ELSEVIER

Deep-Sea Research II 53 (2006) 601–619

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Simulation of upper-ocean biogeochemistry with a flexible-composition phytoplankton model: C, N and Si cycling and Fe limitation in the Southern Ocean

Mathieu Mongin[a,b,*], David M. Nelson[a], Philippe Pondaven[b], Paul Tréguer[b]

[a]*College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97311, USA*
[b]*Institut Universitaire Européen de la Mer-UMR CNRS 6539, Technopole Brest-Iroise, Place Nicolas Copernic, F-29280 Plouzané, France*

Received 30 November 2004; accepted 30 January 2006
Available online 24 May 2006

Abstract

We previously reported the application of an upper-ocean biogeochemical model in which the elemental composition of the phytoplankton is flexible and responds to changes in light and nutrient availability [Mongin, M., Nelson, D., Pondaven, P., Brzezinski, M., Tréguer, P., 2003. Simulation of upper-ocean biogeochemistry with a flexible-composition phytoplankton model: C, N and Si cycling in the western Sargasso Sea. Deep-Sea Research I 50, 1445–1480]. That model, applied in the western Sargasso Sea, considered the cycles of C, N and Si in the upper 400 m and limitation of phytoplankton growth by N, Si and light. We now report a new version of this model that includes Fe cycling and Fe limitation and its application in the Southern Ocean. The model includes two phytoplankton groups, diatoms and non-siliceous forms. Uptake of NO_3^- by phytoplankton is light dependent, but NH_4^+, $Si(OH)_4$ and Fe uptake are not and can therefore continue through the night. The model tracks the resulting C/N and Fe/C ratios of both groups and Si/N ratio of diatoms, and permits uptake of C, N, Fe and Si to proceed independently when those ratios are close to those of nutrient-replete phytoplankton. When they indicate a deficiency cellular C, N, Fe or Si, uptake of the non-limiting elements is controlled by the content of the limiting element in accordance with the cell-quota formulation of [Droop, M., 1974. The nutrient status of algal cell in continuous culture. Journal of the Marine Biological Association of the United Kingdom 54, 825–855]. The model thus identifies the growth-limiting element and quantifies the degree of limitation from the elemental composition of the phytoplankton.

We applied this model at the French KERFIX site in the Indian Ocean sector of the Southern Ocean, using meteorological forcing for that site from 1991 to 1995. As in the Sargasso Sea application, the flexible-composition structure provides simulations that are consistent with field data with only minimal tuning of model parameters. The model reproduces the high-nutrient, low-chlorophyll (HNLC) conditions observed at the KERFIX using much lower and more realistic grazing loss terms than those used in KERFIX simulations that do not include Fe limitation. Cellular Fe/C ratios indicate that both diatoms and non-siliceous phytoplankton are strongly limited by interaction between Fe limitation and low irradiance throughout most of the year in these simulations, with grazing a significant secondary factor.

Keywords: HNLC; Fe; Grazing; Phytoplankton; Elemental ratio; Redfield ratio

---

[*] Corresponding author. *New address*: ACE CRC Private Bag 80 Hobart, Tasmania 7001, Australia.
E-mail address: mathieu.mongin@acecrc.org.au (M. Mongin).

0967-0645/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2006.01.021

1. Introduction

Over the past decade high-nutrient, low-chlorophyll (HNLC) ocean systems have been studied extensively because of their potential importance in controlling ocean/atmosphere CO_2 exchange. Results suggest that primary production in HNLC systems is controlled by some combination of the light/mixing regime, grazing pressure and Fe limitation, as evidenced most clearly in the equatorial Pacific (e.g., Coale et al., 1996; Landry et al., 1997) and Southern Ocean (e.g., Boyd et al., 2000; Price et al., 1994). Martin (1990) showed that Fe could limit nutrient utilization in the Southern Ocean and hypothesized that changes in Fe availability and the resulting efficiency of nutrient use by Southern Ocean phytoplankton may play the dominant role in driving the observed glacial/interglacial oscillations in atmospheric CO_2. Largely as a result of that hypothesis, studies in several HNLC areas have obtained compelling evidence that Fe limits phytoplankton growth, at least under certain conditions, in the equatorial Pacific (Coale et al., 1996), northwestern Pacific (Tsuda et al., 2003) and Southern Ocean (Boyd et al., 2000). However, Martin's original iron hypothesis is still open to some debate with regard to its importance in regulating atmospheric CO_2 levels (Buesseler and Boyd, 2003). The primary reason for this is that, even though Fe fertilization increases primary production, the effect on export production fluxes is poorly documentated, the only Fe-induced bloom yet reported that was followed for long enough to evaluate carbon export was the Subarctic Ecosystem Response to Iron Enrichment Study (SERIES) in the subarctic Pacific (Boyd et al., 2004). Primary production and organic carbon export are not tightly linked in time

This uncertainty is increased by the fact that Fe limitation is just one of several factors that can control primary production in HLNC areas. Both light limitation (Nelson and Smith, 1991) and grazing (Miller et al., 1991) can place constraints on the response of HNLC systems to added Fe, even when iron limitation is present. Beyond that, ecologically important interactions between Fe limitation and grazing pressure (Landry et al., 1997) and light limitation (Sunda and Huntsman, 1997) have been shown. The role of interactive effects of this kind in the ocean is not well understood.

To examine these possibilities in the HNLC waters of the Southern Ocean we used a complex biogeochemical model that simulates Fe limitation, grazing pressure, and light limitation. The model is derived from the flexible-composition phytoplankton model previously applied in the Sargasso Sea (Mongin et al., 2003). That earlier version of the model considered the cycling of C, N and Si and limitation of phytoplankton growth by N, Si and light. To apply the model in the Southern Ocean, an HNLC system from which there is abundant evidence of Fe limitation, we incorporated a Fe cycle and Fe limitation two of key phytoplankton processes, photosynthetic efficiency and nitrate uptake.

Fe is a micronutrient, present in surface waters at very low concentrations and required by phytoplankton in very low proportions to C, N and Si. In contrast to those macronutrient elements, Fe is not a major structural component of phytoplankton cells, but functions mainly as a co-factor for several metabolically important cell enzymes (Raven, 1988). Accordingly, the Fe status of the ecosystem cannot be modeled exactly as that for the other nutrients (Amstrong, 1999).

It has been known for more than 30 years that phytoplankton cells respond to N, P, Si and Fe limitation by adjusting their cellular content of the limiting element downward. While the cellular N and Si content of severely N- or Si-limited cells is typically ~20% of that in nutrient-replete cells (Goldman et al., 1978; Paasche, 1973) the Fe content of strongly Fe-limited cells can be as low as ~2% of that in Fe-replete cells (Davies, 1970). Cellular Fe/C ratios range from $\sim 10^{-6}$ under strong Fe limitation to $\sim 10^{-3}$ under Fe-replete conditions (Sunda and Huntsman, 1995). Effects of Fe limitation on cellular macroelemental composition also have been documented. Under low-Fe, growth conditions, diatoms have Si/N and Si/C ratios up to eight times higher than they do under Fe-replete conditions (Hutchinson and Bruland, 1998; Takeda, 1998; Franck et al., 2000, 2003).

Ecologically, this flexibility is important in letting phytoplankton populations sustain high growth rates in nutrient-depleted habitats. No model that assumes fixed elemental composition for phytoplankton can simulate this important adaptive feature. Photosynthesis and nutrient uptake also respond quite differently to light availability. Photosynthetic C fixation has an absolute light requirement and uptake of NO_3^- is often strongly light-dependent (Raven, 1990; McCarthy et al., 1996), but uptake of NH_+^4 and $Si(OH)_4$ can proceed