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Did dilution limit the phytoplankton response to iron addition in HNLCLSi sub-Antarctic waters during the SAGE experiment?

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ABSTRACT

An *in situ* iron addition experiment (SAGE) was carried out in high-nitrate low-chlorophyll low-silicic acid (HNLCLSi) sub-Antarctic surface waters south-east of New Zealand. In contrast to other iron addition experiments, the phytoplankton response was minor, with a doubling of biomass relative to surrounding waters, with the temporal trends in dissolved iron and macronutrients instead dominated by physical factors such as mixing and dilution. The initial increase in patch surface area indicated a lateral dilution rate of 0.125 d^{-1}, with a second estimate from a model of the decline in peak SF_6 concentration yielding a higher lateral dilution rate of 0.16–0.25 d^{-1}. The model was tested on the SOIREE SF_6 dataset and provided a lateral dilution of 0.07 d^{-1}, consistent with previous published estimates. MODIS ocean colour images showed elevated chlorophyll coincident with the SF_6 patch on day 10 and 12, and an elevated chlorophyll filament at the SAGE experiment location 3–4 days after ship departure, which provided additional lateral dilution estimates of 0.19 and 0.128 d^{-1}. Dissolved iron at the patch centre declined by 85% within two days of the initial infusion, of which dilution accounted for 50–65%; it also decreased rapidly after the 2nd and 3rd infusions but remained elevated after the fourth infusion. Despite decreases in nitrate and silicic acid from day 7 and 10, respectively, the final nutrient concentrations in the patch exceeded the initial concentrations due to supply from lateral intrusion and mixed-layer deepening. The low Si:N loss ratio suggested that the observed limited response to iron was primarily by non-siliceous phytoplankton. Algal growth rate exceeded the minimum dilution rate during two periods (days 3–6 and 10–14), and coincided with net chlorophyll accumulation. However, as the ratio of algal growth to dilution was the lowest reported for an iron addition experiment, dilution was clearly a significant factor in the SAGE experiment recording the lowest phytoplankton response to mesoscale iron addition.

1. Introduction

The high nutrient low chlorophyll (HNLC) status of up to one-third of the oceans has been attributed to limited iron availability in surface waters (de Baar et al., 2005; Boyd et al., 2007). The Southern Ocean is the largest HNLC region, of which the majority is situated in the sub-Antarctic Zone (SAZ) between the sub-tropical and polar fronts. The SAZ is a major contributor to the ocean carbon sink (Sabine et al., 2004) and consequently the factors that limit phytoplankton growth in this region are of global significance. Surface waters in the SAZ are characterized by high levels of macronutrients and low chlorophyll, with limited iron availability (Boyd et al., 2005a); however, the SAZ differs from other HNLC regions in having low silicic acid concentrations (Dugdale et al., 1995). During summer silicic acid may be depleted to <1 μmol/L which is lower than the half-saturation constant for many cultured diatom species (Sarthou et al., 2005; Martin-Jézéquel et al., 2000), and consequently the SAZ is regarded as HNLCLSi. However the SAZ experiences a succession of limiting factors, with light limitation dominating in early spring as a result of deep surface mixed layers (Rintoul and Trull, 2002), followed by stratification of the water column that leads to iron limitation and then Si limitation in summer (Boyd et al., 1999). Although the Si limitation or Fe/Si co-limitation may limit the response of diatoms to iron enrichment, nitrate is always available to support the growth of other phytoplankton groups. Consequently, the timing and magnitude of the response to iron addition in the SAZ, either from natural sources such as dust deposition or deliberate iron addition, may

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differ due to the relationship between silicic acid availability and diatom abundance. Iron addition in these waters may then elicit different responses, in terms of biomass and plankton community composition, to iron addition experiments in other HNLC waters. For example, during the SOFeX-N iron addition experiment in low silicic acid SAZ waters (~2.5 μmol/L), silicic acid limitation of diatom primary production and domination of nutrient uptake by non-siliceous phytoplankton were observed (Coale et al., 2004). This difference in response to iron addition in HNLCLSi waters has implications for carbon export, food webs, and trace gas production.

The response to iron addition may also vary dependent upon the mixing regime. Entrainment of nutrients and loss of iron and phytoplankton biomass as a result of dilution have been identified as important factors in determining the magnitude and duration of response in other iron addition experiments (Abraham et al., 2000; de Baar et al., 2005; Tsumune et al., 2005). This is because the dilution of an isolated patch of phytoplankton may "cap" the increase in phytoplankton concentration (Okubo, 1971), as a proportion of the biomass is exported laterally from the patch centre, with a resultant smaller net biomass increase at the patch centre (McLeod et al., 2002). Conversely the drawdown of nutrients at the patch centre results in a concentration gradient across the patch boundary that maintains entrainment of nutrients at the patch centre via mixing and dilution. This may prolong a phytoplankton bloom by maintaining nutrient supply even when concentrations are limiting (Abraham et al., 2000; Law et al., 2006). In the SAZ dilution may play a critical role, as there may be more than one limiting factor (light/iron/silicic acid). Indeed, mixing and entrainment were critical to the maintenance of the phytoplankton response during the SOFeX-N iron addition experiment in SAZ waters (Coale et al., 2004), with model simulations showing extended bloom duration and magnitude with intermediate dilution relative to zero and high dilution scenarios (Krishnamurthy et al., 2008). On a larger scale, Boyd et al. (1999) suggest that the annual algal silicic acid uptake and occurrence of iron-mediated blooms in SAZ waters require lateral advection of water containing elevated silicic acid.

The SAGE (SOLAS Air–sea Gas Exchange) experiment was an *in situ* iron addition experiment using a SF_6 tracer Lagrangian framework that took place in sub-Antarctic waters in the Bounty Trough, south-east of New Zealand, in March–April 2004 (Fig. 1). The SAGE experiment had dual aims of (a) determining the response of phytoplankton and primary production to an increase in iron availability in a HNLCLSi region, and (b) the generation of a phytoplankton bloom to alter surface CO_2 and trace gas gradients (Harvey et al., 2011). This manuscript describes the physical evolution of the iron-enriched patch, the dissolved iron and macronutrient dynamics, and how these influenced the phytoplankton response to iron addition.

2. Methods

2.1. Pre-release preparation

Four iron infusions were undertaken during the SAGE experiment (see Table 1). For each release two 7500-L tanks were initially half-filled with seawater and acidified to ~pH 2 by addition of 25 L of hydrochloric acid. 1350 kg of $FeSO_4 \cdot 7H_2O$ (4900 mol) were subsequently added, with the aim of initially raising the dissolved iron concentration to ~2 nM. The iron salt was added using a hopper and winch, with the tanks subsequently filled with surface seawater. SF_6 saturation was carried out in two 4000-L tanks of seawater en route to the study site. A headspace of ~5 L volume was continuously flushed with pure SF_6 and continually re-circulated through the water using a diffusion hose and pump until SF_6 saturation was achieved, as determined using a Thermal Conductivity Detector Gas Chromatograph (Law et al., 1998). A drifter buoy (Big-Eye Beacon) attached to a holey-sock drogue was deployed 12 h before the 1st infusion at the nominal patch centre to determine prevailing current velocity and direction.

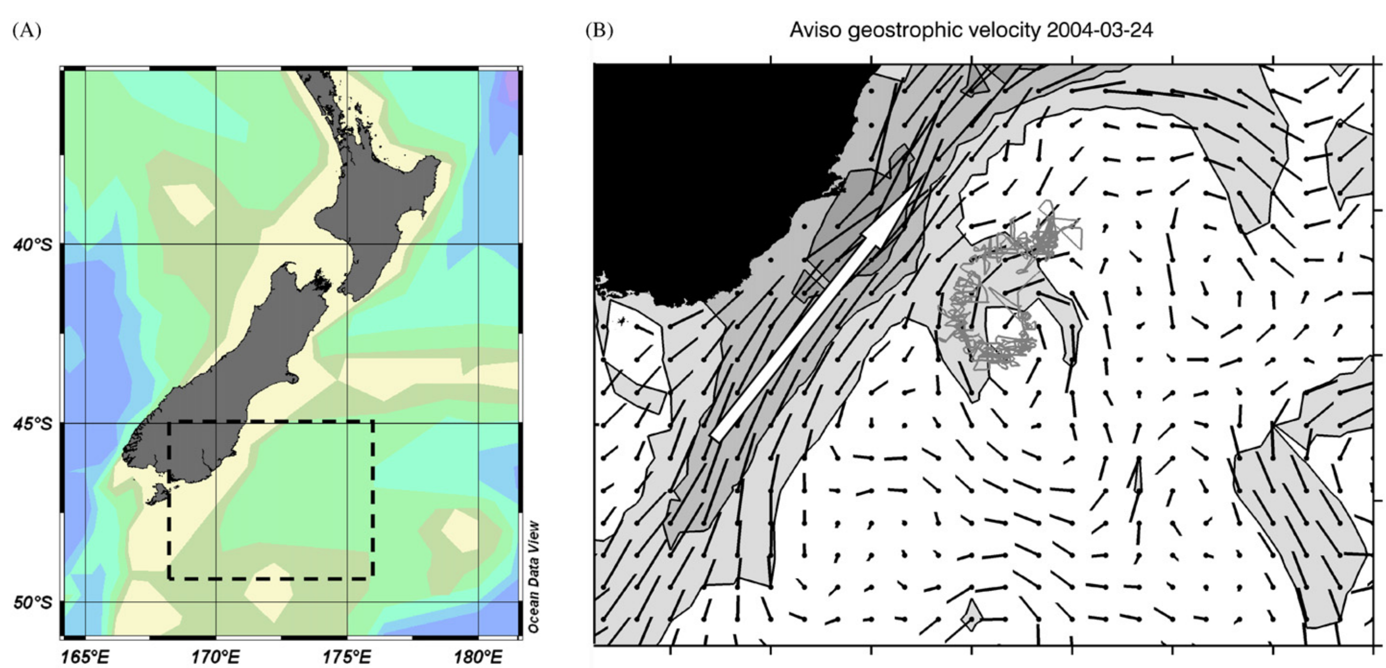

Fig. 1. (A) Location of SAGE experiment in the Bounty Trough, south-east of New Zealand; (B) ship track overlain on geostrophic current velocities (AVISO) on D8, with the filled contours indicating speed in m/s (0-0.1 white, 0.1-0.2 light grey, 0.2-0.3 mid grey, and >0.3 dark grey). The direction and approximate position of the Southland Current is indicated by the white arrow.