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Spatial and temporal variations in variable fluoresence in the Ross Sea (Antarctica): Oceanographic correlates and bloom dynamics

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ABSTRACT

During two cruises to the Ross Sea, Antarctica in austral spring and summer, fast repetition rate fluorometry was used to investigate the relationship between phytoplankton photophysiology and water mass characteristics, micronutrient availability, and composition. Particulate organic matter proxies for phytoplankton biomass (chlorophyll *a*, particulate organic carbon and nitrogen, and biogenic silica) were all elevated in the photic zone during spring and summer. Biogenic silica concentrations were an order of magnitude higher in summer relative to spring, reflecting a shift in composition from *Phaoecystis antarctica* to diatoms. Quantum yields of PS II (F_v/F_m) were generally higher in spring relative to summer, coincident with weaker vertical and horizontal gradients in hydrographic properties. Reduced F_v/F_m values (<0.4) were observed in the upper 30 m in both seasons, with maximum values (ca. 0.55) observed near base and below the euphotic zone. No significant relationship between F_v/F_m values and dissolved Fe could be identified in the merged spring/summer data set. Functional absorption cross sections were significantly higher in spring than summer, presumably reflecting adaptations to lower irradiance in spring; little variation with depth was observed. Phytoplankton composition did not appear to be a major determinant of bulk quantum yield, although diatom-dominated waters exhibited significantly higher functional absorption cross sections when compared to waters dominated by *P. antarctica*. Dominance of *P. antarctica* appears to be related to greater photophysiological resilience and faster photoacclimation to changing light conditions, whereas diatoms were prevalent in shallow summer mixed layers, which likely reflects their enhanced photosynthetic capacity at high irradiance levels.

1. Introduction

Continental shelves around Antarctica have been recognized as critical sinks for atmospheric carbon dioxide. Indeed, it has been estimated that the Ross Sea continental shelf is responsible for more than 25% of the known Southern Ocean sink for anthropogenic CO_2 (Arrigo et al., 2008). Atmosphere to ocean carbon flux on continental shelves is driven by the incorporation of CO_2 by phytoplantkon during the growing season and subsequent vertical export of organic matter to depth. Phytoplankton assemblages in the highly productive continental shelf area of the Ross Sea are dominated by two functional groups: haptophytes and diatoms (Tremblay and Smith, 2007). The haptophytes are overwhelmingly dominated by *Phaeocystis antarctica* (DiTullio et al., 2003), with chlorophyll *a* concentrations of ca. 15 μg L^{-1} being observed in spring, declining to low concentrations by mid-January (Smith et al., 2006, 2011a). *P. antarctica* dominates in relatively deep mixed layers, maintaining high photosynthetic and growth rates despite the reduced irradiance levels characteristic of

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austral spring (Arrigo et al., 1999; Smith et al., 2000). In contrast, diatoms typically flourish during summer, and dominate regions within shallow mixed layers (such as those near ice edges), efficiently harnessing the elevated photon fluxes for photosynthesis (Leventer and Dunbar, 1996; Kropuenske et al., 2009). In addition to blooming in different oceanographic conditions, *P. antarctica* and diatom populations have substantially different elemental stoichiometry, which in turn impacts the magnitude and elemental compositon of the vertical export flux on the continental shelf (Dunbar et al., 2003). It remains unclear whether the specific physiological characteristics of the two functional groups result in dominance at any particular point in time, or the relative importance of micronutrients and irradiance in controlling phyiological characteristics of the algae.

Low iron concentrations have been shown to limit phytoplankton growth in much of the Southern Ocean (Martin et al., 1990a; de Baar et al., 1999; Boyd et al., 2000; Alderkamp et al., 2012b), including the Ross Sea (Martin et al., 1990b; Sedwick and DiTullio, 1997; Sedwick et al., 2000; Olson et al., 2000). Convective overturn during the fall and winter replenishes Fe in surface waters and leaves the early spring water column weakly stratified; thus, irradiance is thought to limit phytoplankton growth and productivity during this season (Smith et al., 2000). However, recent work indicates that dissolved iron concentrations can also be low in the Ross Sea polynya during spring (Sedwick et al., 2011), suggesting that biological iron drawdown early in the season can create iron-limited conditions earlier than had been previously thought. Iron, an essential component of phytoplankton photosynthetic machinery and of other enzymes, such as nitrate reductase, is supplied to the euphotic zone by upwelling of subsurface, relatively iron-rich deep waters, winter convective mixing, melting of sea ice and atmospheric deposition (Sedwick et al., 2000, 2011; Measures and Vink, 2001; Dinniman et al., 2003, 2011).

P. antarctica populations dominate in more deeply mixed water columns, whereas diatoms tend to dominate in more highly stratified waters (Arrigo et al., 1999, 2003; Smith and Asper, 2001). However, the habitats of these two groups overlap, and no statistically significant difference has been demonstrated between mixed layer depths or photosynthetic parameters in waters dominated by either haptophytes or diatoms (van Hilst and Smith, 2002). Furthermore, the limited dissolved iron distribution and cycling data for the Ross Sea do not allow generalizations with regard to the concentrations of dissolved iron in deeply mixed versus stratified waters, given that both vertical mixing and sea-ice melting are thought to supply iron to surface waters in this region (Sedwick et al., 2000, 2011; Coale et al., 2005). In this context, direct observations of the photophysiological status of phytoplankton should provide information on the apparent habitat differentiation between *P. antarctica* and diatoms in the Ross Sea.

Variable fluorescence has been widely used as a method for assessing the photochemical status and response of phytoplankton to a variety of factors, including deficiencies in macro- and micronutrients (Kolber et al., 1994; Behrenfeld and Kolber, 1999; Olson et al., 2000; Parkhill et al., 2001). Hiscock et al. (2007) showed that quantum yields of phytoplankton in the Southern Ocean are responsive to iron availability and suggested that a low quantum yield is indicative of iron stress. One method for measuring variable fluorescence is fast repetition rate fluorometry (FRRF; Kolber et al., 1998). This procedure manipulates the photosystem II (PS II) redox state by reducing the primary electron acceptor with short ($\sim$100 μs) sequences of flashes within a single turnover of the PSII reaction center, allowing assessment of the photosynthetic quantum yield of PSII (F_v/F_m) and the functional absorption cross section of PSII (σ_{PSII}). We conducted an investigation into the controls on phytoplankton photosynthesis, growth and composition during two seasons: early austral summer (December, 2005–January, 2006) and the following spring (November–December, 2006). As part of these cruises, we assessed variable fluorescence distributions within the southern Ross Sea, as well as the relationship among variable fluorescence, phytoplankton assemblage composition, and hydrographic variables. We hypothesized that variations in active fluorescence characteristics would reflect changes in phytoplankton photophysiology and composition, and highlight iron availability as one of the primary factors controlling photosynthetic capacity, which in turn would have a significant impact on phytoplankton quantum yields in the Ross Sea.

2. Materials and methods

All sampling was conducted in the Ross Sea polynya as part of the "Controls on Ross Sea Algal Community Structure (CORSACS)" project during two cruises on the *RVIB Nathaniel B. Palmer* (Cruises NBP06-01, December 2005–January 2006, and NBP06-08, November–December 2006). Results are merged to reflect a seasonal progression due to the changes in ice, the dominant environmental variable, rather than absolute time, as seasonal changes are far

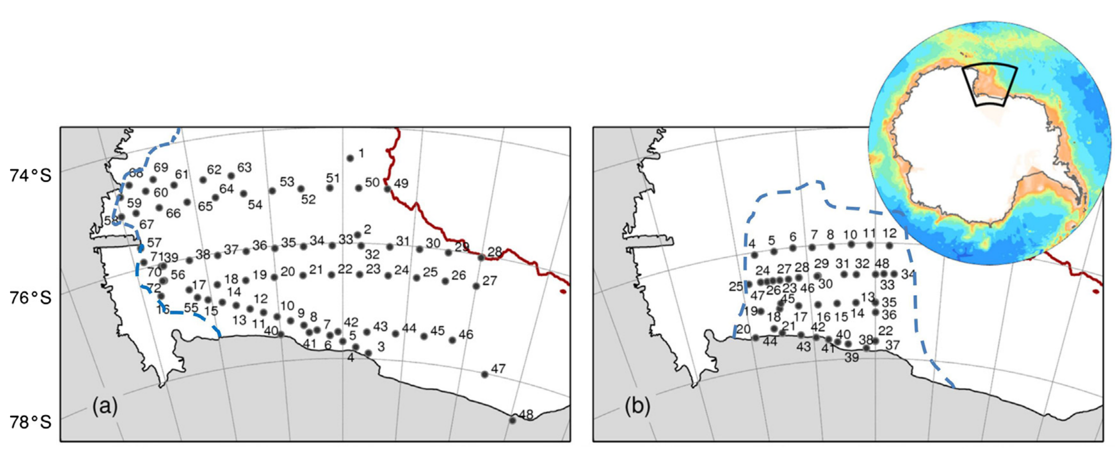

Fig. 1. Map showing the bathymetry of the study area and station locations of *R.V.I.B. N.B. Palmer* cruises (a) NBP06-01 (sampled from December 27, 2005 to January 23, 2006) and (b) NBP06-08 (sampled from November 6 to December 6, 2006). The dashed line on both is the ice distribution at the mid-point of each cruise, and the solid red line is the location of the continental shelf break.