Available online at www.sciencedirect.com
ScienceDirect
Deep-Sea Research II 53 (2006) 2095–2113
DEEP-SEA RESEARCH PART II
www.elsevier.com/locate/dsr2

Phytoplankton processes during a mesoscale iron enrichment in the NE subarctic Pacific: Part I—Biomass and assemblage

Adrian Marchetti[a,*], Nelson D. Sherry[b], Hiroshi Kiyosawa[c], Atsushi Tsuda[d], Paul J. Harrison[e]

[a]*Department of Botany, University of British Columbia, 6270 University Blvd, Vancouver B.C., Canada V6T 1Z4*
[b]*Department of Earth and Ocean Sciences, University of British Columbia, 6270 University Blvd, Vancouver B.C., Canada V6T 1Z4*
[c]*Marine Biological Research Institute of Japan, 4-3-16 Yutaka-cho., Shinagawa-ku, Tokyo 142-0042, Japan*
[d]*Ocean Research Institute, University of Tokyo, Nakano, Tokyo 164-8639, Japan*
[e]*Atmosphere, Marine and Coastal Environment Program, Hong Kong University of Science and Technology, Clear Water Bay, Hong Kong, China*

Received 14 September 2004; accepted 6 May 2006
Available online 12 October 2006

Abstract

We report results from the Subarctic Ecosystem Response to Iron Enrichment Study (SERIES) experiment in waters of the NE subarctic Pacific in which a large scale iron (Fe) enrichment lead to a shift in the phytoplankton assemblage from pico- and nanophytoplankton to one dominated by large diatoms. The phytoplankton response to the added Fe was monitored for 26 days following two infusions into a 77 km^2 patch of seawater. During the course of the experiment, the resulting algal bloom was constrained within the upper 30 m and spread to a region measuring over 1000 km^2. Phytoplankton chlorophyll *a* (chl *a*) increased from 0.3 $mg\,m^{-3}$ to a peak of 6.3 $mg\,m^{-3}$ 18 days after the initial addition of Fe. Water-column integrated chl *a* was enhanced 8-fold, reaching a maximum of 114 $mg\,m^{-2}$ on day 17. The resulting bloom is described in two ecological phases based on dominant phytoplankton groups. In Phase I, which encompassed the initial infusion up to day 10, all size-fractions (0.2–2, 2–20 and $>20\,\mu m$) increased in biomass as indicated by chl *a*, contributing to a surface standing stock of 2 $mg\,m^{-3}$. In Phase II, from days 10 to 18, the bloom was dominated by microphytoplankton ($>20\,\mu m$), with a concomitant decrease in phytoplankton $<20\,\mu m$. Microphytoplankton, which initially accounted for 25% of the phytoplankton biomass and increased by a factor of 50, consisted primarily of the pennate diatom genera, *Pseudo-nitzschia, Neodenticula* and *Thalassiothrix* and the centric diatom genera, *Chaetoceros*, *Rhizosolenia,* and *Proboscia*. Particulate carbon-to-chl *a* (PC: chl *a*) ratios for large cells ($\geq 5\,\mu m$) decreased 5-fold by day 18, indicative of enhanced cellular chl *a* content and increased phytoplankton contributions to PC. Pennate diatoms were most abundant in the patch, although when converted to biovolume, centric diatoms contributed larger amounts of algal carbon (C) to the bloom. A rapid decline in chl *a* on day 19 marked the onset of bloom decline. The magnitude, duration and composition of the phytoplankton response to the Fe enrichment clearly depicted a major shift in the structure of the algal assemblage and increased C export potential.

Keywords: Fe enrichment; NE subarctic Pacific; chlorophyll *a*; Phytoplankton; Diatoms; Carbon-to-chlorophyll ratios

*Corresponding author. School of Oceanography, University of Washington, Box 357940, Seattle, WA 98195, USA. Tel.: +1 206 221 7841; fax: +1 206 543 6073.
E-mail address: amarchetti@ocean.washington.edu (A. Marchetti).

0967-0645/$ - see front matter
doi:10.1016/j.dsr2.2006.05.038

1. Introduction

Initial support for the Fe hypothesis was obtained from shipboard bottle experiments performed in the NE subarctic Pacific (Martin and Fitzwater, 1988; Martin et al., 1989, 1990; Coale, 1991). Iron additions resulted in enhanced phytoplankton growth, providing compelling evidence that algal biomass was primarily regulated by its availability. Since then, considerable advances have been made in our understanding of the extent to which phytoplankton are limited by Fe and the essential role that this trace element performs in cellular processes.

The Fe hypothesis was first proposed to explain the paradox within regions where macronutrients, such as nitrate (NO_3), silicic acid ($Si(OH)_4$) and phosphate (PO_4), were plentiful, but phytoplankton biomass remained comparatively low throughout the year (high-nutrient, low-chlorophyll regions; HNLC). The levels of dissolved Fe in these waters are in subnanomolar concentrations, which limits phytoplankton growth and results in incomplete macronutrient utilization (Martin et al., 1991; Johnson et al., 1997; Fung et al., 2000). These ecosystems are dominated by certain phytoplankton taxa that are more competitive under low Fe conditions due to their high surface area-to-volume ratios and their ability to implement low Fe-requiring metabolic pathways (Sunda et al., 1991; Sunda and Huntsman, 1995, 1997). Though ubiquitously present, larger phytoplankton such as diatoms are generally unable to flourish under these low ambient Fe concentrations and only maintain minimal seed populations.

The ambient phytoplankton assemblage in the NE subarctic Pacific is primarily composed of small ($<5\,\mu m$) flagellates (Booth et al., 1993; Boyd and Harrison, 1999). Diatoms and other large phytoplankton usually comprise between 10% and 30% of total chl *a* (Boyd et al., 1996; Boyd and Harrison, 1999). However, over the duration of a typical summer, dissolved NO_3 and $Si(OH)_4$ are utilized, resulting in a $Si(OH)_4$: NO_3 drawdown ratio of ca. 1.6:1 (Whitney and Freeland, 1999). Within the Gulf of Alaska, surface depletion of $Si(OH)_4$ has also occasionally been observed (Wong and Matear, 1999; Whitney et al., 2005). Thus silicon-requiring diatoms contribute significantly to seasonal nutrient consumption. External sources of Fe required to stimulate growth of these diatom populations are speculated to be sporadic and spatially patchy, either from slow-moving eddies transporting Fe from coastal regions (Johnson et al., 2005) or from dust and wildfire atmospheric deposition (Boyd et al., 1998; Bishop et al., 2002). Therefore, it appears that episodic Fe additions and subsequent increases in phytoplankton growth are a naturally occurring phenomenon in the NE subarctic Pacific.

To date, there have been numerous mesoscale Fe enrichment studies in the Equatorial Pacific (IronEx I, Martin et al., 1994; IronEx II, Coale et al., 1996), Southern Ocean (SOIREE, Boyd et al., 2000; EisenEx, Gervais et al., 2002 and SoFeX; Coale et al., 2004) and the subarctic NW Pacific (SEEDS, Tsuda et al., 2003). All Fe enrichment experiments were performed with common objectives in an attempt to test the Fe hypothesis. These objectives include the documentation and quantification of the system response to Fe enrichment and to verify the extent of C sequestration coinciding with the increase in phytoplankton biomass. Although comparable trends have been observed among Fe enrichments performed in different HNLC regions, the range in Fe-induced bloom longevities and shifts in phytoplankton composition demonstrate considerable variability in the ecosystem responses. The NE subarctic Pacific was the last of the three major HNLC regions where an in situ Fe enrichment experiment had yet to be performed. The region's unique physical and biological properties necessitate an understanding of the geochemical, physiological and ecological responses to Fe enrichment.

In July 2002, a mesoscale Fe addition experiment, Subarctic Ecosystem Response to Iron Enrichment Study (SERIES), was performed in the NE subarctic Pacific. Here we report on the spatial and temporal dynamics in phytoplankton biomass as inferred by chl *a* throughout the bloom. We quantify the algal biomass incorporated into pico-, nano-, and microphytoplankton size-classes by size-fractionated chl *a*. Changes in particulate carbon (PC) are also reported along with the resulting PC: chl *a* ratios. Lastly, a detailed assessment of phytoplankton taxa in the Fe-enriched patch is given as well as estimates of C export potential for the major diatom species composing the bloom. In two companion papers, we describe the phytoplankton nutrient utilization dynamics and changes in primary productivity throughout the mesoscale Fe enrichment (Marchetti et al., this issue-a; Marchetti et al., this issue-b).