

Modelling Plankton Functional Types

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Abstract: The prospect of anthropogenic climate change has generated substantial interest in the role of ocean plankton systems in biogeochemical cycling in the ocean. Plankton may have a significant influence on climate by drawing down carbon dioxide from the atmosphere, sequestering it in the deep ocean, and by producing dimethylsulphide and other volatile compounds that may affect cloud formation over the oceans. Plankton models that include several plankton functional types (PFTs) are needed to resolve the role of plankton in biogeochemical cycling, as different plankton utilise different elements in different ways.

Many contemporary ecosystem models of plankton dynamics may be classed as Kolmogorov systems, as they are of the general form $\dot{u}_i = f_i(u_1, u_2, \dots, u_n, K)$, $i = 1, 2, \dots, n$. Kolmogorov derived conditions on the f_i for predator-prey interactions in the form of Kolmogorov systems (i.e. for $n = 2$) that ensured only ecologically realistic dynamics (stable spiral equilibriums or stable limit cycles that ensure continued co-existence of both predator and prey) were possible. We look at the particular case of a Kolmogorov system with $n = 3$ that conserves the mass of limiting nutrient (many models applied in biological oceanography also have this property). We note that conservation of mass is required for a biogeochemical model to be written as a Kolmogorov system, as the nutrient equation in these models typically cannot be written in Kolmogorov form.

Our analysis provides some useful heuristics to guide modellers when developing and parameterizing PFT models. These heuristics include:

- Complicated models may be broken down into simpler predator-prey and competition models that control the dynamics on the vertices, edges and faces of the full system. Each subsystem of a Kolmogorov system is also a Kolmogorov system.
- The eigenvalues of the ‘competition’ eigenvectors that are orthogonal to each predator-prey face provide a useful indicator of the existence and stability properties of the interior point that is fundamental to a *bona fide* PFT model (where all three PFTs remain extant for all time).

The application of our analysis to an example NP_1P_2Z Kolmogorov system revealed further heuristics that may also be useful for PFT modeling:

- Parameter sets that result in *bona fide* PFT systems are rare: we found an order of magnitude more parameter sets that resulted in pseudo-PFT systems (where which PFT becomes extinct is determined by initial conditions), and an order of magnitude again more parameter sets that resulted in non-PFT systems where extinction is pre-determined by the parameters, irrespective of initial conditions
- *Bona fide* PFT parameter sets are distributed throughout the parameter space; therefore, for any PFT model there may be many *bona fide* parameter sets with significantly different properties

The ubiquity of parameter sets throughout parameter space presents a substantial challenge to PFT modelling. PFT models that are used in simulations of climate change, one of the primary drivers of the development of PFT models, must also respond appropriately to changes in their external environment. Our results suggest that the development of PFT models that can simulate the changes in community composition are unlikely to be achieved by refining measurements of parameters or acquiring longer time series of data; intimate knowledge of the inherent properties of the models allows a more focussed approach.

Keywords: *Plankton functional type models, dynamical systems, parameterization.*

INTRODUCTION

The demand to resolve the roles of different PFTs in biogeochemical cycling in the oceans has meant that PFT models are already being developed and applied. The debate over the merits of including phytoplankton functional types in the ubiquitously successful nutrient – phytoplankton – zooplankton (*NPZ*) models suggests a pressing need for better understanding of the behaviour of these models. The emphasis of attempts to improve the understanding of, and build confidence in, PFT models is often focussed on more and more accurate measurements of PFT traits (parameter values) and more and more accurate data to calibrate and validate the models (Le Quéré et al. 2005). Here, we investigate the dynamics of a simple, generic model with two phytoplankton functional types to see what insights might be gained into the attributes of more complex PFT models. We choose the model and its parameters to ensure ecological realism under the conditions derived by Kolmogorov (1936) and explicated by May and others (May 1973).

We consider the endogenous dynamics of a model with multiple phytoplankton functional types that is a three-dimensional Kolmogorov system:

$$\dot{u}_1 = f_1(u_1, u_2, u_3)u_1, \quad \dot{u}_2 = f_2(u_1, u_2, u_3)u_2, \quad \dot{u}_3 = f_3(u_1, u_2, u_3)u_3, \quad (1)$$

where the u_1 and u_2 represent autotrophs and u_3 their grazer. The f_i describe the net growth and mortality of each species, trophic guild or PFT, that is $f_i = (\text{growth} - \text{predation} - \text{mortality})_i$. These f_i are often nonlinear functions of u_1, u_2, u_3 and include parameters that describe the attributes of the PFTs and how they interact; analytic solutions to such systems are rare. 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 (Franks 2002); this 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 relative concentrations expressed in their nutrient equivalent currency. Conservation of mass causes N to become a ‘virtual’ variable as it allows the \dot{N} equation to be inferred from the other equations. Conservation of mass is generally required for a biogeochemical model to be written as a Kolmogorov system, as the nutrient equation in these models typically cannot be written in Kolmogorov form.

We shall consider the critical points of this system, denoted by $\{u_1^*, u_2^*, u_3^*\}$ and defined by $\dot{u}_i = f_i u_i^* = 0$. 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. Throughout the following, the units are chosen so that $N_T \equiv 1$.

METHOD

We first analyse the dynamics of a generic three state variable Kolmogorov system (equation (1)), and consider the critical points, eigenvalues and eigenvectors of this system. The eigenvalues and eigenvectors describe the local stabilities of the critical points, and together form ‘signposts’ that direct the dynamics of the whole system.

We then consider a specific example in order to examine the parameterizations that result in realistic PFT dynamics. The NP_1P_2Z study system has phytoplankton (P_1, P_2) competing for inorganic nutrient (N) and being grazed by zooplankton (Z). There is significant debate over the appropriate form of the f_i for PFT models (Flynn 2003, Mitra 2009). We choose ‘simple’ f_i that are commonly used to allow for closed form analytic expressions to be found for the critical points and their eigenvalues. The study system has parameter values derived from the literature (see Cropp and Norbury (in press) for full details) and is described by equations (3) - (5):

$$\dot{P}_1 = f_{P_1} P_1 = \left[\frac{\mu N}{N + \kappa} - \frac{\varphi Z}{1 + \varepsilon P_1} - \sigma \right] P_1, \quad (3)$$

$$\dot{P}_2 = f_{P_2} P_2 = \left[\frac{\hat{\mu} N}{N + \hat{\kappa}} - \frac{\hat{\varphi} Z}{1 + \hat{\varepsilon} P_2} - \hat{\sigma} \right] P_2, \quad (4)$$

$$\dot{Z} = f_Z Z = \left[\frac{\varphi(1 - \psi) P_1}{1 + \varepsilon P_1} + \frac{\hat{\varphi}(1 - \hat{\psi}) P_2}{1 + \hat{\varepsilon} P_2} - \sigma_Z \right] Z, \quad (5)$$

$$\dot{N} = -\mu_1 N - \mu_2 N - \mu_3 N = \left[\sigma_Z + \frac{\varphi \psi P_1}{1 + \varepsilon P_1} + \frac{\hat{\varphi} \hat{\psi} P_2}{1 + \hat{\varepsilon} P_2} \right] Z - \left[\frac{\mu N}{N + \kappa} - \sigma \right] P_1 - \left[\frac{\hat{\mu} N}{N + \hat{\kappa}} - \hat{\sigma} \right] P_2. \quad (6)$$

We consider the dynamics of the NP_1P_2Z system under three parameter sets that explicate the dynamics of three classes of PFT systems: *bona fide* PFT systems where all functional types remain extant; pseudo-PFT systems where the initial population sizes determine which type will go extinct; and non-PFT systems where the parameter values determine which type will go extinct irrespective of the initial conditions.

We then consider the ubiquity of parameter sets that result in *bona fide* PFT systems for our exemplar model. The parameter spaces that marine biogeochemical models occupy are notoriously poorly constrained, so we defined a parameter space ranging from 50% of the smallest to 150% of the largest values of each parameter. We randomly sampled 5×10^6 parameter sets from uniform distributions within this space. We used Kolmogorov's (1936) criteria to determine if a parameter set was valid (validity criteria for A, C, D, F in Table 1), calculated the eigenvalues of the inward-pointing eigenvectors of the predator-prey critical points on the faces and classified each parameter set according to the signs of the eigenvalues (*bona fide* criteria for D, F in Table 1).

Table 1: Criteria for classification of parameter sets for the NP_1P_2Z system

VALIDITY	CRITERIA
A	$0 < P_{1A}^* < 1$
C	$0 < P_{2C}^* < 1$
D	$0 < P_{1D}^* < 1$ $0 < Z_D^* < 1$
F	$0 < P_{2F}^* < 1$ $0 < Z_F^* < 1$
<i>Bona fide</i>	CRITERIA
D	$\lambda_{D-2} = f_{P_2} _D > 0$
F	$\lambda_{F-1} = f_{P_1} _F > 0$

RESULTS

Origin Critical Point (O):

Every Kolmogorov system has a critical point at the origin (O) where $u_i^* = 0$ and (usually) $f_i \neq 0$ for all i . The eigenvalues at the origin are:

$$\lambda_{O-1} = f_1|_O > 0, \quad \lambda_{O-2} = f_2|_O > 0, \quad \lambda_{O-3} = f_3|_O < 0, \quad (7)$$

where $f_i|_O$ means that the expression f_i is evaluated at the critical point O.

Prey-only Critical Points (A, C):

The system has an autotroph critical point in each of the predator-prey subsystems. These are defined by $u_1^* \neq 0, u_2^* = 0, u_3^* = 0$ (A) and $u_1^* = 0, u_2^* \neq 0, u_3^* = 0$ (C) and are located where the $f_1 = 0$ isocline in the (u_1, u_3) plane intersects the u_1 axis and where the $f_2 = 0$ isocline in the (u_2, u_3) plane intersects the u_2 axis respectively. The eigenvalues of A and C are given by:

$$\lambda_{A-1} = \frac{\partial f_1}{\partial u_1} u_1|_A < 0, \quad \lambda_{A-2} = f_2|_A, \quad \lambda_{A-3} = f_3|_A > 0, \quad (8)$$

$$\lambda_{C-1} = f_1|_C, \quad \lambda_{C-2} = \frac{\partial f_2}{\partial u_2} u_2|_C < 0, \quad \lambda_{C-3} = f_3|_C > 0. \quad (9)$$

The stable eigenvalues (λ_{A-1} for A and λ_{C-2} for C), which are given by the response of the blooming autotroph to increases in its own biomass, are always negative, as autotroph growth rates reduce as nutrient becomes less available. Systems that comply with Kolomogorov's criteria will always have λ_{A-3} and λ_{C-3} , the eigenvalues associated with grazing pressure, positive (destabilising) at these points. The directions of these eigenvalues will vary according to the nature of the f_i , but will always point into the interior of the (u_1, u_3) plane for A or the (u_2, u_3) plane for C. The eigenvalues associated with the competing autotroph (λ_{A-2} for A and λ_{C-1} for C) may be positive if the competing autotroph's growth from nutrient left by the other exceeds its specific mortality rate, or negative otherwise. The eigenvectors for these critical points are always orthogonal to the (u_1, u_3) plane for A or the (u_2, u_3) plane for C.

Dual Prey-only Critical Point (B):

Systems may have a third autotroph critical point (B), where the competing autotrophs coexist. This point is defined by $u_1^* \neq 0, u_2^* \neq 0, u_3^* = 0$ and is located where the $f_1 = 0$ isocline intersects the $f_2 = 0$ isocline in the (u_1, u_2) plane. The eigenvalues of this point are given by:

$$2\lambda_{B-1,2} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_2}{\partial u_2} u_2 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_2}{\partial u_2} u_2\right)^2 - 4u_1u_2\left(\frac{\partial f_1}{\partial u_1} \frac{\partial f_2}{\partial u_2} - \frac{\partial f_1}{\partial u_2} \frac{\partial f_2}{\partial u_1}\right)}|_B, \quad (10)$$

$$\lambda_{B-3} = f_3|_B > 0. \quad (11)$$

The eigenvalue associated with grazing pressure (λ_{B-3}) is always positive, while the eigenvalues associated with the autotroph growth ($\lambda_{B-1,2}$) will generally have one negative eigenvalue representing autotroph growth on available nutrient. The other eigenvalue may be negative, reflecting co-existence of the autotrophs, or positive indicating competitive exclusion that is dependent on initial conditions.

Predator-Prey Critical Points (D, F):

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

$$2\lambda_{D-1,3} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_3}{\partial u_3} u_3 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_3}{\partial u_3} u_3\right)^2 - 4u_1u_3\left(\frac{\partial f_1}{\partial u_1} \frac{\partial f_3}{\partial u_3} - \frac{\partial f_1}{\partial u_3} \frac{\partial f_3}{\partial u_1}\right)}|_D, \quad (12)$$

$$\lambda_{D-2} = f_2|_D, \quad (13)$$

for D, and by:

$$\lambda_{F-1} = f_1|_F, \quad (14)$$

$$2\lambda_{F-2,3} = \frac{\partial f_2}{\partial u_2} u_2 + \frac{\partial f_3}{\partial u_3} u_3 \pm \sqrt{\left(\frac{\partial f_2}{\partial u_2} u_2 + \frac{\partial f_3}{\partial u_3} u_3\right)^2 - 4u_2u_3\left(\frac{\partial f_2}{\partial u_2} \frac{\partial f_3}{\partial u_3} - \frac{\partial f_2}{\partial u_3} \frac{\partial f_3}{\partial u_2}\right)}|_F, \quad (15)$$

for F. In almost all cases $\lambda_{D-1,3}$ and $\lambda_{F-2,3}$ will be complex numbers, with positive or negative real parts, indicating that trajectories will either spiral into or away from the critical point. The dynamics of the system in the direction orthogonal to these planes is of critical importance to PFT modellers as the eigenvalues in this direction determine whether a system will maintain all plankton extant during simulations. The eigenvalues in this direction are given by λ_{D-2} for D and by λ_{F-1} for F. The signs of these eigenvalues determine whether a predator-prey-prey critical point (E) exists and is stable.

If λ_{D-2} and λ_{F-1} are both positive, E exists in the feasible region of state space and is stable in the direction orthogonal to the predator-prey planes (u_1, u_3) and (u_2, u_3) . In such *bona fide* PFT systems u_1 and u_2 will co-exist, and are both grazed on by u_3 . If λ_{D-2} and λ_{F-1} are both negative, E exists in the feasible region of state space but is unstable in the direction orthogonal to the predator-prey planes (u_1, u_3) and (u_2, u_3) . This means that u_1 and u_2 cannot co-exist, and one must always out-compete the other, with the winner determined by the initial conditions. We shall refer to these cases as pseudo-PFT systems. When λ_{D-2} and λ_{F-1} have opposite signs, E does not exist in the feasible region of state space, and again u_1 and u_2 cannot co-exist. In this case, the winner is pre-determined and the initial conditions have no influence on the outcome of the competition. We shall refer to these as non-PFT systems.

Predator-Prey-Prey Critical Point (E):

As noted above, the system may have a critical point E 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. The eigenvalues of the critical point E are generally difficult to obtain in analytic form, and difficult to interpret, as they involve the roots of a cubic equation derived from the community matrix, and hence are often obtained numerically. However, the global dynamics of the state space must be consistent with the local dynamics determined by the other critical points. Therefore, if the critical points on the faces (D and F) have λ_{D-2} and λ_{F-1} positive, the interior critical point (E) must have negative real eigenvalues (*bona fide* PFT). Similarly, if D and F both have negative real eigenvalues E must have positive real eigenvalues (pseudo-PFT). In the case where D and F have real eigenvalues of opposite signs, E cannot exist in the interior of the state space (non-PFT).

Bona fide PFT systems

We now review the dynamics possible in the NP_1P_2Z system. Figs. 1-3 show the locations of the critical points of each system with two trajectories that start from different initial conditions. The arrows on the faces represent the vector fields of the subsystems (i.e. NP_1Z, NP_2Z or NP_1P_2). These vector fields allow generalized dynamics to be inferred from the individual trajectories shown. Fig. 1 presents typical dynamics for a stable spiral internal critical point (E). The origin (O) and autotroph (A and C) critical points are saddles and the predator-prey critical points on the faces (D and F) both have positive real eigenvalues. The (P_1, Z) face has stable spiral dynamics while the (P_2, Z) face has stable limit cycle dynamics. Every initial condition for the model in Fig. 1 will end up at E. This is perhaps the ideal dynamics for a plankton functional type model, as a balance between all PFT is achieved, and no PFT is ever lost to the system.

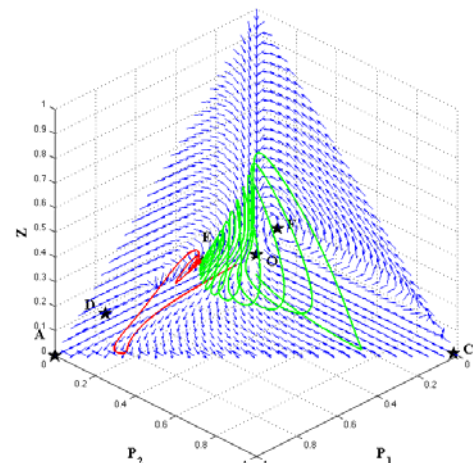


Fig. 1. Critical points and dynamics for the NP_1P_2Z system showing attraction of both trajectories to an internal stable spiral critical point.

Pseudo-PFT systems

Fig. 2 shows a case in which extinction of one P occurs. The (P_1, Z) and (P_2, Z) faces both have stable spiral dynamics and both faces have negative real eigenvalues attracting nearby orbits ‘horizontally’ onto the face. This is perhaps the worst scenario for the dynamics of a plankton functional type model, as which P survives is determined solely by the initial conditions, and is readily influenced by less accurate computation.

Non-PFT systems

Fig. 3 shows a case in which there is no predator-prey-prey critical point in the feasible region of the state space and one PFT will always dominate and the other go extinct. In contrast to the pseudo-PFT systems, in these systems there are no circumstances under which the loser can survive. In Fig. 3 for example, all initial conditions are eventually attracted to the stable spiral critical point on the (P_1, Z) face, even though the initial dynamics suggest that P_2 may dominate.

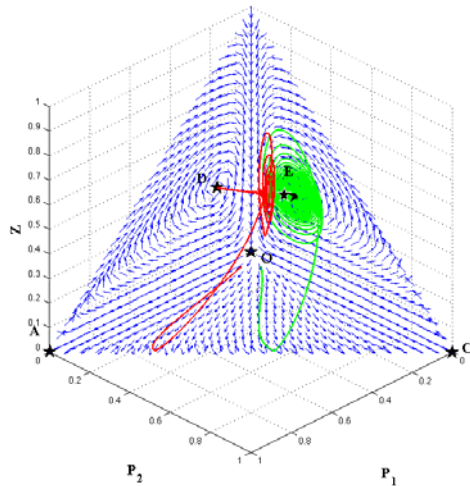


Fig. 2. Critical points and dynamics for the NP_1P_2Z system showing repulsion of both trajectories from an internal unstable spiral critical point to both faces.

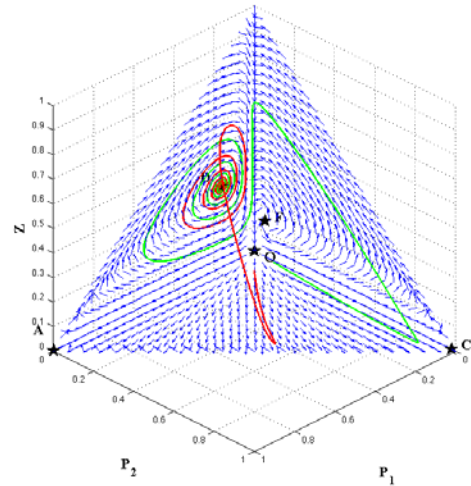


Fig. 3. Critical points and dynamics for the NP_1P_2Z system showing attraction of both trajectories to one face because there is no internal critical point.

Rarity of PFT systems

The criteria for determining valid and *bona fide* parameter sets for the NP_1P_2Z system are presented in Table 1. The 5×10^6 randomly generated parameter sets resulted in 3.1×10^6 (about 62%) valid parameter sets. The distribution of the eigenvalues λ_{D-2} and λ_{F-1} for these parameter sets is shown in Fig. 4. 17,767 (0.6%) of valid parameter sets had both λ_{D-2} and λ_{F-1} positive, indicating that the system had a stable interior predator-prey-prey critical point (E) and would exhibit *bona fide* PFT dynamics (Fig. 1). Pseudo PFT systems were also relatively rare with only a further 228,389 (7.4%) of parameter sets having both eigenvalues negative. The majority of parameter sets (92%) had one positive and one negative eigenvalue, resulting in non-PFT systems.

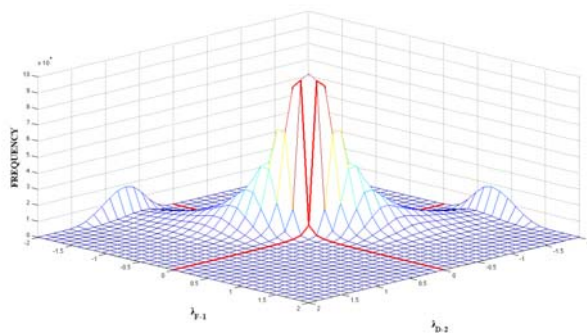


Fig. 4. Frequency distribution of eigenvalues of valid parameter sets.

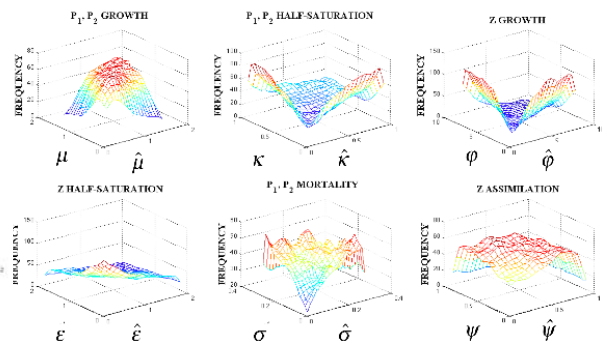


Fig. 5. Frequency distribution of *bona fide* PFT system parameter sets.

Ubiquity of PFT systems

The frequency distributions of the parameters that contributed *bona fide* PFT systems (Fig. 5) reveal that *bona fide* PFT parameter values were found throughout the parameter space, though some parameters were more dense in some areas. *Bona fide* PFT systems are most likely to have competing phytoplankton with similar maximum growth rates ($\mu \approx \hat{\mu}$) but must have different strategies for utilising nutrients ($\kappa \neq \hat{\kappa}$) and/or different grazing susceptibilities ($\varphi \neq \hat{\varphi}$). The grazing functional form used (Lotka-Volterra ($\mathcal{E}, \hat{\mathcal{E}} = 0$) or Michalis-Menten ($\mathcal{E}, \hat{\mathcal{E}} \neq 0$)) had little effect on the ubiquity of *bona fide* PFT systems.

Bona fide PFT systems with phytoplankton that both have low specific mortality rates ($\sigma, \hat{\sigma}$) are rare, although the PFT parameter sets are uniformly distributed throughout the parameter space. A similar distribution is observed for the zooplankton assimilation efficiencies; in this case a substantial number of PFT sets had equally low values for both ψ and $\hat{\psi}$, but large values ($\psi, \hat{\psi} \approx 1$) were rare.

DISCUSSION

The dynamical systems perspective that we have taken in this paper has provided useful insights into how to build more robust PFT models for application in modelling climatically-important biogeochemical cycles in the ocean. Our analysis of the generic Kolmogorov system $\dot{u}_i = f_i(u_1, u_2, u_3)u_i$, $i = 1, 2, 3$ has provided some useful heuristics to guide modellers when developing and parameterizing PFT models:

- Complicated models may be broken down into simpler predator-prey and competition models that control the dynamics on the vertices, edges and faces of the full system. Each subsystem of a Kolmogorov system is also a Kolmogorov system.
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- *Bona fide* PFT parameter sets are distributed throughout the parameter space; therefore, for any PFT model there may be many *bona fide* parameter sets with significantly different properties

The ubiquity of parameter sets throughout parameter space presents a substantial challenge to PFT modelling in determining how PFT models should be parameterised. PFT models that are used in simulations of climate change must also respond appropriately to changes in their external environment. Our results suggest that the development of PFT models that can simulate the changes in community composition that this implies, need, as well as refining measurements of parameters and acquiring longer time series of data, intimate knowledge of the inherent properties of the models.

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