

**The role of grazer predation strategies in the dynamics of consumer-resource
based ecological models**

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22 **Abstract**

23 We analyse a simple plankton system to provide a heuristic for more complex models
24 such as Dynamic Green Ocean Models (DGOMs). Zooplankton foraging is either by
25 generalist grazers that consume whatever they bump into or specialist grazers that
26 actively seek particular prey. The zooplankton may further be classified as either
27 facultative grazers that can survive on any of their prey or obligate grazers that depend
28 on the presence of specific prey.

29 A key result is that different prey dependencies can result in dramatically different
30 impacts of grazing strategies on system outcomes. The grazing strategy can determine
31 whether a system with obligate grazers will be stable, have regular, predictable cycles or
32 be chaotic. Conversely, whether facultative zooplankton functioned as specialist or
33 generalist grazers makes no qualitative difference to the dynamics of the system. These
34 results demonstrate that the effect of different grazing strategies can be critically
35 dependent on the grazer's dependency on specific prey. Great care must be taken when
36 choosing functional forms for population interactions in DGOMs, particularly in
37 scenarios such as climate change where parameters such as mortality and growth
38 coefficients may change. A robust theoretical framework supporting model development
39 and analysis is key to understanding how such choices can affect model properties and
40 hence predictions.

41 **Introduction**

42 The biogeochemical cycling of compounds such as carbon dioxide and dimethyl sulphide
43 by marine plankton may have profound importance for the future climate of the earth.
44 Understanding and predicting such cycling depends on the development of robust,
45 reliable and well-understood models of plankton dynamics in the ocean, and how these
46 systems will respond to changes in climate. The development of Dynamic Green Ocean
47 Models (DGOMs) to address such questions presents interesting theoretical, and
48 pressing practical, issues around the construction and use of complex plankton
49 ecosystem models. DGOMs are being developed to represent the biologically mediated
50 transfer of climatically important gases such as carbon dioxide and dimethylsulphide
51 between the ocean and the atmosphere (for example, Charlson et al., 1987; Falkowski

and Oliver, 2007; Falkowski et al., 1998). Similar models are being developed for coupling to or inclusion in fisheries models to give whole of ecosystem (so-called end-to-end) models for fisheries management (Kishi et al., 2007; Rose et al., 2010). We do not differentiate between these modelling approaches in this work, nor the simpler approach of NPZ modelling that has contributed so much to our understanding of ocean ecosystems (Franks, 2002) – consequently we will use the term DGOM generically to include these and other related approaches.

DGOMs may be complicated, commonly with several competing phytoplankton and several omnivorous zooplankton (Blackford and Gilbert, 2007; Le Quéré et al., 2005). Maintaining populations alive in these models without implementing structural coexistence, where the model equations have a specific form that ensures coexistence of all populations (Bates et al., 2016; Cropp and Norbury, 2012), is extremely difficult. Calibration of these complex models to measured data is challenging with the large number of parameters. This is because of three quite different reasons: the values of the parameters available for tuning are poorly constrained by a paucity of observational data, the models typically require long integration times reducing the number of model evaluations that can feasibly be executed, and parameter sets that result in extinction of one or more populations are ubiquitous (Lignell et al., 2013). Further, recall the famous modelling quote attributed to the mathematician John von Neumann “with four parameters I can fit an elephant, and with five I can make him wiggle his trunk.” (Dyson, 2004) – most DGOMs have hundreds of parameters.

Complicated dynamics including chaos are readily found in unforced, zero-dimensional forms of the relatively simple plankton ecosystem models that underpin DGOMs (Cropp et al., 2014; Hastings and Powell, 1991; Moroz et al., 2016a; Previte and Hoffman, 2010; Woods et al., 2005). It is well known that choices of parameter values and functional forms can significantly influence the dynamical properties of even very simple plankton models (Edwards and Brindley, 1996; Steele and Henderson, 1981). The dependence of the dynamical properties of DGOMs on their formulations has similarly been recognised (Sinha et al., 2010) and model inter-comparison exercises are being used to try to elucidate these dependencies. The complexity of DGOMs means that most attempts to confer them with “desirable” properties proceeds by either numerical experimentation (for example, Anderson et al., 2010; Prowe et al., 2012)) or model inter-comparison

projects, for example, the MARine Ecosystem Model Inter-comparison Project (MAREMIP), (Sailley et al., 2013). Instead, we take a simpler analytic approach by examining the endogenous dynamics of the ecological components of DGOMs without the confounding factors induced by physical forcings or by partial differential equation simulation techniques.

Zooplankton are known to adopt different foraging strategies such as prey selection (Porter, 1973), diurnal vertical migration (Stitch and Lampert, 1984), and even feeding expeditions to abyssal depths (Clarke and Tyler, 2008). Optimizing foraging strategies has been suggested as a primary determinant of evolution in higher organisms such as fish (Giske et al., 1998), and conceivably also drives evolution in zooplankton. Critically, recent research has revealed that marine planktonic omnivores change their feeding behaviour in response to changes in temperature (Wilken et al., 2013), suggesting that understanding how such changes might affect model dynamics may be critical to the performance of DGOMs in climate simulations.

Our key objective in this manuscript is to investigate how changes in foraging strategy and dependence on food sources can impact the dynamics of a heuristic DGOM. Some recent investigations into DGOMs have considered the role of zooplankton predation functional forms in determining model properties (for example, Anderson et al., 2010; Moroz et al., 2016b; Vallina et al., 2014; Visser and Fiksen, 2013). The zooplankton predation functional forms considered in these experiments are generally based on the classic Holling Type II or III forms (Holling, 1959) with modifications to represent zooplankton strategies such as the specialised or generalised feeding strategies described by Koen-Alonso (2007) and prey switching (Gentleman et al., 2003). However, little consensus has been reached on the most useful form of grazing function for plankton systems that underpin both green ocean models and fisheries ecologies (Kishi et al., 2007; Le Quéré et al., 2005). Even when very pragmatic approaches are taken to infer the influence of these functions, in particular how they affect stability and biodiversity, the results are often equivocal (Vallina et al., 2014).

The choice of the functional form used to represent interactions between populations in ecosystems is an ongoing point of contention among ecologists. The theoretical bases for many of the simple two-population interaction terms were set out early, for example,

(Holling, 1959; Ivlev, 1961; Lotka, 1925; Volterra, 1926), but there remains little theoretical or empirical evidence to justify a choice of one form over another. A number of studies have suggested that even simple functional forms may have important influences on properties of the systems. For example, Steele and Henderson (1992) observed that the functional form of zooplankton mortality, often a closure term in plankton models, affected the dynamical stability of simple models, with linear mortality apparently destabilising the system. However, it often turns out that things are more complicated than they first appear, and it now seems that there is no simple relationship between stability and the form of the closure term (Edwards and Brindley, 1996; Edwards and Brindley, 1999; Edwards and Yool, 2000).

The choices made for these functional forms can be important pre-determinants of system properties. For example, Cropp and Norbury (2012) showed that for a general class of models it was possible to ensure that no population ever went extinct in a model of any complexity by choosing functional forms to have certain simply-identified properties. They showed that no population will go extinct in a model where every equation has Kolmogorov form (Kolmogorov, 1936), a common property of ecosystem models, and each population has vanishing loss terms (i.e. Holling Type III terms describing losses to grazing and quadratic mortality terms). Models with these properties are described as having “structural coexistence”, that is, their populations always coexist for any positive parameter set. The efficacy of their approach, and the benefits that it endows on models for parameterisation, has recently been demonstrated by Bates et al. (2015). We know from analysis that structural coexistence models retain their properties for any reasonable (i.e. non-negative) parameter set, a property that might be suspected but not known from numerical analysis. The boundary eigenvalues control the long term, low density growth rates of the population and determine the systems susceptibility to invasion (Chesson, 2000). The analytically known eigenvalues may be used to improve the convergence of optimisation routines, so that we achieve desirable properties such as community structure. Although there are many properties of complex ecosystem models that remain beyond the capacity of mathematical analysis to determine, some are not, and we advocate a balanced approach of analysis and computation. The Conservative Normal (CN) framework that underpins the model has

been published elsewhere (Cropp and Norbury, 2015a) so here is summarised in the Supplementary Material.

The model framework allows us to understand the influence of making certain choices of functional forms on model properties irrespective of wide-ranging parameter values. We choose functional forms to allow population extinctions in our models. This permits us to identify critical parameter values where qualitatively different zooplankton foraging behavior changes. Then we show how the system's dynamical properties are related to these changes in behaviour. Here, we identify *a priori* certain zooplankton grazing properties that have strongly related, but quite different, dynamical behaviours.

The CN framework allows us to differentiate between facultative and obligate grazing, where we define facultative grazing to mean that a zooplankton can survive on any one of its prey independently. We define obligate grazing to mean that a zooplankton is dependent on at least one of its prey being present in order for it to survive. Although it consumes and grows on other prey, it cannot survive if its obligate prey is absent. We also consider whether the zooplankton functions as a generalist or a specialist grazer, analogous to the generalists and specialists defined by Koen-Alonso (2007). Generalist grazing is usually assumed in plankton ecosystem models, but specialist grazing has long been observed in real systems (Porter, 1973), and recent evidence suggests that the majority of plankton are mixotrophic (Flynn et al., 2013; Hartmann et al., 2012). Mixotroph feeding preferences can change with increasing temperature (Wilken et al., 2013), and the role of mixotrophs in controlling the ocean biological carbon pump (Mitra et al., 2014a) presents an imperative for a better understanding of the influence of zooplankton grazing strategies on ecosystem dynamics.

Obligate population interactions, in which the existence of one population is dependent on the presence of another, have been a core component of mutualism theory for a long time (Boucher, 1985; Bronstein, 2015), but the obligate nature of predation interactions has not received the same attention. In this context, "obligate" is usually used in relation to a population's dependence on feeding at a particular trophic level (i.e. an obligate carnivore), rather than on a particular population, but evidence is emerging of populations that are obligate on specific other populations (Harris et al., 2014). Our

framework provides a precise definition of an obligate predator, and here we explore the implication of this trophic strategy for the first time.

Rather than consider these processes in the complicated domain of a “realistic” fully coupled global biophysical model, we take the simpler “caricature model” approach advocated by many investigators that is more amenable to analysis and hence can often provide unequivocal, though constrained, answers (Edwards and Brindley, 1996). In this paper we fix on linear mortality terms and examine the dramatic differences in system dynamics that appear after quite mild variations in the zooplankton grazing strategy.

We find that this simple *NPPZ* plankton ecosystem model, that captures the essence of specialist/obligate predator behaviours, has several distinct dynamical states (a steady coexistence, a large amplitude periodic oscillation, or an unusual long-time steady coexistence with intermittent, rapid population crashes and recoveries) depending on the nature of the zooplankton grazing. Hence, apparently innocuous choices of grazing terms varying from generalist to specialist types which do not appear significantly different, and which may be equivalent up to observational/experimental accuracy, can predetermine the emergent properties of the systems. Here, we observe that the generalist grazer appears to have more reliable and steadier shares of the ecosystem biomass in contrast to the specialist grazer’s very strongly fluctuating biomass share.

We find evidence to support the use of generalist grazing functions for zooplankton in the current generation of DGOMs, where the emphasis is to maintain biodiversity and to represent the dynamics of large groups of plankton (plankton functional types – PFTs) that behave in a similar manner biogeochemically. However, future generations of DGOMs, which resolve bloom succession, for example, may be better served by using specialist grazing functions for the less robust PFTs. The impact of these alternative grazing formulations on model properties suggests that we need to clarify the actual mechanisms of zooplankton grazing.

This work considers the influence of specialist versus generalist feeding functions on ecosystem behaviour, and differentiates facultative from obligate grazing, within a formal, consistent framework built on ecological axioms. It is this framework that allows us to construct specialist grazing functions that do not result in over-grazing, and to define non-overlapping parameter ranges where the zooplankton functions as either a

facultative or an obligate grazer. This is the first work we are aware of to consider simply delineated regimes of facultative and obligate grazing in conjunction with ecologically robust formulations of specialist and generalist foraging.

Methods

We use the CN framework (Supplementary Material) as the theoretical basis for the construction of our model and the determination of the feeding attributes of the zooplankton. Many models in present use and those being developed for DGOMs broadly comply with CN principles, which naturally generalise Holling Type I, II and III forms. Here we take advantage of the insights into model properties that the synthesis of the rules into a limiting nutrient/recycling food web framework provides. This has the following advantages:

- Compliance with the CN rules ensures that the model is ecologically realistic, that is, it satisfies basic ecological assumptions such as:
 - Each population has an explicit, finite resource;
 - A population without resources must decline;
 - A population must be able to grow when its resource(s) are maximal.
- Different types of grazing (such as facultative or obligate) may be precisely defined for the zooplankton population:
 - A grazer that can survive on any one of its multiple prey is defined to be a facultative grazer;
 - A grazer that must have a particular prey present in order to survive (i.e. it cannot grow even when its other prey are at maximal levels) is defined to be obligate on that prey.
- An ecospace (E) is explicitly defined such that all solutions that begin in E remain in E for all time; this ecospace is defined by the constancy of the mass of the finite limiting nutrient resource.

We demonstrate the influence of the grazing strategies and trophic dependencies with a simple *NPPZ* model.

235 The *NPPZ* Model

236 Our approach considers a minimal NP_1P_2Z model of a single limiting nutrient (N), two
 237 phytoplankton populations (P_1 and P_2) and a single zooplankton population (Z) that
 238 grazes on both P_1 and P_2 (equations (1) - (3)). This model is constructed in the CN
 239 framework; a summary is provided in the Supplementary Material and a detailed
 240 explanation may be found in Cropp and Norbury (2015b). To simplify the interpretation
 241 of our computational study we always label P_1 to be the preferred prey so the
 242 zooplankton preferentially consumes P_1 ($\varphi_1 > \varphi_2$). The zooplankton grazing function
 243 includes a parameter (ρ) that allows the functional form to transition smoothly from
 244 generalist grazing ($\rho = 1$) to specialist grazing ($\rho = 0$).

$$245 \quad \dot{P}_1 = P_1 f_{P_1}(P_1, P_2, Z, N) = P_1 \left[\frac{\mu_1 N}{N + \kappa_1} - \frac{\varphi_1 Z}{1 + \varepsilon_1 P_1 + \rho \varepsilon_2 P_2} - \sigma_1 \right], \quad (1)$$

$$246 \quad \dot{P}_2 = P_2 f_{P_2}(P_1, P_2, Z, N) = P_2 \left[\frac{\mu_2 N}{N + \kappa_2} - \frac{\varphi_2 Z}{1 + \rho \varepsilon_1 P_1 + \varepsilon_2 P_2} - \sigma_2 \right], \quad (2)$$

$$247 \quad \dot{Z} = Z f_Z(P_1, P_2, Z, N) = Z \left[\frac{\varphi_1 (1 - \psi_1) Z}{1 + \varepsilon_1 P_1 + \rho \varepsilon_2 P_2} + \frac{\varphi_2 (1 - \psi_2) Z}{1 + \rho \varepsilon_1 P_1 + \varepsilon_2 P_2} - \sigma_Z \right], \quad (3)$$

$$248 \quad \begin{aligned} \dot{N} = I + Z & \left[\sigma_Z + \frac{\varphi_1 \psi_1 Z}{1 + \varepsilon_1 P_1 + \rho \varepsilon_2 P_2} + \frac{\varphi_2 \psi_2 Z}{1 + \rho \varepsilon_1 P_1 + \varepsilon_2 P_2} \right] \\ & + P_1 \left[\sigma_1 - \frac{\mu_1 N}{N + \kappa_1} \right] + P_2 \left[\sigma_2 - \frac{\mu_2 N}{N + \kappa_2} \right] - O \end{aligned} \quad (4)$$

249 The model is formulated as a system open to fluxes of limiting nutrient across its
 250 boundaries, allowing for inputs of new nutrient (I) and outputs of detrital material (O)
 251 to and from the nonliving nutrient compartment (N , equation (4)). For the purposes of
 252 this investigation, we balance the sources and losses and set $I = O$ (Steele and
 253 Henderson, 1992).

254 We produce the numerical investigations by integrating equations (1) - (4) with an
 255 “arbitrary” parameter set derived by non-dimensionalising measured parameter values

(see Table 1). The non-dimensionalisation of applied ecosystem models appears rare, and invariably leads to criticism, with some considering that it obfuscates a direct ecological interpretation of model results. However, it is standard practice in mathematical and physical modelling, as it expresses all parameters in terms of comparable parameters (i.e. it is not how fast a particular rate is, but how fast it is in relation to other rates in the model). Non-dimensionalisation is a critical step in the analytical and numerical analysis of model processes, and is especially important when seeking to determine the influence of different functional forms on model dynamics.

The “life” functions f_{P_1} , f_{P_2} and f_Z (for positive parameters) define the per capita growth rates of the P_1 , P_2 , and Z populations respectively, where \dot{P}_1 means dP_1/dt , etc. The model (1) - (4) complies with the CN framework (Supplementary Material 1). We can then classify the zooplankton as a facultative or obligate grazer based on its parameterisation, and in particular the range that the grazer mortality lies in (see equations (7) and (8)).

Table 1: Measured parameter values for the NP_1P_2Z model. These values have been non-dimensionalised by scaling by a characteristic measured maximum rate of nutrient uptake by phytoplankton (0.27 day^{-1} , Gabric et al. (1999)) and a typical total nutrient concentration (50 mgN m^{-3} , Gabric et al. (1999)).

PARAMETER	PROCESS	VALUE	REFERENCE
μ_1	Maximum rate of N uptake by P_1	1.00	Gabric et al. (1999)
μ_2	Maximum rate of N uptake by P_2	1.15	Muller-Niklas and Herndl (1996)
κ_1	Half-sat const. for P_1 uptake of N	0.25	Slagstad and Stole-Hansen (1991)
κ_2	Half-sat const. for P_2 uptake of N	0.14	Billen and Becquevort (1991)
ϕ_1	Ratio of the maximum Z grazing rate on P_1 to the half-saturation constant for Z uptake of P_1	6.18	Hansen et al. (1996)
ϕ_2	Maximum Z grazing rate on P_2 to	1.85	Gabric et al. (1999)

	the half-saturation constant for Z uptake of P_2		
ε_1	Inverse of the half-saturation constant for Z uptake of P_1	5.50	Fenchel (1982)
ε_2	Inverse of the half-saturation constant for Z uptake of P_2	5.50	Fenchel (1982)
σ_1	P_1 specific mortality rate	0.00	Gabrie et al. (2001)
σ_2	P_2 specific mortality rate	0.26	Moloney et al. (1986)
σ_Z	Default Z specific mortality rate	0.19	Moloney et al. (1986)
ψ_1	Proportion of P_1 uptake excreted by Z	0.40	Moloney et al. (1986)
ψ_2	Proportion of P_2 uptake excreted by Z	0.40	Moloney et al. (1986)
σ_Z^-	Critical Z mortality rate determining the upper bound for facultative grazing	0.1708	Equations (7) and (9)
σ_Z^+	Critical Z mortality rate determining the upper bound for obligate grazing	0.5705	Equations (8) and (10)

274

275 Zooplankton grazing

276 We first consider how zooplankton foraging strategies affect the formulation of the
277 terms used to describe their grazing in models, and then will discuss the details of the
278 NPPZ model that we use to investigate how different terms affect the dynamical
279 behaviour of the model. Generalist grazing functions assume that foraging zooplankton
280 will ingest any prey that they encounter during a generic foraging expedition. We
281 differentiate specialist grazers as zooplankton that actively divide the time they spend
282 foraging for prey between two states, for example, shallow and deep so that they
283 optimise their feeding rates on each prey.

284 *Grazing Terms*

285 We consider a grazer Z feeding on two prey (P_1 and P_2) using a specialist/generalist
 286 feeding function:

$$287 \quad \frac{\varphi_1 P_1}{1 + \varepsilon_1 P_1 + \rho \varepsilon_2 P_2} + \frac{\varphi_2 P_2}{1 + \rho \varepsilon_1 P_1 + \varepsilon_2 P_2} = \begin{cases} \text{Specialist when } \rho = 0 \\ \text{Generalist when } \rho = 1 \end{cases}, \quad (5)$$

288 that enable us to use a simple computational switch to transition between specialist and
 289 generalist grazing types using a single parameter (ρ). This allows us to change the
 290 functional form of grazing smoothly within the computer model. The derivation of this
 291 equation is provided in the Supplementary Material.

292 To facilitate an equitable comparison between grazing functions, free of the influence of
 293 artefacts from different parameter values, we require that specialist and generalist
 294 grazers perform equally well when only one prey exists so the only difference between
 295 the grazing functions is the shape of their surface (Fig 1). This assumption dictates that
 296 the specialist grazer optimises its foraging strategy according to the relative abundance
 297 of the prey populations. Further, to enable comparison of the grazing functional forms
 298 on equal terms we reduce the number of confounding factors and set $\varepsilon_1 = \varepsilon_2$. This
 299 assumption makes a direct ecological interpretation of our results less intuitive, but we
 300 take the view that the effect of the functional forms is more important than the effect of
 301 these parameter values, and the relatively straight-forward examination of the influence
 302 of parameter values within a particular grazing strategy is easily undertaken by those
 303 with particular interest in this aspect.

304

305 *Facultative/Obligate Grazing*

306 The dynamical implications of the obligation of grazers on a particular prey are an issue
 307 not commonly examined in ecosystem or population modelling. Changes in the
 308 environment of a grazer that, for example increase its density-independent mortality
 309 rate, could result in a zooplankton population that could previously survive on a number

of phytoplankton prey becoming dependent on a particular prey. This may occur in simulation models without the modeler necessarily becoming aware that a fundamental change in the nature of the trophic interactions in the model has occurred. The CN framework (see Supplementary Material 1) provides a simple rule (#3) for defining in equations (7) and (8) the difference between a facultative and obligate zooplankton grazer.

Zooplankton food “heaven” arises when the ecospace E is comprised of 100% prey P_1 and P_2 . The maximum resource per capita grazing sign condition (see Supplementary Material) for Z ($f_Z|_{R_Z=1} > 0$) is evaluated along the line of maximum resource $R_Z = P_1 + P_2 = 1$. (Note that we have scaled the measurements of the populations to be in the same currency of the key limiting nutrient. Then $P_1 + P_2 = 1$ means that 100% of this currency is in the phytoplankton populations – hence 0% is in the zooplankton population and the inorganic nutrient pool so that $Z = 0 = N$.) The grazing sign condition (see Supplementary Material) then provides the parameter constraint (where we assume assimilation rates $0 < \psi_1, \psi_2 < 1$ and introduce the coefficient of zooplankton mortality, σ_Z):

$$\frac{\varphi_1(1-\psi_1)P_1}{1+\varepsilon_1P_1+\rho\varepsilon_2P_2} + \frac{\varphi_2(1-\psi_2)P_2}{1+\rho\varepsilon_1P_1+\varepsilon_2P_2} - \sigma_Z > 0 \quad \text{for } P_1 + P_2 = 1. \quad (6)$$

We define Z to be a facultative grazer if it can survive on either P_1 or P_2 independently, that is, we evaluate (6) at its resource maxima $P_1 = 1$ and $P_2 = 1$ to obtain the constraint:

$$0 < \sigma_Z < \min \left\{ \frac{\varphi_1(1-\psi_1)}{1+\varepsilon_1}, \frac{\varphi_2(1-\psi_2)}{1+\varepsilon_2} \right\} \equiv \frac{\varphi_2(1-\psi_2)}{1+\varepsilon_2} \equiv \sigma_Z^-. \quad (7)$$

We also consider the case of an obligate grazer, where Z has the property:

$$\sigma_Z^- < \sigma_Z < \max \left\{ \frac{\varphi_1(1-\psi_1)}{1+\varepsilon_1}, \frac{\varphi_2(1-\psi_2)}{1+\varepsilon_2} \right\} \equiv \frac{\varphi_1(1-\psi_1)}{1+\varepsilon_1} \equiv \sigma_Z^+. \quad (8)$$

332 In this case, $f_Z|_{P_1=1} > 0$ but $f_Z|_{P_2=1} < 0$ indicating that Z cannot survive on P_2 alone – it is
 333 now obligate on the presence of P_1 upon which it can survive in the absence of P_2 .

334 We consider parameter ranges where Z can always survive on P_1 alone ($0 < \sigma_Z < \sigma_Z^+$),
 335 where it can survive on P_1 and/or P_2 alone ($0 < \sigma_Z < \sigma_Z^-$), and where it can't survive on
 336 P_2 alone when $\sigma_Z^- < \sigma_Z < \sigma_Z^+$ (see Figure 1 and equations (7) and (8) for definitions of σ_Z^-
 337 and σ_Z^+). Here σ_Z^- gives the transition from facultative grazing to obligate grazing on P_1
 338 as the grazer mortality rate σ_Z increases past σ_Z^- (remember Z always prefers, or grows
 339 better on, P_1).

340 Using the growth and grazing parameter values of Table 1, Z is a facultative grazer if:

$$341 \quad 0 < \sigma_Z < \sigma_Z^- = 0.1708, \quad (9)$$

342 and is an obligate grazer if:

$$343 \quad \sigma_Z^- = 0.1708 < \sigma_Z < 0.5705 = \sigma_Z^+. \quad (10)$$

344 If $\sigma_Z > 0.5705$ then Z is not a viable population as it cannot grow under any
 345 circumstances, and cannot survive anywhere in E . Note that the definition of Z as a
 346 facultative or obligate grazer is independent of its grazing strategy, so we must examine
 347 all four combinations of generalist and specialist feeding with facultative and obligate
 348 omnivory (see Table2).

349 We examine here the cases where Z changes from a specialist to an generalist grazer,
 350 and σ_Z varies so that Z transitions from facultative to obligate. We explore the
 351 ecological implications of this behaviour in more detail with particular regard to the
 352 influence of grazing strategies and different forms of omnivory. We consider the
 353 following cases that arise from Figure 1 (Table 2). The model integrations use an
 354 adaptive time step 4-5th order Runge-Kutta algorithm provided in Matlab as ode45.
 355 Integrations were made for 2,000 or 5,000 (non-dimensional) time steps using the
 356 parameter values provided in Table A1 in Supplementary Material Three with values of
 357 zooplankton mortality between 0 and $\sigma_Z^+ = 0.5705$, and with ρ either 0 or 1.

358

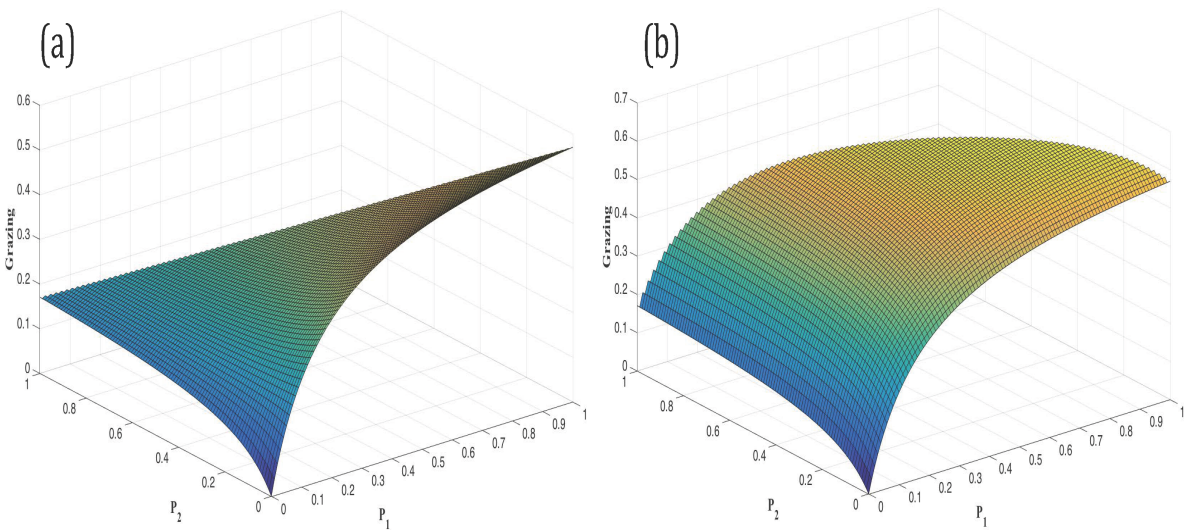
Table 2. The four cases of grazing behaviour.

		Prey dependence	
		$0 < \sigma_z < \sigma_z^-$	$\sigma_z^- < \sigma_z < \sigma_z^+$
Foraging strategy	$\rho = 1$	Facultative generalist	Obligate generalist
	$\rho = 0$	Facultative specialist	Obligate specialist

359

360 *Grazing Surfaces*

361 Figure 1 confirms that an “optimal” strategy for Z is for it to act as a specialist grazer as
362 this allows it to achieve maximal food intake. While our specialist and generalist grazing
363 functions are identical in the absence of alternative prey, the specialist function provides
364 Z with a grazing advantage when $P_1 + P_2 \approx 1$. Note that Figure 1 reveals the advantage of
365 specialist grazing, with the maximum specialist grazing rate never less than, and up to
366 20% greater than, the equivalent generalist grazing rate for any prey abundances.
367 Further, the volume under the specialist surface is nearly 50% greater than the volume
368 under the generalist surface, revealing that the specialist strategy always results in a
369 higher ingestion rate for Z, and is significantly better than a simple examination of the
370 maximum grazing rate might suggest.



371

Figure 1. Grazing surfaces for generalist (a) and specialist (b) functional forms using the parameter set in Table A1. Subtracting σ_z from these surfaces gives f_z and translates the surfaces down the z axis. σ_z^- is evident as the intercept of the left-hand corners of the surfaces with the z axis, and σ_z^+ is evident as the intercept of the right-hand corners of the surfaces with the z axis. Note that the axes do not have units as the model has been scaled and that the surfaces are only defined for the front triangle of the diagram up to the line $P_1 + P_2 = 1$, evident as a straight edge to the surface in (a) and the curved edge to the surface in (b).

We note that specialist grazing formulations are sometimes criticised in consumer-resource models that do not have mass conservation because they allow unbounded grazing – as the number of prey populations increases the total grazing also increases without bound. However, when they are implemented in models where mass is conserved (as is fundamental to the CN framework) grazing is always bounded.

Key system behaviour

We first note some key properties of the system (1) - (4) for the parameter choices in Table 1 that are important but are not the focus of this work:

- When $Z \equiv 0$, P_1 and P_2 are R^* competitors (Tilman, 2007) with the “immortal” phytoplankton (or autotroph) P_1 always eventually dominating P_2 (but only at a marginal level – i.e. between $N \approx 0.05$ and $N = 0$) even when P_2 grows better on an ample nutrient supply;
- Z prefers P_1 over P_2 in the ratio 3:1, but we have made P_1 immortal ($\sigma_1 = 0$) so it dominates by R^* theory, and is the more “reliable” food source;
- But for $\sigma_z \approx 0.1$ we have P_2 and Z coexisting successfully with P_1 becoming negligibly small (Z is extremely successful with approximately 50% of the biomass while P_2 stably secures approx. 20%, and the nutrient pool has about 30%);

- The above switches in system behaviour occur for both generalist and specialist grazers at $\sigma_z \approx \sigma_z^- = 0.1708$ (see (9)), but are controlled by an interior equilibrium point in quite different ways for the two grazing types;
- For $\sigma_z \geq \sigma_z^-$ the dynamics for specialist grazers changes in that the stable coexistence between P_2 and Z can now be invaded by “random” P_1 blooms, which dramatically destabilise the system;
- For specialist grazers, recovery to the pseudo-steady P_2 dominant state always occurs, and the system awaits another (unpredictable) P_1 outbreak;
- In contrast, the generalist grazer coexists fairly stably with smaller, but increasing, variation in biomass fraction as the mortality factor σ_z increases from σ_z^- to σ_z^+ .

This last mentioned more stable, and robust, behaviour is a desirable feature for GCM climate modelling studies where only a few plankton communities are modelled. Later we discuss the ecological interpretation and significance of the grazing function.

Ecologically viable equilibrium points

Every three-population CN system has eight sets of equations that define its critical points. These sets of equations are defined by the various ways of setting all three time derivatives to zero and describe equilibrium points ranging from a point (C_0) at the origin of the ecospace, where all populations are zero, to a point in the interior of the ecospace where all populations are non-zero (C_7). Here, of the eight equilibrium points that the model possesses, we only discuss in detail the behaviours of the two boundary equilibrium points $C_5 = \{N, P_1, 0, Z\}$ and $C_6 = \{N, 0, P_2, Z\}$, and the coexistence equilibrium point $C_7 = \{N, P_1, P_2, Z\}$, the only points that move in response to the parameter changes. We note that all the boundary points may affect the dynamics of the system, depending on the grazing properties of the zooplankton.

Analytic expressions for the locations of these points are provided in Supplementary Material 2 - $C_1 = \{N, P_1, 0, 0\}$ and $C_2 = \{N, 0, P_2, 0\}$ are autotroph equilibrium points for

425 the prey populations P_1 and P_2 respectively (so that C_1 and C_2 are stable in the absence
 426 of Z and each other). P_1 and P_2 compete according to R^* theory when $Z \equiv 0$, with P_1
 427 always dominant over P_2 , by our labelling, so that C_2 is unstable in the C_1 direction.
 428 Consequently, by R^* theory, $C_4 = \{N, P_1, P_2, 0\}$ does not exist in E (nor does the
 429 unphysical point $C_3 = \{N, 0, 0, Z\}$ since Z is a pure grazer). Note that $C_0 - C_2$ do not
 430 depend on σ_Z and C_3 and C_4 are always outside E and hence we do not discuss them
 431 further. However, C_1, C_2 do control the ends of the paths of the C_5, C_6 equilibrium
 432 points as σ_Z increases to σ_Z^+, σ_Z^- respectively.

433 Note that for ease of discussion here we use equilibrium “point” to mean steady state
 434 solution(s) defined by the zero time derivatives. As the system (1) - (4) is nonlinear,
 435 each equilibrium “point” may in fact have several (or no) points in different locations in
 436 the closure of the ecospace E . The multiple point circumstance is rare in this model
 437 parameterisation and not relevant to this discussion. Although only equilibria in E and
 438 on its boundary are ecologically relevant, it is often useful to keep track of them
 439 numerically as σ_Z varies, even when they leave E .

440 We consider the sensitivity of properties of the specialist ($\rho = 0$) and generalist ($\rho = 1$)
 441 grazer models with respect to variations in the zooplankton mortality rate σ_Z for
 442 $0 < \sigma_Z < 0.60$. This transitions Z from facultative to obligate omnivory at
 443 $\sigma_Z = \sigma_Z^- = 0.1708$, and from obligate omnivory to an unviable Z population at
 444 $\sigma_Z = \sigma_Z^+ = 0.5705$. These changes in the zooplankton mortality rate affect the dynamics
 445 of the system by changing the locations and stability properties of the equilibrium
 446 points. While these points respond to changes in σ_Z smoothly and continuously, we
 447 refer to important changes in their properties as bifurcations. Key bifurcations in
 448 ecosystem models occur when two equilibrium points collide and exchange stability
 449 (“transcritical” bifurcations, which are often associated with the extinction of a
 450 population) or when a point independently changes stability (“Hopf” bifurcations,
 451 associated with destabilization of systems).

Changes in system behaviour related to bifurcations occur when for instance the C_7 interior equilibrium point crosses the boundary of E at C_6 when $\sigma_z^- = 0.1708$. When the paths of locations of C_6 and C_7 intersect as σ_z increases past σ_z^- we find an exchange of stabilities from C_6 to C_7 . The dynamical system behaviour generally depends on the existence of C_7 and its stability, and then the grazer's life experience strongly depends on whether it is an obligate specialist or not. Note that stability here refers to Lyapunov (or local) stability – the system returns to stable equilibrium points after a small perturbation away, but is repelled by unstable points – see Kot (2001) or Pastor (2008) for elegant explanations.

Results and Discussion

The first result to observe from the analysis of the equilibrium points is that the locations of the two boundary equilibrium points, C_5 and C_6 (Fig 2) are independent of the functional form of the zooplankton's feeding strategy, that is whether it is a specialist or a generalist grazer. The location of the coexistence point C_7 in E is constrained to lie on a line joining C_6 (at $\sigma_z = \sigma_z^-$) and C_5 (at $\sigma_z = \sigma_z^+$). This suggests that whether an obligate grazer is generalist or specialist may make only a subtle difference to the population behaviour. But, this turns out not to be the case for an unexpected reason.

Figure 2 confirms that the locations of the boundary equilibrium points C_5 and C_6 vary with zooplankton mortality σ_z but are insensitive to the zooplankton grazing strategy ρ . The sensitivities of C_5 and C_6 to σ_z are, however, quite different, with C_6 rapidly moving away from the Z axis and exiting E through C_2 before C_5 has moved significantly. The behaviour of the interior point C_7 , and consequently the dynamical behaviour of the system, is however clearly sensitive to ρ . When Z is a generalist grazer (Fig 2(a)), C_7 enters E via a transcritical bifurcation with C_6 and then proceeds across E in a straight line where N and Z are constant, defined by $N = 0.05$, $Z = 0.15$, and $P_1 + P_2 = 0.80$. Note that when Z is a generalist grazer C_7 is a stable equilibrium point

everywhere in E , as shown in Figures 2(a) and 3(a, c). In contrast, when Z is a specialist grazer C_7 is stable on entering E (at approximately $\sigma_z \approx 0.169$, Fig 2(b)) but almost immediately loses stability (at $\sigma_z \approx 0.173$). It moves across E much more slowly than when Z is a generalist grazer, and is less than half-way across E when C_5 becomes stable (at $\sigma_z \approx 0.473$) and thereafter controls the dynamics of the system (Fig 3(b, d)).

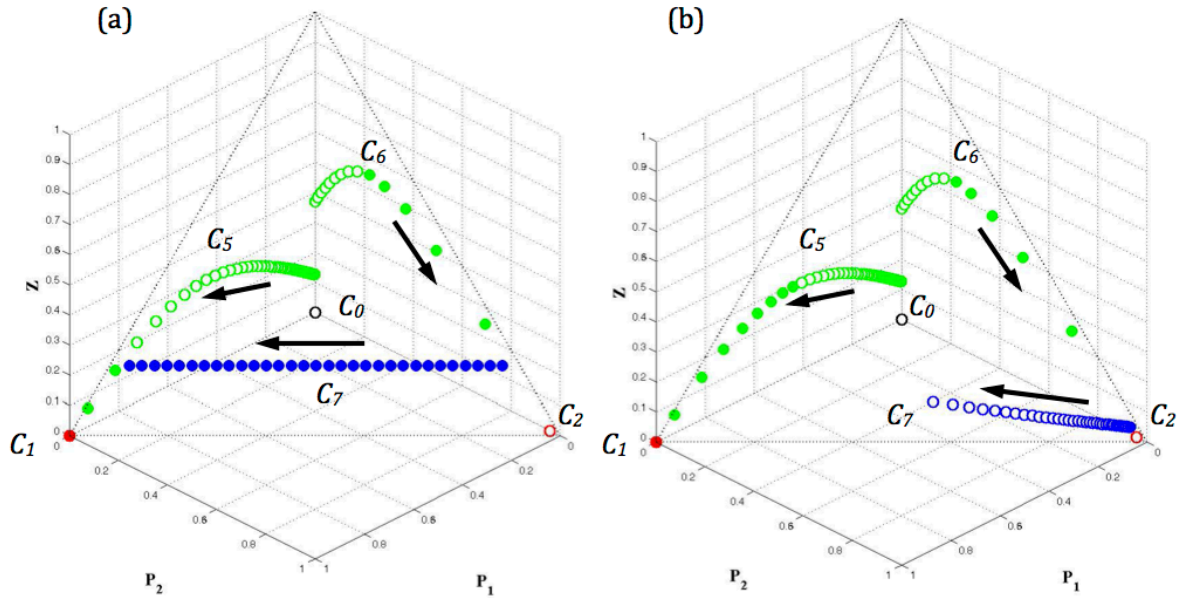


Figure 2. Ecospace for the generalist (a) and specialist (b) NPPZ model showing all equilibrium points in the ecospace (open or closed circles) for values of $0 < \sigma_z < 0.6$. The open circles show unstable equilibrium points, while the closed circles show stable equilibrium points. C_0 , C_1 and C_2 do not move in response to changes in σ_z but C_1 and C_2 change stability in transcritical bifurcations with C_5 and C_6 respectively. C_5 and C_6 are also involved in transcritical bifurcations with C_7 as it leaves and enters the ecospace E respectively. Note that C_5 and C_6 are located on the Z axis for $\sigma_z = 0$. The black arrows show the direction of movement of the equilibrium points as σ_z increases. One circle is plotted for each equilibrium point at each step in σ_z unless it is outside E . σ_z increments in steps of 0.012. Note that C_6 moves very rapidly down the (P_2, Z) face before leaving E through C_2 . Refer to the text for descriptions of the critical points and to the Supplementary Material for analytical expressions for their locations. Animations of

these figures showing how the points move as σ_z changes are provided in the online
Supplementary Material.

As σ_z increases from 0.173, C_7 influences the dynamics less and less, and the population levels eventually cease to be influenced by C_7 at all. This behaviour is observable in Figures 3(b) and (d), which reveal chaotic dynamics in the specialist system when $\sigma_z = 0.30$. The trajectory in Figure 3(b) reveals that the system changes velocity as it circulates on its chaotic attractor in E by several orders of magnitude. It also reveals the sensitivity of each subsequent bloom to how the previous bloom collapses, as trajectories that flow down the Z axis toward the origin may leave the origin, roughly in the P_1, P_2 plane, along different paths. When σ_z increases beyond the intermediate values (i.e. approximately in the middle of the obligate range so $\sigma_z \approx 0.5(\sigma_z^- + \sigma_z^+) \approx 0.3$) shown in Figure 3, the system behaviour settles into an “obligate regime”, approximately the antithesis of the “facultative regime”.

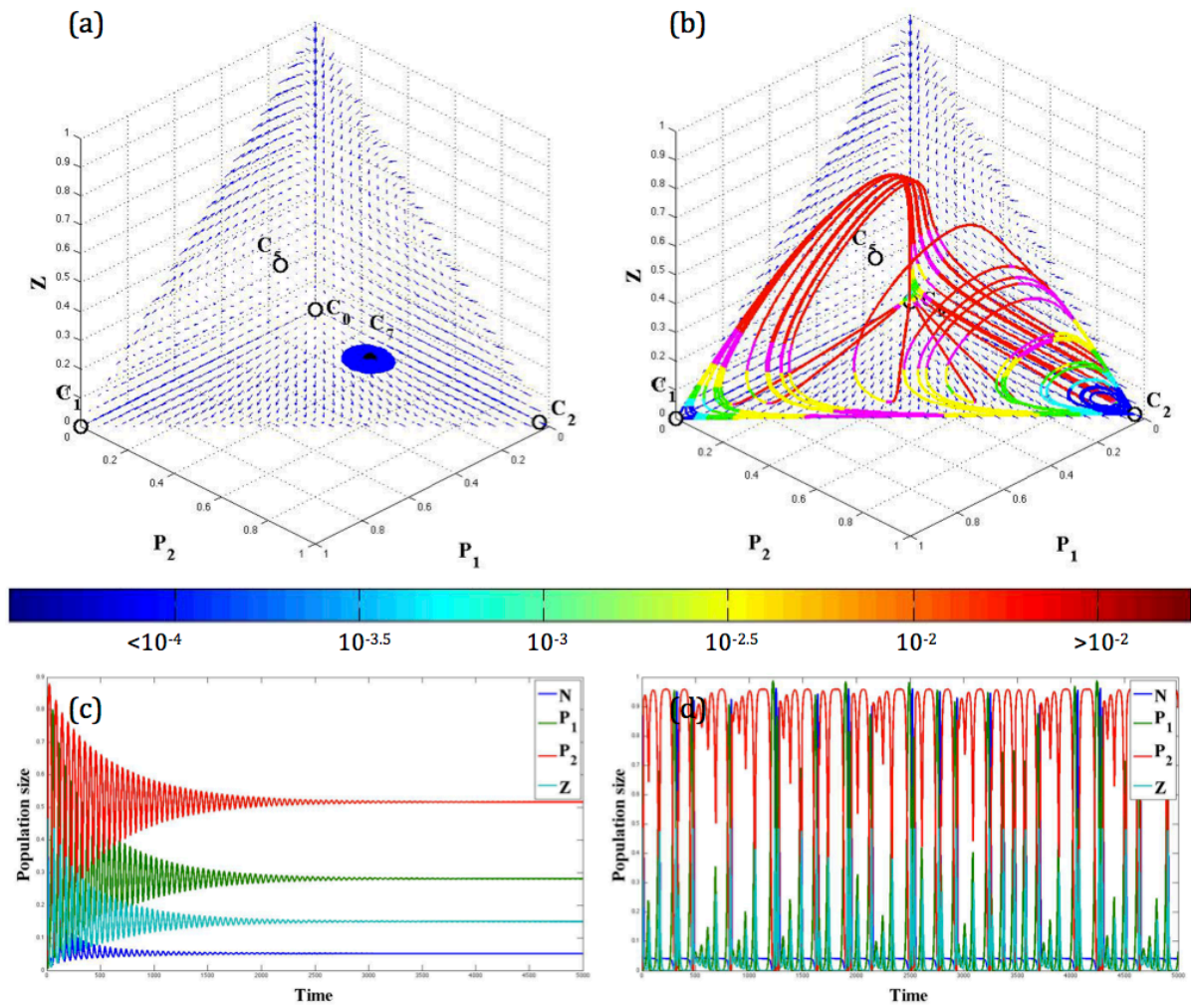


Figure 3. Trajectory (a, b), and population time series (c, d) for a typical obligate generalist grazer (a and c, $\rho = 1$, $\sigma_z = 0.35$) and a typical obligate specialist grazer (b and d, $\rho = 0$, $\sigma_z = 0.35$). The system was integrated for 5,000 time steps and the last half are shown in the trajectories to eliminate transients. All data (including transients) are shown in the time series. Note that 1,000 time steps are approximately equivalent to three months at this scaling. All the equilibrium points shown are unstable except for the interior coexistence point. The trajectories in (a) and (b) are coloured according to the non-dimensional velocity at each point: the colour bar indicates the relative velocities around the stable (a) and chaotic (b) attractors.

It is not evident from Figure 3 that the obligate generalist grazer and the obligate specialist grazer utilised very different prey ingestion ratios. The actual prey ingested during the simulations shown in Figure 3 are shown in Figure 4. The time series of the

ingestion rates (Fig. 4(a, b)) show that the obligate generalist grazer stabilized at a prey
 ingestion rate ratio where the zooplankton ingested P_1 at about 2.5 times the rate it
 ingested P_2 , but its diet was always composed of both prey. The obligate specialist grazer
 in contrast generally ingested either P_1 or P_2 , and both together sometimes stably, and
 sometimes when transitioning from grazing on one to the other. The maximum grazing
 rate on P_1 was about 3.3 times the maximum grazing rate on P_2 . Whereas the obligate
 generalist grazer would, in an unperturbed state, have an unvarying diet, the obligate
 specialist grazer has a continually varying diet, occupying the entire potential grazing
 surface, and we might expect that perturbations to the prey populations could have very
 different impacts.

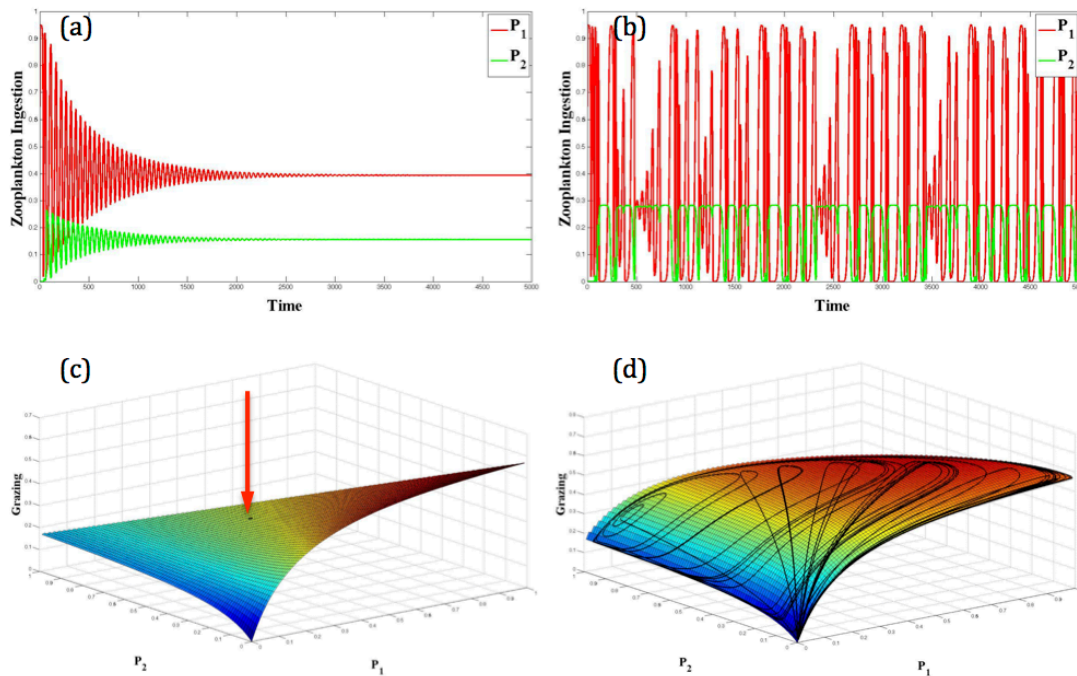


Figure 4. Zooplankton ingestion rate time series (a, b) are shown on the grazing surfaces (c, d) for the simulation shown in Figure 3. Panels (a, c) show ingestion rates for the typical obligate generalist grazer ($\rho = 1$, $\sigma_Z = 0.35$) and panels (b, d) show ingestion rates for the typical obligate specialist grazer ($\rho = 0$, $\sigma_Z = 0.35$). The red arrow in (c) shows the equilibrium point for the obligate generalist grazer, and the black lines in (d) show which of the potential ingestion rates were actually used by the obligate specialist grazer.

542 The four grazing behaviour cases identified in Table 1 are shown in Figure 5. The
 543 facultative generalist and facultative specialist cases (Fig. 5 (a, b)) are effectively
 544 identical, with the “immortal” P_1 being grazed into extinction and the system settling
 545 onto a stable limit cycle of alternating P_2 and Z blooms. Here, the grazer Z drives P_1 to
 546 extinction despite it not having a natural mortality. This outcome can be achieved
 547 because Z is a “facultative” grazer that can survive on either P_1 or P_2 independently. In
 548 the facultative regime then, choosing Z to be an generalist or a specialist grazer makes
 549 little difference to the system dynamics. However, the dynamics in Figure 5 (a), (b),
 550 which occur for most of the parameter range $0 < \sigma_z < \sigma_z^-$, are not a solution desired by
 551 DGOM modellers, as each population (functional type) is included to fulfil a specific
 552 biogeochemical role.

553 Increasing σ_z substantially, past the intermediate region where the specialist system is
 554 chaotic (Fig. 3(b), (d)) until $\sigma_z \approx \sigma_z^+$, leads again to similar dynamics in both the obligate
 555 generalist and specialist systems. However, now the system has P_2 being grazed into
 556 extinction and settling onto a stable limit cycle of alternating P_1 and Z blooms. As we
 557 near this situation, where the generalist and specialist systems are again effectively the
 558 same, the solutions are quite different (Fig. 5 (c), (d)). In the generalist system (Fig. 5(c))
 559 the three populations exist in a stable equilibrium, and P_2 smoothly declines to zero as
 560 $\sigma_z \rightarrow 0.549$. P_2 's behaviour in the specialist system is quite different, as it periodically
 561 blooms from very low levels to briefly dominate the biomass in the system (Fig. 5(d))
 562 before collapsing as P_1 then blooms. The succession from a P_2 dominated community to
 563 a P_1 dominated community occurs along a line ($P_1 + P_2 \approx 0.96$) very close to the lid of the
 564 ecospace, in the only region of E where P_1 can outcompete P_2 .

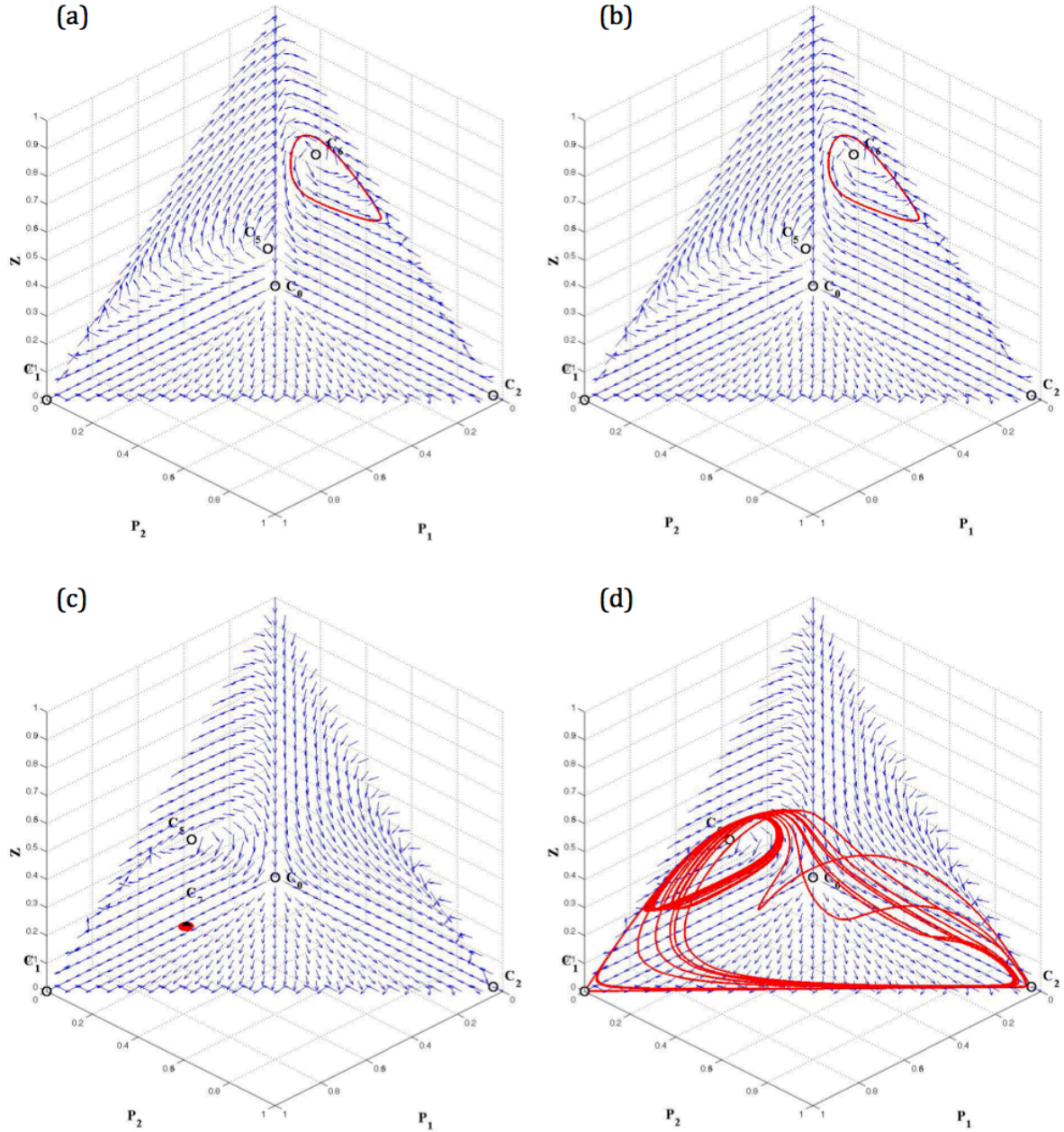


Figure 5. Trajectory of the *NPPZ* system with transients eliminated. Blue arrows show the vector fields on the boundaries of *E* – the length of each arrow is proportional to the strength of each vector. (a) facultative generalist ($\rho = 1, \sigma_z = 0.10$); (b) facultative specialist ($\rho = 0, \sigma_z = 0.10$); (c) obligate generalist ($\rho = 1, \sigma_z = 0.45$); (d) obligate specialist ($\rho = 0, \sigma_z = 0.45$).

Figure 5(a, b) shows that C_6 controls the dynamics of the system when Z is a facultative generalist grazer and drives P_1 to extinction, despite P_1 not having a natural mortality.

573 This outcome can be achieved because Z prefers P_1 and can survive on P_1 or P_2
 574 independently. When C_6 is unstable (as shown here), the dynamics is a stable oscillation
 575 (limit cycle) near C_6 . Figure 5(c) reveals C_7 is a strong influence on the dynamics of the
 576 system when Z is an obligate generalist. In this case the system has a stable limit cycle
 577 around C_7 . Here, all populations coexist with blooms in P_1 followed by a bloom in Z . As
 578 the Z population increases it rapidly grazes P_1 down to levels where it can no longer
 579 sustain Z 's growth, and the grazer population then collapses from want of food. This
 580 provides P_2 with the opportunity to bloom on the newly re-mineralised inorganic
 581 nutrient. However, as P_2 consumes inorganic nutrient N it reduces the available nutrient
 582 to the point where it can no longer grow. At the C_2 values $P_2 = 0.9591$, $N = 0.0409$ P_1
 583 remains able to regrow by invading the P_2 dominant bloom (due to its zero natural
 584 mortality), and it eventually outcompetes P_2 and the cycle repeats. Note that the region
 585 of the ecospace where P_1 can outcompete P_2 is restricted to a small region within
 586 $\frac{\kappa_2 \sigma_2}{\mu_2 - \sigma_2} = 0.0409$ of the lid (i.e. when the available inorganic nutrient falls to about 4% of
 587 the total nutrient).

588 The case for a specialist grazer with a low mortality rate (Fig. 5(a)) is similar to the case
 589 for a generalist grazer with a low mortality rate (Fig. 5(b)). In both cases, Z drives the
 590 "immortal" P_1 to extinction with its heavy grazing pressure. Z then coexists in a stable
 591 equilibrium with the less palatable/preferred P_2 , but at a population size several times
 592 that of its prey, a very unusual state for a grazer.

593 We parameterised our simple models of interacting plankton populations so that in the
 594 absence of a grazing zooplankton population, P_1 is eventually a more successful
 595 competitor than P_2 (despite P_2 initially growing faster when nutrient levels are high).
 596 The zero isoclines of these prey populations in our model do not intersect in the
 597 ecospace E for very small Z , and the outcome of their competition, when P_1 drives P_2 to
 598 extinction, is determined by R^* theory. The zooplankton has a distinct preference for P_1

599 and grows much better on it ($\phi_1 > \phi_2$), and thus “kills the winner” as suggested by
600 Vallina et al. (2014). When grazing is significant (for instance, the Z mortality range
601 $0 < \sigma_z < 0.24$), the “weaker” competitor P_2 dominates P_1 – thus the grazer’s preference
602 for the dominant (and immortal in the absence of predation) prey outweighs the prey’s
603 ability to compete. Under this facultative grazing strategy, where Z can survive by solely
604 grazing either of the phytoplankton populations, the zooplankton typically make up
605 more than 50% of the biomass.

606 When the generalist grazer grazing pressure weakens (due to its increasing mortality
607 rate) and Z becomes obligate on P_1 (in the range $0.1708 = \sigma_z^- < \sigma_z < \sigma_z^+ = 0.5705$) then P_1 ,
608 increasingly with σ_z increasing, regains dominance over P_2 in the ecosystem. Note that
609 Z rarely takes more than 20% of the biomass under this generalist grazing strategy, but
610 it exists in a stable equilibrium with its prey. This renders the system amenable to
611 simple tuning to reproduce observed data, however, P_2 has been driven to extinction
612 when this occurs.

613 In contrast, the specialist grazer strategy initiates a more chaotic invasion sequence,
614 with first P_2 and then P_1 blooming, which happens over most of the obligate regime. For
615 the specialist grazing strategy (Fig. 5(d)), we see strongly fluctuating P_1 – Z orbits
616 interspersed with zones where $Z < 1\%$ while P_1 and P_2 take turns in accounting for over
617 95% of the biomass. No longer does the interior coexistence state (C_7) closely control
618 the solution as it did for the generalist obligate grazer. When σ_z approaches σ_z^+ , the
619 ecology shows the appearance of a more fragile orbit – a fairly extreme dynamical
620 outcome where an apparently robust system witnesses invasions or outbreaks of a
621 competitor that has a population size so small as to be unobservable for all practical
622 purposes. Here the long (decadal) averages of the primary producers’ fraction of the
623 biomass approximates 95%. The price that the specialist grazer Z pays for this reliable
624 food supply is that its own population falls to a very low level interspersed with an
625 occasional bloom where it briefly accumulates 20% of the biomass.

Plankton systems with facultative grazers appear to be unaffected by whether the grazing strategy is generalist or specialist. In this case, Z grazes P_1 to extinction and survives on P_2 . Figure 5 (a) and (b) show Z taking up approximately 60% of the biomass - such inversion of the trophic pyramid is known as the “clear water” stage in lakes (Straskraba et al., 1999).

When Z is an obligate grazer, changing from a generalist to a specialist grazing strategy leads to a dramatic change in the dynamical outcomes. For the generalist grazer we have the stable equilibrium of Figure 5(c), where P_1, P_2, Z oscillate in small blooms while tending to the values given by the C_7 equilibrium point. Here P_1 and P_2 take up most of the biomass, but Z now retains a smaller share of the biomass (about 5-10%). This is in keeping with classical views of “trophic pyramids” where the total biomass in each level is approximately 10% of the biomass in the trophic level below (Begon et al., 2005; Krebs, 2000). However, when Z is a specialist obligate grazer the system is chaotic with most of the biomass in P_1 and Z , alternating with blooms where P_2 briefly dominates the system. The dynamics of this plankton system depend on the properties of the zooplankton grazer: facultative grazers generally produce stable systems; whereas obligate grazers may produce stable or chaotic dynamics depending on their grazing strategy.

Conclusions

We have shown that a fundamental choice of zooplankton grazing strategy, whether it is a specialist or generalist grazer, can have dramatically different impacts on model dynamics depending on whether the zooplankton is functioning as a facultative or obligate grazer. We show that the transition from facultative to obligate grazer can occur under a change in parameters that might be expected in climate change scenarios, and that may not be obvious unless the model is examined in a formal consumer resource framework. The implication for DGOM and similar models is that models that produce quite stable and consistent dynamics when the zooplankton functions as a facultative grazer could produce very different dynamics when the zooplankton becomes an obligate grazer, as may occur in climate change scenarios.

The demand for DGOMs to predict how the biogeochemical cycling of key compounds such as carbon dioxide and dimethylsulphide will influence climate change, and be affected by climate change, has placed plankton modellers in the invidious position of having to provide predictive models both in the absence of a solid theoretical understanding of the population interactions involved and a paucity of empirical data to test their models against. At best, these models can hope to be plausible. In cases where analogous models reproduce contemporary data equally well, but produce different predictions of the future, there is little to support choosing one model over another. Model inter-comparison projects such as MAREMIP (Sailley et al., 2013)) are useful tools to tease out why models might produce different predictions, but the endogenous dynamics arising from the properties of the plankton population interactions can be obfuscated by physical forcings and numerical artefacts.

We have shown that systems with obligate grazers may be more susceptible to chaotic dynamics than systems with facultative grazers. Despite the apparent undesirability of chaotic dynamics for climate prediction, chaotic dynamics have been suggested to explain biodiversity in plankton (Huisman and Weissing, 1999; Scheffer et al., 2003). Biodiversity in homogeneous environments is a key attribute that DGOMs should be able to reproduce, although the evidence for chaotic dynamics facilitating biodiversity is equivocal (Schippers et al., 2001). This is not a pressing question at the current stage of development of DGOMs, where their application is primarily to model the influence of plankton on climate, but may be a crucial question in the next stage of development, where the impact of climate on plankton systems, together with the high trophic level populations they support, and the consequent feedback on climate, is the key question.

DGOMs are designed to simulate the carbon uptake in, and export from, the well-mixed upper ocean layers, and our results suggest that the choice of a generalist grazing functional form will give models that can be readily, and stably, tuned to historical data. These models will respond quite benignly to global warming, which may increase water temperatures past the thermal optimum for zooplankton, and thus increase the zooplankton mortality coefficient into the obligate region. Conversely, zooplankton may increase their ingestion rates in response to climate change (Wilken et al., 2013), effectively reducing their mortality coefficient, as it is the relative size that is important not the absolute value. This pushes an obligate zooplankton population into the

687 facultative region. Our results suggest that DGOM developers should be aware of the
688 implications of these changes in feeding strategy for the dynamical properties of their
689 models.

690 Unfortunately, the development of the complex marine plankton models central to
691 DGOMs has proceeded perforce, as Anderson (2005) suggests, by “running before we
692 can walk”. Zooplankton grazing formulations have been recognised as an impediment to
693 development of these models (Franks, 2002), in fact Mitra et al. (2014b) categorise the
694 knowledge level of all aspects of modelling zooplankton grazing as limited or minimal. It
695 is well known that different choices of functional forms in ecosystem models can lead to
696 very different properties (Edwards and Brindley, 1996; Edwards and Brindley, 1999;
697 Steele and Henderson, 1981; Steele and Henderson, 1992), with chaotic dynamics being
698 possible even in very simple models (Hastings and Powell, 1991; Previte and Hoffman,
699 2010; Woods et al., 2005). It has been suggested that the palatability of prey can affect
700 zooplankton grazing and influence bloom development (Mitra and Flynn, 2006).
701 Zooplankton grazing formulations have been identified as potentially key determinants
702 of differing dynamics of DGOMs (Gentleman et al., 2003; Vallina et al., 2014), and this
703 view is supported and extended by our results.

704 We considered two aspects of zooplankton grazing that have not to our knowledge been
705 considered in previous work, specialist vs generalist foraging, and obligate vs facultative
706 grazing. Both of these choices, that model developers must make, turn out to have
707 important implications for model dynamics. While known to occur in plankton
708 ecosystems, our results suggest that the distinction between obligate and facultative
709 grazing should be a focus of empirical research to determine its ubiquity in real
710 ecosystems. When a zooplankton population is a facultative grazer (that is, it can survive
711 on either of its food sources independently), whether it forages as a specialist or a
712 generalist does not make any qualitative difference to the dynamics of the model.
713 However, when the zooplankton population is obligate on the existence of a specific food
714 source, specialist grazing induces chaotic dynamics. It is an interesting observation that
715 such nutritionally advantageous strategies for the zooplankton (Gentleman et al., 2003)
716 may destabilize the system. Conversely, generalist foraging appears to suppress any
717 chaotic dynamics for obligate grazers and allows the non-critical food source to resist
718 extinction for longer.

These results do not make the job of the developers of DGOMs easier, but rather provides them with additional decisions and/or assumptions that must be made when developing models. Our results contribute to the pool of knowledge that model developers use to inform these decisions and to evaluate what the impact of those decisions might be on their model predictions. The changed outcomes in terms of which phytoplankton population dominates the ecology needs to be evaluated depending on the use of the model:

- The primary producer that wins under R^* theory (Tilman, 1977) will dominate the system when obligate grazers are sufficiently weakened (as the zooplankton mortality σ_z increases towards the corresponding critical value σ_z^+), which could follow global warming or over-fishing of higher trophic levels that lead to increased natural mortality or external grazing pressure on the zooplankton;
- In contrast, the less-preferred primary producer will dominate the system under stronger grazer preference for the R^* winner. Then the zooplankton preferentially grazes the notionally dominant (and in this case “immortal”) phytoplankton down, which remains the status quo for the facultative regime and nearly half the obligate regime in our example.

Our simple model suggests which functional forms lead to “desirable” modelling outcomes for ecosystem behaviour and supports similar findings from studies of other zooplankton grazing formulations (Gentleman et al., 2003; Steele and Henderson, 1992; Vallina et al., 2014). Unfortunately it can’t tell us which option represents the most influential, the most realistic, or even the most common interactions in real plankton ecosystems, but it does suggest that it is important to resolve this question. It also raises the question of whether the plankton functional type responsible for controlling the carbon cycle in a model should be given properties more like our P_1 (slower growing, more palatable/nutritious, low natural mortality) or our P_2 (faster growing, competes for scarce nutrients better, less palatable/nutritious, high natural mortality). This is not to suggest that the parameterisation of complex ecosystem models should proceed in denial of measured data on parameter values, but it must be recognised that parameter values are system-dependent. For example, there are no universal phytoplankton growth rates or universal zooplankton mortality rates. These values vary according to

the biotic and abiotic environment in which the population exists. The measured parameter values that form the basis of the parameter spaces searched for parameter sets for ecosystem models often come from studies of many different populations in many different places at many different times. Anecdotal evidence suggests that it is not uncommon for parameterisation routines searching these spaces to struggle to find parameter sets for which the models even work, let alone produce plausible answers. This study tries to clarify the influence of, and simplify those decisions about, the functional forms and the associated parameters to ensure realistic outcomes of the modelling process.

The role of zooplankton grazing strategies in determining the presence of chaotic dynamics in plankton systems has not received a lot of attention. A study by Gragnani et al. (1999) found that changing zooplankton (*Daphnia*) selectivity and the nutritional values of its prey, green algae and filamentous cyanobacteria, could introduce chaotic dynamics into a model with a stable equilibrium. This empirical study was similar in conception to this our theoretical one, effectively an *NPPZ* model with conservation of mass and generalist zooplankton grazing, but it included a 'self-shading' feedback on the autotroph growth rate and Holling Type III zooplankton mortality. While coming to broadly similar conclusions that the zooplankton grazing can determine the presence or absence of chaotic dynamics, they did not investigate different foraging strategies. Their use of different autotroph growth and zooplankton mortality terms further emphasises the importance of understanding the choices made when constructing models. For example, Hastings and Powell (1991) and Scheffer (1991) describe how they carefully selected the function forms for their model equations to ensure chaos, although both chose very simple zooplankton grazing terms.

The dimension of the system may also have important consequences for choices made. Our results with two phytoplankton populations and one zooplankton population show that generalist zooplankton grazing suppresses chaotic dynamics. Beninca et al. (2009) showed that chaotic dynamics were possible with generalist zooplankton grazing in a similar system with two phytoplankton and two zooplankton. The presence of chaos in this case relied on there being competitive coupling between both the phytoplankton and the zooplankton populations. Although this system remained of sufficient dimension for chaos to occur, the removal of a zooplankton population in this case suppressed the

chaotic dynamics, consistent with our results. This is also consistent with the general rubric proposed by Fussmann and Heber (2002) that the propensity for chaos increases as trophic complexity increases.

We have focused on the ‘endogenous’ dynamics of this system that arise solely from the interactions of the three populations. DGOMs, however, solve the equations describing the population interactions in a ‘physical’ scenario, that includes the influence of depth- and seasonally-varying forcings such as irradiance and temperature, and processes such as advection and mixing that move members of populations around. Further, the numerical integration schemes used to solve the pdes of many DGOMs lack the numerical precision of the schemes used to solve the odes that describe the population interactions alone. Anecdotal evidence suggests that the chaotic dynamics evident in ode models often disappear when the same equations are solved in forced pde form. Whether this is due to the external forcings, physical processes or the numerical integration schemes provides an avenue of further investigation.

The crucial choice of grazing strategies (generalist versus specialist) pragmatically depends on many objectives: whether the application outcome requires stable equilibrium populations or plankton successions; whether system change should be sensitive to keystone species or not, etc. Which choice best represents the real world remains moot, but the key result of this work is that we need to be aware that these seemingly minor choices may dramatically affect model behaviours. In particular, plankton models that are being developed to simulate gas exchange between the ocean and atmosphere in a changing climate may make dramatically different predictions as a result of seemingly innocuous decisions on the part of the model developers, and consequently may have profound implications for predictions of future climate (Charlson et al., 1987; Falkowski et al., 2003; Falkowski and Oliver, 2007). Our results support the conclusions of Mitra et al. (2014b) that a significant research effort is required to address the paucity of theoretical and empirical constraints on the formulation of zooplankton grazing strategies used in plankton models for all applications.

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