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Abrupt transitions in dynamics of a NPZD model across Southern Ocean fronts

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ABSTRACT

The Southern Ocean is the largest high nutrient, low chlorophyll region in the global ocean and is subject to strong iron limitation. Iron availability is associated with the interaction between the Antarctic Circumpolar Current (ACC) and topographic features such as the Kerguelen Plateau in the Indian Sector of the Southern Ocean. The fronts of the ACC also provide important environmental delineations for Southern Ocean ecosystem structure. Here, we implement a NPZD (nitrogen, phytoplankton, zooplankton, detritus) model together with an optimal control algorithm along three meridional transects across the Antarctic Circumpolar Current. Our study represents the first spatial application of this model, and considers potential environmental drivers of parameter variability and community dynamics.

In iron-limited open ocean regions, this model captures seasonal processes well but does not converge in more complex regions, such as the iron fertilized Kerguelen Plateau and sea ice areas. All variables show marked meridional changes, which are likely associated with the fronts of the Antarctic Circumpolar Current. This technique indicates that the different bodies of water associated with the circumpolar current exhibit different ecosystem dynamics, a result that is likely caused by distinct NPZD communities. Overall, our findings contribute to broadscale understanding of the drivers of lower trophic level ecosystem dynamics across physical boundaries in the Indian Sector of the Southern Ocean, and can be used to help guide further modelling efforts.

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1. Introduction

1.1. The southern ocean ecosystem

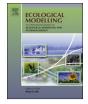
The Southern Ocean with its energetic Antarctic Circumpolar Current (ACC) is the largest high nutrient, low chlorophyll (HNLC) region in the global ocean (Martin et al., 1990; Minas and Minas 1992) and is subject to complex plankton bloom processes. Without any continental boundaries along its path, the ACC plays a key role in global climate, transmitting signals between the Atlantic, Pacific and Indian Ocean (Gille 2002). As stated by Martin et al. (1990), iron fertilization of the Southern Ocean could have the potential to evoke a plankton bloom big enough for carbon dioxide drawdown binding the majority of CO₂ produced through anthropogenic

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http://dx.doi.org/10.1016/j.ecolmodel.2017.05.030 0304-3800/© 2017 Elsevier B.V. All rights reserved. burning of fossil fuels. In more recent studies the link between the limited availability of iron and low primary production has been confirmed (De Baar et al., 1995; Boyd et al., 2000), while regions with silicate depletion, limiting diatom production, have also been identified (Coale et al., 2004).

The interaction of the large-scale mean flow of the ACC with its energetic eddy field leads to multiple fronts across the ACC (Sokolov and Rintoul 2007). These fronts separate water masses, with each of these masses have distinct physical properties and consequent plankton, nutrient and iron concentrations (Sohrin et al., 2000) and have a large impact upon the intensity of blooms. This phenomenon proves to be particularly important when looking at the complex plankton blooms occurring annually around the Kerguelen Plateau (70°E) as the fronts interacting with topographical features create upwelling, supplying iron to the upper ocean (Mongin et al., 2009). Understanding the complex processes in this vast and important HNLC region is essential not only for fisheries and sustainable management of the natural resources of the Southern Ocean (Croxall





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and Nicol 2004), but also for the global climate due to its role in the carbon cycle (Gille 2002; Gutt et al., 2015).

1.2. NPZD models and optimal control

In developing any ecosystem model there is a need to find an appropriate balance between simplicity – lower computational costs, fewer unknown parameters, simple interpretation – and complexity. For lower trophic-level marine ecosystem models, a common means of resolving this compromise is to combine the different variables of the ecosystem into four bulk-variable categories: Dissolved organic nitrogen (N), phytoplankton (P), zooplankton (Z) and detritus (D) (Oschlies and Garçon, 1999Oschlies and Garçon 1999) thus combining species of similar physiological characteristics. This approach is called a NPZD model and has been applied successfully to various regions in the global ocean (Schartau and Oschlies 2003a,b; Xu et al., 2008, Kidston et al., 2011).

Traditionally NPZD models have assumed a static species composition. Recent work (Jarbi et al., 2012; Mattern et al., 2012; Melbourne-Thomas et al., 2015) has included a time-dependent parameter in order to represent a varying species composition and complex seasonal processes, resulting in a closer fit to observations. Melbourne-Thomas et al. (2015) used an optimal control approach to model ecosystem dynamics at two locations south of Tasmania in the Southern Ocean (140°E, 52°S & 58°S). They allowed one parameter, the photosynthetic efficiency α , to vary as a function of time. Photosynthetic efficiency reflects the ability of the phytoplankton community to convert light into energy. It is primarily influenced by the species composition of phytoplankton, temperature and light availability (Harrison and Platt 1986; van Hilst and Smith Jr 2002, Falkowski and Raven 2013), all of which vary throughout the year in the Southern Ocean.

The aim of this paper is to extend the NPZD model of Melbourne-Thomas et al. (2015) and apply it to three full transects in the Southern Ocean, including one immediately downstream of the Kerguelen Plateau. This represents the first spatial application of this type of model for the region, and provides an opportunity to evaluate the potential importance of environmental drivers in determining modelled plankton community characteristics. Specifically, the transect-level spatial replication offers us detailed information about the model's ability to reproduce existing bloom patterns as environmental forcing factors and NPZD communities change. Covering areas of iron and silicate fertilization (e.g. the Kerguelen Plateau) to iron depleted open ocean regions and sea ice areas in high latitudes with scarce observational data we investigate the models sensitivity and restrictions in its applicability. We interpret our results taking into account the Antarctic Circumpolar Currents (ACC) frontal positions and the seasonal patterns of the time-varying photosynthetic efficiency parameter. The outcomes and sensitivity to environmental forcing of this simple model give us important insights into the relationships between the different forcing variables governing the system state.

2. Material and methods

2.1. The model

We use the NPZD model of Melbourne-Thomas et al. (2015) which in turn is based on the four-component NPZD model by Oschlies and Garçon (1999) (Fig. 1). In contrast to the model by Oschlies and Garçon (1999), the mixed layer depth (MLD) and its daily rate of change (Evans and Parslow 1985; Matear 1995) is not modelled but taken from observational data (see Section 3.2). Zooplankton is the only motile entity and thus is the only component that changes with a decrease or increase of MLD due to active

movements following the mixed layer. Within the mixed layer all components are assumed to be present in a uniform distribution. We use a quadratic phytoplankton mortality rate (Kidston et al., 2011) as this fits the population dynamics better than a linear rate.

The evolution of the components of N, P, Z and D is defined using the following equations:

$$\begin{aligned} \frac{dN}{dt} &= \mu_D D + \gamma_2 Z - \bar{J}(M, t, N) P + \frac{w^+(t)(N_0 - N)}{M}, \\ \frac{dP}{dt} &= \bar{J}(M, t, N) P - G(P) Z - \mu_P^2 P^2 - \frac{w^+(t) P}{M}, \\ \frac{dZ}{dt} &= \gamma_1 G(P) Z - \gamma_2 Z - \mu_Z Z^2 - \frac{w(t) Z}{M}, \\ \frac{dD}{dt} &= (1 - \gamma_1) G(P) Z + \mu_Z Z^2 + \mu_P^2 P^2 - \mu_D D - \frac{(w_D + w^+(t)) P}{M}. \end{aligned}$$

where N₀ is the nitrogen concentration below the mixed layer (Matear 1995; Kidston et al., 2011), M is the mixed layer depth, $w^+ = max(w(t), 0)$, where w(t) is the daily rate of change in M and all other variables and their parameter values are defined in Table 1.

Using a Holling-type III function the decline in phytoplankton due to zooplankton grazing is defined as (for parameters see Table 1.):

$$G(P) = \frac{g\varepsilon P^2}{g + \varepsilon P^{2'}}$$

and the daily average growth of phytoplankton is calculated as:

$$\bar{J}(M, t, N) = \min\left(\bar{J}(M, t)\right) J_{max} \frac{N}{K+N}$$

Following Oschlies and Garçon (1999), the nutrient limitation $(J_{max} = ab^T)$ is assumed to be independent from light limitation $(\bar{I}(M,t))$. To obtain the latter averaged over the MLD we integrate over one day-night cycle (Matear 1995; Kidston et al., 2011)

$$\bar{J}(M,t) = 2\frac{1}{M} \int^{\tau} \int^{M} J(I) dz dt$$

Here 2τ is the day length (as calculated from Brock (1981)), *I* denotes the photosynthetically active portion of incident solar radiation as a function of depth, while *J*(*I*) calculates the photosynthesis-irradiance relationship (P-I-curve) as defined by the Smith function (Smith 1936; Jassby and Platt 1976):

$$J(I) = \frac{J_{max}\alpha I(z,t)}{\sqrt{J_{max}^2 + (\alpha I(z,t))^{2'}}}$$

where α is the parameter value of the photosynthetic efficiency. I(z,t) is calculated as

$$I(z, t) = I(0, t) e^{(-k_W z)} PAR$$

I(0,t) is equivalent to the incident solar radiation observed directly under the surface of the water and \bar{z} is the effective vertical coordinate with θ as the angle of incidence at noon (for the water depth of *z* in metres)

$$\bar{z} = \frac{z}{\sqrt{1 - (\cos\theta/1.33)^2}}.$$

Assuming a triangular shape of the incident solar radiation throughout the day (Evans and Parslow 1985), the mean incident solar radiation is converted to peak radiation at noon.

All these equations and algorithms were implemented using R (R Development Core Team, 2011) and are provided in the supplementary data along with instructions and comments.

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