage of valid parameter sets increased approximately linearly with the number of PFTs that had nonlinear mortality, indicating that the inclusion of nonlinear mortality is indeed a useful tool in building *bona fide* PFT models.

The distributions of the competition eigenvalues of the valid parameter sets other than [0000], [0100], [0011] and [0111] (see below) are shown in Figs 2-4. In these figures, eigenvalue combinations that result in *bona fide* PFT systems are located in the front quadrant ($\lambda_{B-3} > 0$ and $\lambda_{C-2} > 0$), pseudo-PFT systems in the rear quadrant ($\lambda_{B-3} < 0$ and $\lambda_{C-2} < 0$), and non-PFT systems in the left and right quadrants. A characteristic of all these distributions is that they are all asymmetric, with the asymmetry determined by which zPFT has nonlinear mortality and/or whether omnivory of Z_2 on Z_1 is allowed. Table 3 indicates that pseudo-PFT parameter sets, for which the initial conditions determine which zPFT will ultimately survive, are the least common type of PFT system for NPZ_1Z_2 systems. No pseudo-PFT parameter sets were observed for systems without zooplankton omnivory, or for systems for which the omnivore had nonlinear mortality. Pseudo-PFT systems were observed only for less than 6% of systems that had an omnivore with linear mortality.

Classes of *bona fide* PFT parameter sets

Our results reveal that the *bona fide* NPZ_1Z_2 systems may be classified into several subtypes characterised by the functional forms and/or trophic structures of the models. The analysis showed that the sixteen model formulations could be classified according to the probability of finding parameter sets that resulted in *bona fide* dynamics:

- always *bona fide* PFT systems: no omnivory and both zPFT have nonlinear mortality ([0011] and [0111])
- common (high probability) *bona fide* PFT systems: no omnivory and one zPFT has linear mortality and the other nonlinear mortality ([0001], [0010], [0101] and [0110])

- intermediate (moderate probability) *bona fide* PFT systems: omnivory and the top predator has linear mortality ([1000], [1010], [1100] and [1110])
- rare (low probability) *bona fide* PFT systems: omnivory and the top predator has nonlinear mortality ([1001], [1011], [1101] and [1111])
- never *bona fide* PFT systems: no omnivory and both zPFT have linear mortality ([0000] and [0100])

This categorisation, based on probabilities of finding *bona fide* parameter sets, will be used in the figures and discussion of the properties of the models as other similarities are also captured by this classification scheme.

Systems that always or never have co-existing zPFTs ([0000], [0100], [0011] and [0111]) have very uninteresting properties in the context of this paper, with their eigenvalues all symmetrically grouped near zero and uniform parameter distributions, so we somewhat pragmatically group these together as uninteresting systems and ignore them in the following analysis. We now consider only the properties of the other three types of system.

Properties of common *bona fide* PFT systems

Common *bona fide* PFT systems have zooplankton that are not omnivorous and have one zPFT with linear mortality and one zPFT with nonlinear mortality. The valid parameters for these systems have asymmetric distributions of the competition eigenvalues λ_{B-3} and λ_{C-2} (Fig 2) with the asymmetry being determined by which of the zPFT has nonlinear mortality. The zPFT with nonlinear mortality has the competition eigenvalue of its predator-prey critical point negative, indicating that it will send the competing zPFT extinct. Therefore, in the approximately 80% of these valid parameter sets that produce non-PFT systems, the zPFT with nonlinear mortality will dominate and the zPFT with linear mortality will become extinct. However, approximately 20% of these parameter sets will produce *bona fide* PFT systems, in which the other attributes of the zPFT with linear mortality compensate for the competitive advantage endowed upon the competing zPFT by nonlinear mortality and allow both PFTs to coexist.

The attributes of the competing zooplankton that allow coexistence in common *bona fide* PFT systems, as described by the parameter distributions, are shown in Fig 5. In order to coexist the

zPFT with nonlinear mortality (Z_{NL}) must exert very light grazing pressure on the pPFT (ϕ_{NL} small) and be an inefficient converter of food to biomass (ψ_{NL} large), while the zPFT with linear mortality (Z_L) exerts moderate to heavy grazing pressure (ϕ_L moderate to large) and efficiently converts food to biomass (ψ_L small). Similarly, Z_L must have very low mortality coefficient (σ_L) while Z_{NL} has a moderate to large coefficient (σ_{NL}). The ‘half-saturation’ constants (ε_1 and ε_2) have little influence on the coexistence of the zPFTs, suggesting that stable equilibria or stable limit cycles are equally likely.

Properties of intermediate *bona fide* PFT systems

Intermediate *bona fide* PFT systems have an omnivorous zPFT (Z_2) that has linear mortality. The valid parameters for these systems also have asymmetric distributions of the competition eigenvalues λ_{B-3} and λ_{C-2} (Fig 3) with the asymmetry being dominated by the omnivore. These systems have the most potential behaviours, with Table 3 revealing that 7-10% of valid parameter sets produce *bona fide* PFT systems, 1-6% produce pseudo-PFT systems and 85-90% produce non-PFT systems. Of the non-PFT systems, Fig 3 reveals that the Z_2 will send Z_1 extinct in most cases, but there are some parameter sets that allow Z_1 to send Z_2 extinct.

Comparison of the parameter distributions of these *bona fide* PFT systems (Fig 6) with Fig 5 reveals that the zooplankton attributes that allow coexistence in these systems are quite different from common *bona fide* PFT systems. The likelihood of coexistence in these systems is insensitive to the rate of Z_2 grazing on phytoplankton (ϕ_2), but is increased if Z_1 grazes heavily on the pPFT (ϕ_1 moderate to large). Low to moderate coefficients for Z_1 respiration (ψ_1) again maximise the potential for coexistence, which is more likely if Z_2 inefficiently converts food to biomass, but in contrast to common systems, there is an optimal maximum value for Z_2 respiration of about $\psi_2 = 0.9$.

The distribution of parameter values for the Z_2 mortality coefficient (σ_2) also has an optimum value in these systems, but is relatively insensitive to the Z_1 mortality coefficient (σ_1). In this case,

$\sigma_2 \approx 0.25$ appears to provide the optimum likelihood of coexistence (the actual value of σ_2 used in model simulations will depend on the values of the pPFT growth parameters, as we have used non-dimensional parameters in our analysis). Again, the ‘half-saturation’ constants for zPFT grazing on the pPFT (ε_1 and ε_2) have little influence on the coexistence of the zPFTs.

Properties of rare *bona fide* PFT systems

Rare *bona fide* PFT systems have an omnivorous zPFT (Z_2) that has nonlinear mortality. The valid parameters for these systems have strongly asymmetric distributions of the competition eigenvalues λ_{B-3} and λ_{C-2} (Fig 4) with the system either supporting both zPFTs (less than 5% of valid parameter sets) or in 95% of cases Z_2 drives Z_1 to extinction. No parameter sets were found such that these systems exhibited pseudo-PFT dynamics where the initial conditions determined which zPFT went extinct.

The distributions of the parameters of these systems (Fig 7) reveal similar heuristics to those of common *bona fide* PFT systems, with very similar distributions of grazing pressures (φ_1, φ_2) and assimilation efficiencies (ψ_1, ψ_2). These parameter distributions indicate that the omnivorous zPFT needs to be a ‘lazy’ and inefficient predator for the other zPFT to survive. Similarly, coexistence is more likely if the prey zPFT is a voracious grazer and converts food to biomass efficiently. The distribution of mortality parameters is more similar to that of intermediate *bona fide* PFT systems, in that coexistence is essentially determined by the omnivore’s mortality coefficient and is insensitive to the prey zPFT’s mortality rate. This relationship is different from that observed for intermediate systems, as the likelihood of coexistence appears to increase linearly with the omnivore’s mortality coefficient.

DISCUSSION

The results of the analysis of the NPZ_1Z_2 system in this paper are broadly consistent with the results of the analysis of the NP_1P_2Z system discussed in CN09 in that:

- *Bona fide* PFT parameter sets are rare in parameter space: less than 10% of valid parameter sets produced *bona fide* dynamics in omnivorous systems; if omnivory was prohibited, approximately 20% of valid parameter sets produced *bona fide* dynamics. This is compared to 0.6% for the NP_1P_2Z system analysed in CN09.
- *Bona fide* PFT parameter sets are distributed throughout parameter space for many systems. Generally, *bona fide* parameter sets are more common in some regions of parameter space than others, but depending on the process formulations (f_i) used, some regions of parameter space are highly unlikely to produce *bona fide* PFT systems.
- PFT models require finely tuned parameter sets in order to keep all functional types extant.

We reiterate that in drawing these conclusions we have not considered systems that always have an internal critical point ([0011] and [0111]) and those that never have an internal critical point ([0000] and [0100]). These systems all have uniform parameter distributions that do not contribute to our analysis.

The analyses of CN09 and this paper have revealed that NP_1P_2Z and NPZ_1Z_2 systems have quite different likelihoods of parameter sets that result in pseudo-PFT systems, where the winner of competition between functional types is determined by the initial conditions. CN09 found that about 7% of valid parameter sets resulted in pseudo-PFT dynamics, whereas this analysis found many systems for which these dynamics appear not possible. Of the 16 model formulations examined, pseudo-PFT dynamics were only found in four systems; of these systems, less than 6% of valid parameter sets produced pseudo-PFT systems. These systems all included omnivory where the omnivorous zPFT had linear mortality.

The additional insights that analysis of the NPZ_1Z_2 systems provides over the analysis of the NP_1P_2Z system of CN09 are that omnivory and mortality are important contributors to the likelihood of finding *bona fide* PFT parameter sets where competing zPFTs can coexist indefinitely. This is consistent with other studies that have observed the importance of these factors for the dynamics and stability of food web models (Steele and Henderson 1992, Edwards and Yool 2000, Emmerson and Yearsley 2004).

Symmetry

The analysis of the NPZ_1Z_2 model in this paper has noted similarities with the analysis of the NP_1P_2Z model reported in CN09. However, the models differ quite fundamentally in their symmetry properties. The NP_1P_2Z model analysed in CN09 had a symmetric trophic topology, and the frequency distributions of the competition eigenvalues (Fig 7 in CN09) and the competition parameters of the *bona fide* parameter sets (Fig 9 in CN09) were also symmetric. While rare, the *bona fide* parameters were distributed ubiquitously throughout the parameter space, with no regions of the space having zero density of *bona fide* parameters.

The analysis of the NPZ_1Z_2 system in this paper suggests that, in contrast to systems with multiple autotrophs, symmetric trophic topologies are rare in systems with multiple grazers that exist in constant, homogeneous environments. The purely symmetric systems ([0000], [0011], [0100] and [0111]) could never have, or always had, stable interior critical points for all valid parameter sets. The asymmetry of *bona fide* NPZ_1Z_2 systems is evident throughout the distributions of the eigenvalues (Figs 2-4) and most of the competition parameters (Figs 5-7). In systems that do not have omnivory, the asymmetry is driven by the form of the zPFT mortality terms, whereas in systems that include omnivory the asymmetry is driven by the direction of the omnivory, but its effects may be modified by the form of the zPFT mortality terms. Further, in contrast to the competition parameter distributions of the NP_1P_2Z model reported in CN09 there are substantial regions of the competition parameter space where the density of *bona fide* parameter sets falls to zero. This is particularly evident for the mortality parameters (σ_1 and σ_2) and the assimilation efficiency parameters (ψ_1 and ψ_2) in systems without omnivory (Fig 5) and in the systems with omnivory in which the top predator has nonlinear mortality (Fig 7). The distributions are less strongly asymmetric in systems that have omnivory in which the prey zPFT has nonlinear mortality and the predator zPFT has linear mortality (Fig 6). The parameter distributions of these systems reveal optimal parameter combinations driven by trade-offs between the competitive advantages provided to the prey zPFT by nonlinear mortality and those provided to the predator zPFT by omnivory.

Omnivory and mortality

While once Gause's (1934) 'competitive exclusion principle' was considered to be the norm, recent workers have suggested that attributes such as density-dependent mortality can prevent competitive exclusion (Ruan et al. 2007). The form that such density-dependent mortality should take is, however, a matter of debate (Edwards and Brindley 1999, Edwards and Yool 2000, Edwards and Bees 2001, Mitra 2009). Ruan et al (2007) considered competing predators without omnivory where the grazers had Holling Type II grazing interactions (equivalent in our model to $\phi = 0$ and $\varepsilon_1, \varepsilon_2 \neq 0$) and concluded that the use of a density-dependant (in fact quadratic) mortality term for one competitor 'not only ensures the survival of itself, but also guarantees the existence of the other competitor, which would otherwise be out-competed'. Ruan et al. (2007) considered only the cases for which the internal predator-predator-prey critical point existed, and determined conditions for its stability. In the parlance of this paper, they examined the influence of nonlinear mortality on the stability of the interior critical point and concluded that systems with nonlinear mortality could not have pseudo-PFT parameter sets. Our analysis (of models with quite different functional forms) agrees with their conclusion; when one or other zPFT in our NPZ_1Z_2 system without omnivory had nonlinear mortality we did not find any parameter sets that resulted in pseudo-PFT systems, suggesting that this may be a quite general property of PFT systems.

The role of omnivory in maintaining competing species extant in food web models has also received recent attention, with Vandermeer (2006) concluding that omnivory may be stabilizing or destabilising (where they use 'stable' to mean the persistence of the competing species), depending on the structure of the food web. Our results are consistent with Vandemeer's conclusions; if omnivory is added to model structures in which one or both zPFTs have nonlinear mortality ([0001], [0010], [0011], [0101], [0110] or [0111]), the addition of omnivory is 'destabilising'. In these cases, the addition of omnivory reduces the likelihood of finding *bona fide* parameter sets from around 20% (or 100% in the cases of [0011] and [0111]) to 3-10%. Conversely, the addition of omnivory to systems that are unstable, in that competitors cannot coexist ([0000] and [0100]), 'stabilises' the systems, with the likelihood of finding *bona fide* parameter sets increasing from zero to around 7%.

Interaction strengths

Our *bona fide* systems reveal a skewed distribution of interaction strengths (parameter values and fluxes) toward weaker interactions, and we note that this appears a common property of stable high-

dimension ecosystem models. This property was observed by McCann et al (1998) in a study of six food-web models, and appears common to stable food webs with omnivores in particular (Namba et al. 2008). For example Emmerson and Yearsley (2004) examined randomly generated Lotka-Volterra systems and concluded that species were more likely to coexist in omnivorous food webs if the omnivorous interactions were weak. Similarly, McCann and Hastings (1997) noted that relatively strong omnivory could cause a three-species food web model to lose its interior critical point.

Weak interactions, however, generally result in food webs that are slow to recover from perturbation (Emmerson and Yearsley 2004), and that may be less resistant to species loss (Borvall et al. 2000). This presents what may be an interesting conundrum, as ecological parameter spaces are poorly constrained, and modellers generally have little option but to use parameter sets that ‘best’ reproduce observed data. The paucity of *bona fide* parameter sets in the regions of parameter space that produce high-interaction strength models, and the significant computational demands associated with parameterising even quite modestly complex PFT models, suggest that such ‘best-fit’ approaches will be biased toward systems with low interaction strengths. While these regions of parameter space may produce *bona fide* PFT systems that do a reasonable job of reproducing observed data, there is some reason to question whether these regions are representative of the ecosystems that exist in nature.

Unfortunately, unlike modellers of physical systems, ecosystem modellers as yet have little overarching theory to guide them in parameterising models (Hood et al. 2007). The consideration of theories that shape ecosystem adaptation was perhaps initiated in the contemporary era by Lotka (1922), who suggested that natural selection would operate, within the constraints of the environment and the potential of the organisms, to maximise the energy flux through an ecosystem. Odum (1983) elaborated this concept into the ‘maximum power principle’ and similarly suggested that ecosystems would maximise the flow of useful energy, while Schneider (1988) proposed a theory of maximum entropy production. Recently, Kleidon (2004, 2009) has extended the concept of maximum entropy production to the Earth system.

Cropp and Gabric (2002) synthesised these, and related concepts of maximum exergy (Jorgensen 1992) and maximum ascendancy (Ulanowicz 1980), with ecological considerations such as maximum production per unit biomass (Lotka 1922, Odum and Pinkerton 1955) and resilience (DeAngelis 1992) into ecologically-defined ‘thermodynamic imperatives’ and simulated the effect

of these imperatives on the evolution of the biotic constituents of a simple ecosystem model. They discovered that the outcomes produced by these imperatives were consistent, and that the parameter set that maximised the resilience of the system also optimised the other imperatives. Most importantly in the context of this paper, these parameter sets also maximised the interaction strengths. Laws (2003) has since demonstrated the efficacy of using this maximum resilience approach for fitting ecosystem models to data, suggesting that real ecosystems may have parameter sets that result in resilient systems with large interaction strengths.

Our results suggest that unsophisticated searches of parameter space looking merely for parameter sets that allow the models to reproduce observed data with some ‘acceptable’ level of veracity may not be the most useful approach. Such searches are more likely to be successful in regions of parameter space that result in PFT systems with low interaction strengths because *bona fide* parameter sets are more abundant there. Conversely, parameter sets that generate high interaction strengths are sparse in the parameter space, but satisfy broader theoretical concepts of the properties of ecosystems. Parameterisation approaches that simultaneously maximise interaction strengths and minimise the discrepancy between observations and model predictions are likely to produce better models than simple approaches that seek only to mimic data. The more sophisticated approach is likely to be most effective in high latitude regions of the ocean that function in accordance with Sverdrup’s (1953) criteria for bloom development. In these regions, ecosystem dynamics closely track physical forcings such as irradiance and temperature, suggesting that the ecosystems are highly resilient (Gabric et al. 2003).

CONCLUSIONS

The analysis of this predator-predator-prey (NPZ_1Z_2) system again emphasises the great advantage of Kolmogorov systems that analytic expressions for the eigenvalues that control the ability of a PFT to invade and/or coexist in an ecosystem may be obtained directly from inspection of the governing equations. We recall that these eigenvalues are explicit representations of the long-term low-density growth rates that are central to invasion theory developed from terrestrial plant communities.

This work also provides some useful heuristics to guide biogeochemical modellers in the construction and parameterisation of PFT models. These heuristics extend the heuristics for the predator-prey-prey (NP_1P_2Z) model reported in CN09 (Cropp and Norbury 2009a) and include:

- In contrast to symmetric prey-prey-predator systems, that contribute insights in to the properties of competing prey in homogenous, stable environments, symmetric predator-predator-prey models can apparently contribute little.
- Consequently, distributions of competition parameters that lead to *bona fide* dynamics in predator-predator-prey models are strongly asymmetric. Unlike predator-prey-prey systems, there are likely to be regions of parameter space where the likelihood of finding *bona fide* parameter sets falls to zero.
- The use of nonlinear mortality terms for predators makes them ‘super-competitors’ that are very resistant to extinction. Systems with multiple predators that include omnivory are therefore more likely to have *bona fide* dynamics if the top predator has linear mortality and their competitor/prey has nonlinear mortality.
- Distributions of interaction strengths of *bone fide* PFT systems are skewed towards weak interactions, suggesting that calibration exercises to find parameter sets that mimic observations are more likely to produce models with this attribute. However, theoretical considerations suggest that modellers should search for such parameter sets in the regions of parameter space where interactions are strong, but *bone fide* parameter sets are rare.

We also note that whereas the consideration of competition in terrestrial plant communities has resulted in an emphasis on the role of spatial and temporal variation in ensuring coexistence, our analysis shows that coexistence in competitive plankton communities is possible in constant, homogeneous environments.

It would appear from a comment made by a reviewer of CN09 that the initial response of PFT modellers to the difficulties of parameterising PFT models, that we have explicated in CN09 and again in this paper, has been to include computational ‘fixes’ in their code that prevent PFTs from going extinct in simulations. This increases the probability of finding useful parameter sets, making such models much easier to parameterise. However, we suggest that such fixes inevitably lead to flawed models, that in particular are unable to predict changes in community structure and species extinctions in the plankton that may already be happening (Montes-Hugo et al. 2009).

We hope that the heuristics we have presented here, in conjunction with those presented in CN09, will prove useful in the construction and parameterisation of particularly those plankton biogeochemical models currently being developed to model the contribution of ocean biota to climate, and alleviate the temptation of such ‘fixes’. In particular, we note that the use of eigenvalue properties to search a model’s parameter space can provide significant benefits in terms of computational load, and reductions of CPU time of six orders of magnitude are not unrealistic.

Finally, we observe that while the heuristics presented in this paper may be combined to guide the development of higher-dimension PFT models to ensure *bona fide* dynamics, more behaviours are possible in the higher-dimension models. Our analyses therefore need to be extended to incorporate these additional potential behaviours, and we hope to present these analyses in forthcoming work.

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FIGURE LEGENDS

Figure 1. Generic diagram of one autotroph and two grazer isoclines showing intersection of the grazer isoclines ($f_2 = 0$ and $f_3 = 0$) with the autotroph isocline ($f_1 = 0$) to give an internal critical point (D). The competition eigenvalues (equivalent to the competing species long-term low-density growth rates) that are crucial to coexistence are shown as the black double-ended arrows at critical points B and C.

Figure 2. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for common systems. Recall that we use codes such as [0101] to denote the values of $[\phi, \alpha, \gamma, \delta]$. Eigenvalue combinations that result in *bona fide* PFT systems are located in the front quadrant ($\lambda_{B-3} > 0$ and $\lambda_{C-2} > 0$), pseudo-PFT systems in the rear quadrant ($\lambda_{B-3} < 0$ and $\lambda_{C-2} < 0$), and non-PFT systems in the left and right quadrants.

Figure 3. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for intermediate systems. Details as for Fig 2.

Figure 4. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for rare systems. Details as for Fig 2.

Figure 5. Typical frequency distributions of the four competition zPFT parameter pairs for common systems. The parameter pairs are grazing (ϕ_1, ϕ_2) (a), half-saturation ($\varepsilon_1, \varepsilon_2$) (b), mortality (σ_1, σ_2) (c) and assimilation efficiency (ψ_1, ψ_2) (d). Distributions shown are for system [0001]; the other common systems ([0010], [0101] and [0110]) have the same distributions.

Figure 6. Typical frequency distributions of the four competition zPFT parameter pairs for intermediate systems. Panels as for Fig 5. Distributions shown are for system [1000]; the other intermediate systems ([1010], [1100] and [1110]) have the same distributions.

Figure 7. Typical frequency distributions of the four competition zPFT parameter pairs for rare systems. Panels as for Fig 5. Distributions shown are for system [1001]; the other rare systems ([1011], [1101] and [1111]) have the same distributions.

TABLES

Table 1: Parameter bounds used to constrain the parameter searches for the NPZ_1Z_2 model. These values are identical to those used in CN09 and have been non-dimensionalised from measured values.

PAR	PROCESS	VALUE
μ	Maximum rate of N uptake by P_1	0.25 – 1.70
κ	Half-saturation constant for P_1 uptake of N	0.00 – 1.00
$\phi_1, \phi_2, \tilde{\phi}$	Z_1 or Z_2 grazing rate (per ind) on Z_1 and/or P	0.75 – 9.00
$\varepsilon_1, \varepsilon_1, \tilde{\varepsilon}$	Half-saturation constant for Z_1 or Z_2 uptake of Z_1 and/or P	0.00 – 2.00
$\sigma, \sigma_1, \sigma_2$	P, Z_1 or Z_2 specific mortality rate	0.00 – 0.50
α, γ, δ	P, Z_1 or Z_2 mortality exponents	0 or 1
$\psi_1, \psi_2, \tilde{\psi}$	Proportion of P or Z_1 uptake excreted by Z_1 or Z_2	0.01 – 0.99

Table 2: Criteria for classification of parameter sets for the NPZ_1Z_2 system.

CRITICAL PT	CRITERION	METRIC
<u>Validity</u>		
A	$0 < P_A^* < 1$	$0 < \frac{\mu - \sigma(1 + \kappa)}{\mu - \sigma} < 1, \quad (\alpha = 0)$
		$0 < \frac{\mu + \sigma(1 + \kappa) \pm \sqrt{[\mu + \sigma(1 + \kappa)]^2 - 4\mu\sigma}}{2\sigma} < 1, \quad (\alpha = 1)$
B ¹	$0 < P_B^* < 1$	$0 < \frac{\sigma_1 Z_{1B}^{*\gamma}}{\varphi_1(1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1B}^{*\gamma}} < 1$
	$0 < Z_{1B}^* < 1$	$0 < \left(\frac{1 + \varepsilon_1 P_B^*}{\varphi_1(N_B^* + \kappa)} \right) \left[\sigma_1(N_B^* + \kappa) P_{1B}^{*\alpha} - \mu N_B^* \right] < 1$
C ²	$0 < P_C^* < 1$	$0 < \frac{\sigma_2 Z_{2C}^{*\gamma}}{\varphi_2(1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2C}^{*\gamma}} < 1$
	$0 < Z_{2C}^* < 1$	$0 < \left(\frac{1 + \varepsilon_2 P_C^*}{\varphi_2(N_C^* + \kappa)} \right) \left[\sigma_2(N_C^* + \kappa) P_{2C}^{*\alpha} - \mu N_C^* \right] < 1$
<u>Bona fide</u>		
B	$\lambda_{B-3} = f_{Z_2} \big _B > 0$	$\frac{\varphi_2(1 - \psi_2)P_B^*}{1 + \varepsilon_2 P_B^*} + \frac{\phi(1 - \psi)Z_{1B}^*}{1 + \varepsilon Z_{1B}^*} - \sigma_2 Z_{2B}^{*\delta} > 0$
C	$\lambda_{C-2} = f_{Z_1} \big _C > 0$	$\frac{\varphi_1(1 - \psi_1)P_C^*}{1 + \varepsilon_1 P_C^*} - \frac{\phi Z_{2C}^*}{1 + \varepsilon Z_{1C}^*} - \sigma_1 Z_{1C}^{*\gamma} > 0$

¹ N_B^* is given by equation (29) or (30)² N_C^* is given by equation (33) or (34)

Table 3: Results of searches of the parameter space for the NPZ_1Z_2 model. One million randomly selected parameter sets were evaluated for validity and for the existence and stability of an interior point for each model formulation.

PARAMETER				VALID		<i>Bona fide</i> PFT		Pseudo-PFT		Non-PFT	
$\tilde{\phi}$	α	γ	δ	No	%	No	%	No	%	No	%
0	0	0	0	609,584	61	0	0	0	0	609,584	100
0	0	0	1	664,287	66	124,835	18.8	0	0	539,452	81.2
0	0	1	0	663,559	66	124,145	18.7	0	0	539,414	81.3
0	0	1	1	768,969	77	768,969	100	0	0	0	0
0	1	0	0	704,617	70	0	0	0	0	704,617	100
0	1	0	1	740,382	74	169,296	22.9	0	0	571,086	77.1
0	1	1	0	739,888	74	169,798	22.9	0	0	570,090	77.1
0	1	1	1	830,548	83	830,548	100	0	0	0	0
$\neq 0$	0	0	0	609,689	61	42,829	7.0	9,915	1.6	556,945	91.4
$\neq 0$	0	0	1	663,204	66	21,917	3.3	0	0	641,287	96.7
$\neq 0$	0	1	0	663,801	66	58,727	8.8	39,329	5.9	565,745	85.3
$\neq 0$	0	1	1	768,747	77	37,152	4.8	0	0	731,595	95.2
$\neq 0$	1	0	0	705,172	71	53,088	7.5	8,802	1.2	643,283	91.3
$\neq 0$	1	0	1	740,108	74	27,505	3.7	0	0	712,603	96.3
$\neq 0$	1	1	0	740,489	74	70,720	9.5	30,638	4.1	639,131	86.4
$\neq 0$	1	1	1	830,522	83	40,467	4.9	0	0	790,055	95

NOTE: As the value of $\tilde{\phi}$ has no effect on the validity of each parameter set, comparison of equivalent functional forms for $\phi = 0$ and $\phi \neq 0$ provides an indication of the variation in the results associated with the random selection of the parameter sets. This is of the order of less than 0.1%. However, we also note that the percentages of the different solutions for each model will change if the parameter space is changed; the search results should therefore be considered indicative of the types of properties we can expect from generic formulations. Examination of different specific formulations would also change the percentages.

988

989 **APPENDIX**

990

991 We describe the locations and eigenvalues of the critical points of the NPZ_1Z_2 model with linear
 992 phytoplankton mortality ($\alpha = 0$) and quadratic phytoplankton mortality ($\alpha = 1$).

993

994 **Origin Critical Point (O):**

995

996 The critical point at the origin is defined by $P_O^* = Z_{1O}^* = Z_{2O}^* = 0$, $N_O^* = 1$ and has the eigenvalues:

997

$$\lambda_{O-1} = f_P|_O = \frac{\mu}{1 + \kappa} - \sigma \quad (17)$$

998

$$\lambda_{O-2} = f_{Z_1}|_O = -\sigma_1 Z_{1O}' . \quad (18)$$

999

$$\lambda_{O-3} = f_{Z_2}|_O = -\sigma_2 Z_{2O}^\delta . \quad (19)$$

1000 Note that when $\gamma \neq 0$ and $\delta \neq 0$, $\lambda_{O-2} = 0$ and $\lambda_{O-3} = 0$. This indicates that higher-order terms of
 1001 the system must be considered to elucidate these eigenvalues. However, consideration of these
 1002 terms will produce negative values for λ_{O-2} and λ_{O-3} .

1003

1004 **Prey-only Critical Point (A):**

1005

1006 The prey-only critical point is defined by $Z_{1A}^* = Z_{2A}^* = 0$ and for $\alpha = 0$ is located at:

1007

$$P_A^* = \frac{\mu - \sigma(1 + \kappa)}{\mu - \sigma}, \quad (20)$$

1008

$$N_A^* = \frac{\sigma\kappa}{\mu - \sigma}. \quad (21)$$

1009 For $\alpha = 1$ the point is located at:

$$P_A^* = \frac{\mu + \sigma(1 + \kappa) \pm \sqrt{[\mu + \sigma(1 + \kappa)]^2 - 4\mu\sigma}}{2\sigma}, \quad (22)$$

$$N_A^* = 1 - P_A^*. \quad (23)$$

This point has the eigenvalues:

$$\lambda_{A-1} = \frac{\partial f_1}{\partial u_1} u_1 \Big|_A = -\frac{\mu\kappa}{(N_A^* + \kappa)^2} - \alpha\sigma, \quad (24)$$

$$\lambda_{A-2} = f_{Z_1} \Big|_A = \frac{\varphi_1(1 - \psi_1)P_A^*}{1 + \varepsilon_1 P_A^*} - \sigma_1 Z_{1A}^\gamma, \quad (25)$$

$$\lambda_{A-3} = f_{Z_2} \Big|_A = \frac{\varphi_2(1 - \psi_2)P_A^*}{1 + \varepsilon_2 P_A^*} - \sigma_2 Z_{2A}^\delta. \quad (26)$$

Note that $\lambda_{A-1} < 0$ and $\lambda_{A-2}, \lambda_{A-3} > 0$ for nonlinear mortality ($\gamma, \delta \neq 0$) and will be smaller in magnitude for linear mortality, but not negative if the parameter set complies with Kolmogorov's criteria.

Predator-Prey Critical Points (B, C):

The predator-prey critical point on the (P, Z_1) face is given by $Z_{2B}^* = 0$ and:

$$Z_{1B}^* = \left(\frac{1 + \varepsilon_1 P_B^*}{\varphi_1(N_B^* + \kappa)} \right) \left[\sigma_1(N_B^* + \kappa)P_{1B}^{*\alpha} - \mu N_B^* \right], \quad (27)$$

$$P_B^* = \frac{\sigma_1 Z_{1B}^{*\gamma}}{\varphi_1(1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1B}^{*\gamma}}. \quad (28)$$

Then for $\gamma = 0$

$$2\varphi_1 N_B^* = \left[\left(1 + \varepsilon_1 P_B^*\right) \left(\sigma_1 P_B^{*\alpha} - \mu\right) + \varphi_1 \left(P_B^* + \kappa - 1\right) \right] \pm \sqrt{\left[\left(1 + \varepsilon_1 P_B^*\right) \left(\sigma_1 P_B^{*\alpha} - \mu\right) + \varphi_1 \left(P_B^* + \kappa - 1\right) \right]^2 - 4\kappa \left[\sigma_1 \left(1 + \varepsilon_1 P_B^*\right) P_B^{*\alpha} - \varphi_1 \left(P_B^* - 1\right) \right]} \quad (29)$$

and for $\gamma = 1$:

$$N_B^* = 1 - P_B^{*\alpha} - Z_{1B}^*, \quad (30)$$

and we obtain the solution for the critical point with quadratic zooplankton mortality numerically.

Similarly, the predator-prey critical point on the (P, Z_2) face is given by $Z_{1C}^* = 0$ and:

$$Z_{2C}^* = \left(\frac{1 + \varepsilon_2 P_C^*}{\varphi_2 (N_C^* + \kappa)} \right) \left[\sigma_2 (N_C^* + \kappa) P_{2C}^{*\alpha} - \mu N_C^* \right], \quad (31)$$

$$P_C^* = \frac{\sigma_2 Z_{2C}^{*\gamma}}{\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2C}^{*\gamma}}. \quad (32)$$

Then for $\gamma = 0$

$$2\varphi_2 N_C^* = \left[\left(1 + \varepsilon_2 P_C^*\right) \left(\sigma_2 P_C^{*\alpha} - \mu\right) + \varphi_2 \left(P_C^* + \kappa - 1\right) \right] \pm \sqrt{\left[\left(1 + \varepsilon_2 P_C^*\right) \left(\sigma_2 P_C^{*\alpha} - \mu\right) + \varphi_2 \left(P_C^* + \kappa - 1\right) \right]^2 - 4\kappa \left[\sigma_2 \left(1 + \varepsilon_2 P_C^*\right) P_C^{*\alpha} - \varphi_2 \left(P_C^* - 1\right) \right]} \quad (33)$$

and for $\gamma = 1$:

$$N_C^* = 1 - P_C^* - Z_{2C}^*, \quad (34)$$

and we obtain the solution for the critical point with quadratic zooplankton mortality numerically.

Predator-Predator-Prey Critical Point (D):

1044 The predator-predator-prey critical point is defined by $N_D^*, P_D^*, Z_{1D}^*, Z_{2D}^* \neq 0$. The following
 1045 relationships are solved iteratively to obtain the location of the critical point. For $\gamma = 0$, $f_2 = 0$ and
 1046 $f_3 = 0$ provide relationships for P_D^* that must be reconciled; $f_2 = 0$ gives:

$$1047 \quad P_D^* = \frac{\phi Z_{2D}^* + \sigma_1 (1 + \varepsilon Z_{1D}^*)}{(1 + \varepsilon Z_{1D}^*) [\varphi_1 (1 - \psi_1) - \varepsilon_1 \sigma_1] - \varepsilon_1 \phi Z_{2D}^*}, \quad (35)$$

1048 and $f_3 = 0$ gives:

$$1049 \quad P_D^* = \frac{\sigma_2 (1 + \varepsilon Z_{1D}^*) - \phi (1 - \psi) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2] - \varepsilon_2 \phi (1 - \psi) Z_{1D}^*}. \quad (36)$$

1050

1051 Similarly, for $\gamma = 1$, $f_2 = 0$ and $f_3 = 0$ provide relationships for P that must be reconciled; $f_2 = 0$
 1052 gives:

$$1053 \quad P_D^* = \frac{\phi Z_{2D}^* + \sigma_1 (1 + \varepsilon Z_{1D}^*) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_1 (1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1D}^*] - \varepsilon_1 \phi Z_{2D}^*}, \quad (37)$$

1054 and $f_3 = 0$ gives:

$$1055 \quad P_D^* = \frac{\sigma_2 (1 + \varepsilon Z_{1D}^*) Z_{2D}^* - \phi (1 - \psi) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2D}^*] - \varepsilon_2 \phi (1 - \psi) Z_{1D}^*}. \quad (38)$$

1056 When reconciled, equations (35) and (36), and equations (37) and (38) define Z_{2D}^* in terms of Z_{1D}^* .

1057 These relationships provide complicated expressions that must be solved iteratively and which
 1058 provide little insight into the location or sensitivity of the critical points, which we hence do not
 1059 give here.

1060

1061

Figure 1
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Figure 2
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