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Phytoplankton growth in the Australian sector of the Southern Ocean, examined by optimising ecosystem model parameters

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ABSTRACT

SeaWiFS surface chlorophyll estimates and Levitus nitrate estimates in the Southern Ocean south of Australia (140°E) show that this region is characterised by a high-nitrate low-chlorophyll (HNLC) regime typical of Southern Ocean waters. The HNLC conditions become more prominent moving south from the Sub-Antarctic Zone, with surface chlorophyll generally decreasing and nitrate increasing with latitude. Parameter optimisation experiments were performed using simulated annealing to fit a zero-dimensional nitrogen-based four-component ecosystem model to SeaWiFS surface chlorophyll data in the Sub-Antarctic Zone (SAZ), Polar Frontal Zone (PFZ) and Antarctic Zone (AZ). We hypothesise that bioavailability of iron limits phytoplankton growth in this region. A physiological indicator of iron availability was investigated by optimising three of the model parameters defining maximum photosynthetic growth and maximum photosynthetic efficiency of phytoplankton. The effect of zooplankton grazing and light, mixed layer depth and temperature forcing data on the optimisation results was investigated in further optimisation experiments. An error analysis of the optimised parameter estimates was performed by analysing the Hessian matrix of the cost function.

The parameter optimisations indicate that phytoplankton growth rates in the Polar Frontal Zone and Antarctic Zone are limited by some process not explicitly included in this model, with iron availability being the most likely candidate. Based on these optimisations we support the theory that micronutrient availability is the primary cause of the HNLC conditions in the Australian sector of the Southern Ocean.

1. Introduction

In large areas of the world's oceans there is an excess of nitrate and phosphate that remain unutilised in the surface waters where phytoplankton populations do not manage to bloom sufficiently to strip out the nutrients. There has been considerable debate about the principle factors causing anomalously low phytoplankton biomass in relation to nutrients in the Southern Ocean, the equatorial Pacific and the North Pacific. The Southern Ocean HNLC (high nutrient low chlorophyll) region is particularly important because it is one of the major regions of intermediate and deep-water formation (Sarmiento and Orr, 1991) and Sub-Antarctic waters are an important sink for anthropogenic carbon dioxide (CO_2) (Metzl et al., 1999).

Growth limitation by micronutrients (Boyd et al., 2000; Coale, 1991; Sedwick et al., 1999), limited light availability in the high latitudes (Holm-Hansen et al., 1977; Mitchell and Holm-Hansen, 1991; Smith and Nelson, 1985), suppression of phytoplankton populations by zooplankton grazing (Duce and Tindale, 1991; Miller et al., 1991; Minas and Minas, 1992; Tsuda et al., 2007), or some combination of these factors (Boyd et al., 2001; Chavez et al., 1991; Landry et al., 1997) have been considered to explain HNLC regions.

The most likely micronutrient in limiting phytoplankton growth in HNLC regions is iron (Kolber et al., 1994; Martin and Fitzwater, 1988). Silica is also a possibility (Ku et al., 1995; Leynaert et al., 1996). Iron is an essential nutrient for phytoplankton growth, required for the synthesis of chlorophyll and for the photosynthetic production of organic compounds (Street and Paytan, 2005).

The role of iron in limiting phytoplankton growth in HNLC regions has been given added importance since Martin et al. (1990) proposed the ‘Iron Hypothesis’ speculating that iron deficiency was alleviated in glacial periods due do Aeolian dust deposition in a windier and dryer climate. They hypothesised that this allowed increased phytoplankton productivity and export of CO_2, resulting in the reduced atmospheric CO_2 concentrations that characterise glacial periods. Iron fertilisation of HNLC regions of the ocean has been proposed as a geo-engineering approach to mitigate climate change, by stimulating a phytoplankton bloom large enough to remove substantial amounts of CO_2 from the atmosphere (Denman, 2008). Additionally, natural delivery of iron to the Southern Ocean by dust from land masses and advective sources from shelf sediments is projected be

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significantly altered under future climate change scenarios (Bowie et al., 2011).

A number of iron enrichment experiments and incubation experiments (Bakker et al., 2005; Blain et al., 2004; Boyd et al., 2000; Coale et al., 1996; Franck et al., 2000; Martin et al., 1994; Timmermans et al., 1998; Tsuda et al., 2003) have demonstrated an increase in phytoplankton growth and primary productivity with iron enrichment of surface ocean waters. The Southern Ocean Iron Release Experiment (SOIREE), an in situ mesoscale iron fertilisation experiment, provided evidence of enhanced algal growth rates due to iron enrichment at 140°E, 61°S (Boyd et al., 2000); however many of the previous Southern Ocean studies provided ambiguous results, with increases in chlorophyll in both iron enriched treatments and control treatments (reviewed in de Baar and Boyd, 2000).

Although results support the importance of iron in regulating primary productivity, they do not imply that iron is the ultimate control (Fennel et al., 2003). Recent studies show that the factors controlling phytoplankton biomass in the Southern Ocean are still open to debate. Boyd et al. (2001) studied the effect of iron supply and irradiance on phytoplankton growth in the SAZ (Sub-Antarctic Zone) and PFZ (Polar Frontal Zone) of the Australian sector of the Southern Ocean and found that in both regions iron was limiting algal growth rates whilst in the PFZ light was also limiting growth. In contrast van Oijen et al. (2004) studied the effect of iron supply and irradiance on phytoplankton growth in the Atlantic sector of the Southern Ocean and found that low phytoplankton biomass was mainly caused by light limitation rather than iron. Conversely Banse (1996) studied the effects of underwater irradiance, iron and grazing on SAZ chlorophyll and found that zooplankton grazing was controlling the phytoplankton populations.

Ecosystem models provide a useful tool to separate the factors indicated in the control of phytoplankton biomass and look at different processes individually. Complex models have been developed to simulate the role of iron on marine ecosystems. Fasham et al. (2006) developed a multi nutrient model incorporating iron cycling and performed a parameter optimisation to fit the model to iron replete and iron limited conditions. They showed that underwater light levels have a more limiting effect on phytoplankton growth than iron supply at their experiment site in the Indian Ocean sector of the Southern Ocean. Mongin et al. (2006) applied a flexible composition model incorporating iron cycling, phytoplankton iron/carbon ratios and iron limitation to the same region and found phytoplankton growth to be strongly limited by an interaction of iron and light, with grazing also being a significant factor.

There have been a number of iron modelling studies that do not explicitly include iron as a state variable (Denman and Pena, 1999; Fennel et al., 2003; Hense et al., 2000). Fennel et al. (2003) looked at the effect of iron on phytoplankton photosynthetic growth rates to investigate inter-glacial changes in CO_2 concentrations. Hense et al. (2000) used a 5–7 compartment model to investigate the role of iron limitation in the PFZ by using different Si:N uptake ratios and reduced phytoplankton growth rates. Denman and Pena (1999) used a 4 compartment NPZD (Nitrate–Phytoplankton–Zooplankton–Detritus) model to simulate the planktonic ecosystem and examine iron limitation in the North Pacific by reducing growth rates of phytoplankton. They found that the annual cycle of surface layer nitrate concentrations in this region was best reproduced by reducing the maximum photosynthetic growth by a factor of 3.0–3.5.

Here we present a modelling study to explore the limitation of phytoplankton growth in the HNLC regime in the Australian sector of the Southern Ocean (Fig. 1). The HNLC conditions in this region become more prominent moving south from the SAZ, with surface chlorophyll generally decreasing and nitrate increasing with latitude (Figs. 2 and 4). We perform parameter optimisation experiments using simulated annealing to fit a zero dimensional nitrogen based model to SeaWiFS surface chlorophyll data in three distinct regions of the Southern Ocean in the Sub-Antarctic Zone, Polar Frontal Zone and Antarctic Zone. Possible reasons for the latitudinal variation in phytoplankton biomass in this region are discussed in light of what our parameter estimates indicate about the ecosystem functioning. We hypothesise that iron is limiting phytoplankton growth but other explanations such as light availability, temperature and zooplankton grazing are also considered.

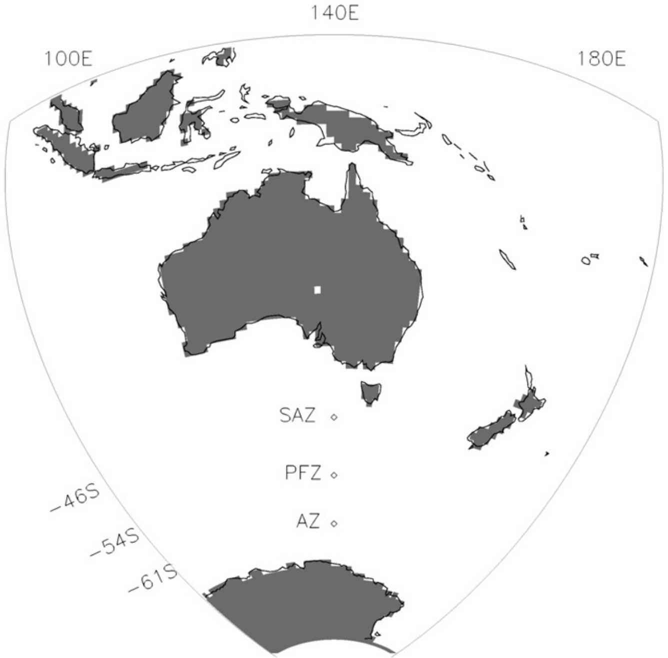

Fig. 1. Location of the study area, showing and the three experiment sites in the SAZ, PFZ and AZ in the Australian sector of the Southern Ocean.

Current knowledge of iron cycling in seawater, and the availability of iron to phytoplankton, shows that the cycling of iron is complex and qualitatively different from the cycling of macronutrients (Fennel et al., 2003). The processes relating to the cycling of iron are poorly quantified, particularly those that affect bioavailability and biological uptake (Johnson et al., 1997; Wells et al., 1995). The main physiological response of phytoplankton to iron deficiency is a reduction in light saturated photosynthetic growth and an increase in the initial slope of the P–I curve, the photosynthetic efficiency. Greene et al. (1991) found a 2-fold reduction in light saturated photosynthesis and a 1.3 fold increase in the initial slope of the P–I curve between iron replete and iron deficient cells. This, combined with the lack of observations of iron in the Southern Ocean to validate complex model parameterisations, governs the decision to use a simple NPZD model, which does not explicitly include iron as a state variable (Oschlies and Garcon, 1999), and optimise the parameters for maximum photosynthetic growth and photosynthetic efficiency.

This paper is organised as follows: Section 2 describes the oceanographic characteristics of the study region. Section 3 explains the experimental design of this study. Section 4 presents and discusses the results of our experiments. Section 5 summarises this study.

2. Oceanographic characteristics

In this section the physical characteristics of the experiment locations are described and the forcing used to run the model is explained.

2.1. Physical setting

The Southern Ocean is separated from the warmer and saltier waters of the subtropical oceans by pronounced meridional gradients in