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Chaos in plankton models: Foraging strategy and seasonal forcing

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ABSTRACT

The dynamics of plankton ecosystems have long been of interest to ecologists and mathematicians, with some of the earliest examples of chaotic dynamics being provided by ecological models. Mortality terms were initially identified as determinants of chaos in simple ecosystem models, but relatively little attention has been given to the role of grazing terms. The behaviour of omnivores has arisen as a particularly interesting case. Recent experiments have revealed that plankton omnivores may change their feeding behaviour in response to changes in temperature, and is therefore of interest to plankton modellers contributing models of biogeochemical cycling in the ocean to climate models. In this paper we consider the role of an omnivorous zooplankton's foraging strategy, seasonal variations and the choice of functional forms on the dynamics of a simple two prey–one predator plankton model, within a Conservative-Normal framework. We find that assumptions about the way the predator forages for food, the specific form for grazing and mortality terms, and seasonal changes in the environment all qualitatively affect the predictions that the model will produce. In particular, discriminate foraging and seasonal variations engender chaotic dynamics while Holling Type III grazing and quadratic mortality terms suppress chaotic dynamics.

1. Introduction

Phytoplankton and zooplankton together form the basis of the oceans' food chain. Through photosynthesis, limited by the availability of dissolved nutrients and solar irradiance, phytoplankton convert carbon dioxide from the Earth's atmosphere, drawing it down into the deep oceans, in the process producing half of the world's atmospheric oxygen (Bork et al., 2015). Phytoplankton are the primary organic food source for zooplankton, which are in turn the food source for fish and whales.

The potential importance of plankton as key indicators of climate change cannot be underestimated, since the viability of various phytoplankton depends upon water temperature and acidity. Long term climate change could affect phytoplankton populations, their seasonal blooms and/or their extinction (Falkowski, 2012) and in turn, feed back on climate change through changes in biogeochemical cycling of climatically important compounds such as carbon dioxide and dimethylsulphide (Charlson et al., 1987). PlankTOM5 (Le Quéré et al., 2005) and PlankTOM10 (Kwiatkowski et al., 2014) are two examples of global marine ecosystem models, containing many different plankton functional types, aimed at studying the interactions between ocean biogeochemistry and climate change (Mitra et al., 2014). Recent analysis of data has shown the complexity of plankton grazing interactions (Flynn et al., 2013), and its sensitivity to changes in ocean temperature (Wilken et al., 2013).

The Conservative-Normal approach involves a set of ecological rules that characterise the food web, and from which properties of the system can be determined. It was first formulated in a series of papers by Cropp and Norbury (2012a,b) up to two different phytoplankton and two different zooplankton populations with a single nutrient constraining the populations. They used Holling Type II functional forms. Bates et al. (2015) used the Conservative-Normal framework to develop a system of twenty-one coupled nonlinear ordinary differential equations to model a near-shore Antarctic food web. As well as various types of phytoplankton, zooplankton and benthic feeders, the model included fish, whales, seals, penguins and seabirds. The choice of Holling Type III functional forms and nonlinear mortality functions, cast in a Kolmogorov framework, ensured the structural coexistence of each member of the ecosystem as every boundary critical point of the system (where one or more populations were extinct) was locally unstable.

Cropp and co-workers have investigated the role of different types of grazer predation in a prey–prey–predator model with two phytoplankton populations (prey) and one zooplankton population (predator) with Holling Type II functional forms. Linear stability and bifurcation analyses showed that under *indiscriminate* predation (where the predator searches for and eats prey indiscriminately according to what it encounters), only steady states or

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Table 1
The parameters in (2.1), their interpretations and values.

Par.	Process	Value
μ_1	Maximum (seasonal average) rate of N uptake by P_1	1.00
μ_2	Maximum (seasonal average) rate of N uptake by P_2	1.15
κ_1	Half-saturation constant for N uptake by P_2	0.25
κ_2	Half-saturation constant for N uptake by P_2	0.07
ϕ_1	Z grazing rate on P_1	6.18
ϕ_2	Z grazing rate on P_2	1.85
ϵ_1	Half-saturation constant for Z uptake of P_1	5.50
ϵ_2	Half-saturation constant for NZ uptake of P_2	5.50
σ_1	P_1 specific mortality rate	0.00
σ_2	P_2 specific mortality rate	0.26
σ_Z	Z specific mortality rate	0.19
ψ_1	Proportion of P_1 uptake excreted by Z	0.40
ψ_2	Proportion of P_2 uptake excreted by Z	0.40

simple periodic limit cycle solutions obtain. For *discriminate* predation (where the predator preferentially searches for a particular prey, but will eat other prey that it encounters), more complicated periodic as well as chaotic states are also possible.

Here we extend the analysis to consider a *transitionalist* model, which contains these two limits as special cases. We utilise our foraging transition parameter with the commonly used closure parameter (the mortality coefficient of the zooplankton) to produce a two-parameter bifurcation diagram, summarising the nonlinear dynamics and placing the two special cases into context. We also consider the effects of seasonal forcing on the system under both discriminate and in discriminate grazing and finally, vary the underlying functional forms of the grazing terms from Holling Type II to Holling Type III and the mortality terms from linear to nonlinear to extend our investigation to models with structural coexistence.

2. The plankton model

We investigate a model comprising two different phytoplankton populations, P_1, P_2, being grazed upon by one zooplankton population, Z, in the presence of a limiting nutrient N (Cropp and Norbury, 2009):

$$\dot{P_1} = P_1\left[\frac{\mu_1 N}{N+\kappa_1} - \frac{\phi_1 Z}{1+\epsilon_1 P_1 + \rho\epsilon_2 P_2} - \sigma_1\right] = P_1 f(P_1, P_2, Z), \tag{2.1a}$$

$$\dot{P_2} = P_2\left[\frac{\mu_2 N}{N+\kappa_2} - \frac{\phi_2 Z}{1+\rho\epsilon_1 P_1 + \epsilon_2 P_2} - \sigma_2\right] = P_2 g(P_1, P_2, Z), \tag{2.1b}$$

$$\dot{Z} = Z\left[\frac{\phi_1(1-\psi_1)P_1}{1+\epsilon_1 P_1 + \rho\epsilon_2 P_2} + \frac{\phi_2(1-\psi_2)P_2}{1+\rho\epsilon_1 P_1 + \epsilon_2 P_2} - \sigma_Z\right] = Zh(P_1, P_2, Z), \tag{2.1c}$$

together with the nutrient N mass conservation condition:

$$\dot{N} = -\dot{P_1} - \dot{P_2} - \dot{Z}, \tag{2.2}$$

where $P_1 + P_2 + Z + N = 1$. Here the populations P_i and Z are measured by the fractions of limiting nutrient bound into their biomass – N is then the fraction of limiting nutrient (available to the populations) in the nutrient pool. Apart from ρ, the various parameters appearing in (2.1) are explained in Table 1, together with their measured parameter values in the field (see Cropp and Norbury, 2009 for further details). When $\rho = 0$, we obtain the discriminate model considered by Cropp and Norbury (2009), while for $\rho = 1$, we obtain the indiscriminate model considered by Cropp et al. and Moroz et al. We term (2.1) the *transitional* model for which $0 \le \rho \le 1$. The $\rho = 0$ and $\rho = 1$ basic models have ecological significance, while the transitional model enables us to put the two limits into context: we think of ρ as a bifurcation parameter. We extend our bifurcation analysis to $\rho = 1.4$ to capture the complete behaviour of the model.

The transitional model (2.1) also satisfies the Conservative-Normal (CN) parameter constraints (see Cropp and Norbury, 2009). The resource conditions that $f > 0$ and $g > 0$ when $N = 1$ and $Z = 0$ give

$$\sigma_1 < \frac{\mu_1}{1+\kappa_1}, \quad \sigma_2 < \frac{\mu_2}{1+\kappa_2}, \tag{2.3}$$

which translates to $0 < \sigma_1 < 0.8$ and $0 < \sigma_2 < 1.07$ for the measured values in Table 1. Requiring $h > 0$ at the extremities of $P_1 + P_2 = 1$ gives

$$\sigma_Z < \min\left\{\frac{\phi_1(1-\psi_1)}{1+\epsilon_1}, \frac{\phi_2(1-\psi_2)}{1+\epsilon_2}\right\}, \tag{2.4}$$

so that Z survives on either P_1 or P_2 (or a combination of the two): a ‘facultative omnivore’. This is part of a ‘normal’ ecology. From Table 1 this gives $0 < \sigma_Z < 0.17$. However when

$$0.17 < \sigma_Z < \max\left\{\frac{\phi_1(1-\psi_1)}{1+\epsilon_1}, \frac{\phi_2(1-\psi_2)}{1+\epsilon_2}\right\}, \tag{2.5}$$

we obtain an ‘exotic’ ecology, and Z becomes an ‘obligate omnivore’ for $0.17 < \sigma_Z < 0.57$: Z grazes on both P_1 and P_2, but P_1 must be present for Z to survive, so that Z is obligate on P_1.

While (2.5) violates the resource condition on the sign of h at $P_2 = 1$, bifurcation and stability analyses in Moroz et al. show that with Table 1 measured parameter values, the ‘min’ constraint permits only two-dimensional oscillatory behaviour in the (P_2, Z)-plane, whereas the ‘max’ constraint allows three-dimensional periodic oscillations in (P_1, P_2, Z)-space, as well as period-doubling bifurcations and chaos.

The foraging strategy parameter ρ, that transitions from discriminate to indiscriminate grazing, and the zooplankton mortality parameter σ_Z, that determines the prey-dependence of the zooplankton and also closes the model, provide natural bifurcation parameters with which to investigate the dynamical properties of the model. While σ_Z transitions smoothly and we can identify critical values for it at which the trophic classification of the zooplankton population changes, the foraging parameter ρ is only explicitly ecologically defined for $\rho = 0$ and $\rho = 1$. However, we will show that the system smoothly transitions between $\rho = 0$ and $\rho = 1$, and argue that these transition values might reasonably be interpreted to represent transitional foraging strategies. We also extend the examination of the linear stability boundaries of the system for $\rho > 1$ for reasons that are detailed in Section 3.7 and Fig. 1. These values represent enhanced indiscriminate foraging, where the foraging efficiency exceeds the handling time.

3. Critical points

The linear stability analysis of the critical points of (2.1) and (2.2) uses the same notation and labelling as Cropp and Norbury (2009). Indeed the analyses for the origin and prey-only critical points are identical.

3.1. Origin critical point

There is a critical point at the origin, given by $(P_1, P_2, Z, N) = (0, 0, 0, 1)$, whose linear stability is determined from the eigenvalues

$$\lambda_{01} = \frac{\mu_1}{1+\kappa_1} - \sigma_1, \quad \lambda_{02} = \frac{\mu_2}{1+\kappa_2} - \sigma_2, \quad \lambda_{03} = -\sigma_Z. \tag{3.1}$$

From (2.3), we see that this critical point is an unstable saddle.