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Temporal progression of photosynthetic-strategy in phytoplankton in the Ross Sea, Antarctica

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ABSTRACT

The bioavailability of iron influences the distribution, biomass and productivity of phytoplankton in the Ross Sea, one of the most productive regions in the Southern Ocean. We mapped the spatial and temporal extent and severity of iron-limitation of the native phytoplankton assemblage using long- (>24 h) and short-term (24 h) iron-addition experiments along with physiological and molecular characterisations during a cruise to the Ross Sea in December–February 2012. Phytoplankton increased their photosynthetic efficiency in response to iron addition, suggesting proximal iron limitation throughout most of the Ross Sea during summer. Molecular and physiological data further indicate that as nitrate is removed from the surface ocean the phytoplankton community transitions to one displaying an iron-efficient photosynthetic strategy characterised by an increase in the size of photosystem II (PSII) photochemical cross section (σ_{PSII}) and a decrease in the chlorophyll-normalised PSII abundance. These results suggest that phytoplankton with the ability to reduce their photosynthetic iron requirements are selected as the growing season progresses, which may drive the well-documented progression from Phaeocystis antarctica- assemblages to diatom-dominated phytoplankton. Such a shift in the assemblage-level photosynthetic strategy potentially mediates further drawdown of nitrate following the development of iron deficient conditions in the Ross Sea.

1. Introduction

The Ross Sea continental shelf is the most productive region in the Southern Ocean (Arrigo and van Dijken, 2004; Peloquin and Smith, 2007), with an annual productivity >200 g C m^{-2} (Smith et al., 2006), which may account for as much as 27% of the estimated total Southern Ocean biological CO_2 uptake (Arrigo et al., 2008). An understanding of the controls on primary productivity is therefore needed given the potential for future changes in stratification (Boyd et al., 2008; Smith et al., 2014) and nutrient inputs to this region (Mahowald and Luo, 2003; Tagliabue et al., 2008).

A persistent polynya in the southern Ross Sea greatly increases in size in the early austral spring (Arrigo and van Dijken, 2003; Reddy et al., 2007), and hosts large seasonal phytoplankton blooms, typically dominated by the colonial haptophyte Phaeocystis antarctica (P. antarctica) in spring through early summer (November–December), with an increase in abundance of diatoms in mid- to late summer (Arrigo and van Dijken, 2004; Arrigo et al., 1998; DiTullio and Smith, 1996; Goffart et al., 2000; Smith and Gordon, 1997; Smith et al., 2000). Understanding the causes and consequences of this seasonal phytoplankton progression is important, as the spatial and temporal distribution and abundance of P. antarctica and diatoms have significant biogeochemical consequences on, for example, the elemental composition and flux of biogenic material from the euphotic zone (Arrigo et al., 1999; DeMaster et al., 1992; Smith and Dunbar, 1998; Tagliabue and Arrigo, 2005).

Iron (Fe) and irradiance are assumed to exert the major 'bottom-up' controls on phytoplankton biogeography and productivity in the Ross Sea, given the incomplete macronutrient removal at the end of the growing season (Arrigo and van Dijken, 2003; Arrigo et al., 1998; Coale et al., 2003; Fitzwater et al., 2000; Sedwick et al., 2000; Sedwick et al., 2007; Smith et al., 2003; Smith et al., 2000; Tagliabue and Arrigo, 2003). Light availability may limit spring phytoplankton growth when vertical mixing is deep and daily integrated irradiance is low, this mixing will

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also supply dissolved iron (DFe) to the euphotic zone (McGillicuddy et al., 2015). As the growing season progresses and the water column stratifies, the flux of DFe from below is likely reduced and may therefore become a more significant factor in limiting phytoplankton growth rates. Indeed, shipboard iron-addition experiments have repeatedly demonstrated the role of iron limitation in the Ross Sea (Bertrand et al., 2007; Coale et al., 2003; Cochlan et al., 2002; Martin et al., 1990; Olson et al., 2000; Sedwick and DiTullio, 1997; Sedwick et al., 2000), consistent with other metrics of Fe stress including high levels of flavodoxin (Maucher and DiTullio, 2003) and enhanced biological drawdown of silicate relative to nitrate (Arrigo et al., 2000; Smith et al., 2006).

Changes in phytoplankton composition from P. antarctica to diatom species may be linked to the co-limitation and interaction between iron and light. Boyd (2002) speculated that P. antarctica growth is limited by Fe availability from spring through late summer. Sedwick et al. (2007) further proposed that decreases in iron availability through spring are mitigated by increases in irradiance, thereby decreasing phytoplankton iron requirements. The differences in intracellular iron requirements alongside changes in the light environment may explain the community succession of the Ross Sea, where diatoms can outcompete P. antarctica in the late summer (Strzepek et al., 2012).

Phytoplankton that dominate in the Ross Sea may therefore need to be adapted to highly variable iron concentrations and light availability (Sedwick et al., 2011). An antagonistic relationship between irradiance and photosynthetic Fe demand may be predicted given that lower irradiances can increase Fe requirements associated with the synthesis of the additional photosynthetic units required to increase light absorption (Maldonado et al., 1999; Raven, 1990; Sunda and Huntsman, 1997). Each photosynthetic electron transfer chain requires 22–23 Fe atoms, and the photosynthetic apparatus can be the largest sink of Fe within a phytoplankton cell (Raven, 1990; Shi et al., 2007; Strzepek and Harrison, 2004). In contrast to the tight link between cellular Fe requirements and light harvesting capacity, studies on Southern Ocean diatoms and P. antarctica in culture suggest the Fe burden of photosynthesis may be significantly reduced for these species through increases in the size rather than the number of photosynthetic units (termed sigma-type acclimation) in response to iron/ and light limitation (Strzepek et al., 2012; Strzepek et al., 2011). Effectively, these Southern Ocean taxa appear to invest relatively more resources in the generation of a larger light-harvesting apparatus, rather than in the Fe-rich photosynthetic catalysts of photosystems I and II (Strzepek et al., 2012). This Fe-efficient strategy appears to be most pronounced for Southern Ocean diatoms, which, in culture can have some of the largest light harvesting antennae reported (Strzepek et al., 2012), a phenotype which is more commonly associated with small cells (Suggett et al., 2009). The photosynthetic strategy of Southern Ocean diatoms may therefore contribute to the apparently low Fe requirement and cellular Fe:C ratio of these species (Coale et al., 2003; Kustka et al., 2015; Sedwick et al., 2007; Strzepek et al., 2012; Strzepek et al., 2011), and as such drive the seasonal progression from P. antarctica to diatoms in the Ross Sea.

In December–February 2012 a research cruise was conducted as part of the multidisciplinary research project Processes Regulating Iron Supply at the Mesoscale – Ross Sea (PRISM-RS), in an effort to identify and quantify the major sources of iron to the surface waters of the Ross Sea during the growing season. As part of this study, physiological and molecular measurements were combined with shipboard incubation experiments in an effort to define the spatial and temporal extent of phytoplankton iron limitation and reveal the photosynthetic strategy of the phytoplankton assemblages.

2. Materials and methods

2.1. Oceanographic sampling

The samples and data presented here were obtained during a cruise of the RVIB Nathaniel B. Palmer to the Ross Sea (cruise NBP12-01) from 24th December 2011 to 10th February 2012 (DOY 358–041). During the cruise, 29 short-term (24 h) and 3 long-term (168 h) incubation experiments were performed (Fig. 1a). Short-term experiments were used to determine rapid iron induced changes in the phytoplankton photophysiological status; whereas long-term experiments determined whether relief from iron limitation could drive changes in biomass. For the long-term incubation experiments, uncontaminated whole seawater was collected from ~5 m depth while slowly underway, using a trace-metal clean towed fish system (Sedwick et al., 2011). Uncontaminated whole seawater for the short-term incubation experiments was collected from ~10 m depth in Teflon-lined, external closure 5 L Niskin-X samplers (General Oceanics) deployed on a trace metal clean CTD rosette system (Marsay et al., 2014). Samples for additional analysis were also collected along the cruise track.

2.2. Bioassay incubation experiments

Incubation experiments were performed using methods similar to those employed previously in the Southern Ocean (Moore et al., 2007; Nielsdóttir et al., 2012) and the high latitude North Atlantic (HLNA) (Nielsdóttir et al., 2009; Ryan-Keogh et al., 2013). Water for the experiments (see Section 2.1, above) was transferred unscreened into acid-washed 1.0-L polycarbonate bottles (Nalgene) for the short-term incubation experiments and 4.5-L polycarbonate bottles for the long-term incubation experiments. Incubation bottles were filled in a random order, with triplicate samples for initial measurements in the long-term incubation experiments collected at the beginning, middle and end of the filling process. Initial samples for the short-term incubation experiments were collected from the same Niskin-X sampling bottle. The short-term experiments were run for 24 h and the long-term experiments were run for 168 h; both experiments consisted of two treatments: an unamended control treatment and 2.0 nmol L^{-1} Fe treatment (hereafter, +Fe). All experimental incubations were conducted as biological duplicates or triplicates.

All bottle tops were externally sealed with film (Parafilm™), and bottles were double bagged with clear polyethylene bags to minimize risks of contamination during the incubation. On-deck incubators were shaded using LEE "blue lagoon" filters to provide light levels corresponding to ~35% of above-surface irradiance (Hinz et al., 2012; Nielsdóttir et al., 2009; Ryan-Keogh et al., 2013). Flowing surface seawater was used to control the temperature in the incubators. Subsampling of long-term incubations for measurements of chlorophyll a, dissolved macronutrient concentrations and phytoplankton physiological parameters occurred after 24, 72, 120 and 168 h. Sub-sampling of short-term incubation experiments for the same parameters occurred after 24 h. All experiments were set up and sub-sampled under a class-100 laminar flow hood within a trace metal clean environment.

2.3. Chlorophyll a and nutrient analysis

Samples for chlorophyll a (Chl) analysis (250 mL) were filtered onto GF/F filters and then extracted into 90% acetone for 24 h in the dark at 4 °C, followed by analysis with a fluorometer (TD70; Turner Designs) (Welschmeyer, 1994). Macronutrient samples were drawn into 50 mL diluvials and refrigerated at 4 °C until analysis, which typically commenced within 12 h of sampling. Nitrate plus nitrite (DIN), phosphate, ammonium and silicate were determined shipboard on a five-channel Lachat Instruments QuikChem FIA+ 8000s series AutoAnalyser (Armstrong et al., 1967; Atlas et al., 1971; Bernhardt and Wilhelms, 1967; Patton, 1983). Dissolved iron was determined post-cruise using flow injection analysis modified from Measures et al. (1995), as described by Sedwick et al. (2011); accuracy of the DFe method was verified by analysis of SAFe reference seawater samples (Johnson et al., 2007).

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