



Introduction

Shedding dynamic light on Fe limitation (DynaLiFe)

1. Primary production in the Southern Ocean

The Southern Ocean (waters south of 50°S) consists broadly of three distinct open water ecological regimes: the pelagic, the marginal ice zone (MIZ), and the continental shelf. The pelagic Southern Ocean ranges in size from 23.8 to 38.7 × 10⁶ km² and is always much larger than either the MIZ or the shelf due to the large area of the permanently open ocean zone (23.8 × 10⁶ km²). The MIZ, a component of the sea ice zone (20 × 10⁶ km²), attains its maximum extent of only 6 × 10⁶ km² in December. The continental shelf is comparatively small, and is ice-covered for most of the year, becoming ice-free between November and April, attaining its maximum open water area of 0.9 × 10⁶ km² (Arrigo et al., 1998).

During the austral spring and summer, rates of daily net primary production (NPP) in the Southern Ocean vary considerably within these ecological regimes, ranging from 159 mg C m⁻² d⁻¹ in the pelagic province to ~500 mg C m⁻² d⁻¹ on the continental shelf (Arrigo et al., 2008). Due to its large size, the pelagic province contributes 90.6% of total Southern Ocean annual NPP, while the much smaller MIZ and continental shelf contribute approximately 6.0% and 3.4%, respectively, although they exhibit much higher daily rates of NPP (Arrigo et al., 1998, 2008).

The high rates of NPP on the continental shelf are due in part to the presence of numerous coastal polynyas (areas of open water surrounded by sea ice), which are the earliest sites with ice-free waters in the spring. The polynyas are located in relatively shallow waters and generally have high nutrient concentrations that stimulate very productive seasonal phytoplankton blooms. Daily rates of NPP exceeding 1000 mg C m⁻² d⁻¹ are common in these polynyas and rates exceeding 3000 mg C m⁻² d⁻¹ have been reported. Among the most productive of the 37 identified polynyas surrounding the Antarctic continent are those in the Amundsen Sea, located in the western Antarctic (Arrigo and Van Dijken, 2003). The Amundsen Sea contains two polynyas, the Pine Island Polynya in the east with a mean area of 17,632 km² and Amundsen Polynya in the west with a mean area of 27,333 km². Although these polynyas are relatively small, the amount of phytoplankton biomass they support is higher per unit area than any other Antarctic polynya, including the very productive Ross Sea polynya (Arrigo and Van Dijken, 2003).

Several fast-flowing glaciers that are thinning rapidly drain into the Amundsen Sea, most notably the Pine Island Glacier (PIG), the Thwaites Glacier, and the Dotson Ice Shelf (Pritchard et al., 2009). The thinning of these ice sheets is mainly attributed to the presence of relatively warm Circumpolar Deep Water (CDW) on the Amundsen Sea continental shelf. In the Pine Island Polynya, this warm water enters the cavity beneath the floating

terminus of the PIG and drives basal melting. The resulting dilution by the glacial melt initiates a circulation pattern whereby fresher and cooler meltwater modified CDW flows up the underside of the floating ice sheets into the Amundsen Sea (Jenkins et al., 2010; Jacobs et al., 2011). How both the thinning ice sheets and unique circulation patterns contribute to the extraordinarily high rates of phytoplankton production are unknown and are part of the rationale behind the DynaLiFe field program.

Two phytoplankton taxa, the prymnesiophyte *Phaeocystis antarctica* and diatoms (both of which are ubiquitous bloom formers in Southern Ocean waters), dominate primary production on the continental shelf and in the coastal polynyas. For example, phytoplankton blooms in the Ross Sea polynya are consistently dominated by either diatoms or *P. antarctica*, with a bloom of the latter species covering an area of >100,000 km² (Arrigo and McClain, 1994). Similarly, *P. antarctica* and chain-forming diatoms accounted for 70% of the total phytoplankton biomass in waters around the northern tip of the Antarctic Peninsula (Kang et al., 2001). At a coastal site in east Antarctica during austral summer, the breakout of seasonal fast ice was associated with a succession of dominant phytoplankton from *Cryptomonas* sp. to *Phaeocystis* to diatoms (Robinson et al., 1999). *P. antarctica* and diatoms were also dominant between Prydz Bay, Antarctica, and Australia (Wright et al., 1996). Waters in the Bransfield Strait region were dominated by nanoflagellates such as *Cryptomonas* sp. and by *P. antarctica*, which accounted for 83% of the total phytoplankton carbon (Kang and Lee, 1995).

The dominance of these two phytoplankton taxa in the Southern Ocean controls both the biogeochemistry and the ecology of the waters where they bloom. For example, previous data suggest that *P. antarctica* takes up twice as much CO₂ per mole of PO₄ removed than do diatoms (Arrigo et al., 1999, 2002). Other evidence suggests that *P. antarctica* is not readily grazed by microzooplankton (Caron et al., 2000; Tagliabue and Arrigo, 2003). Therefore, *P. antarctica* is thought to form the base of a marine food web that is substantially different from that supported by diatoms.

2. What controls phytoplankton distributions?

In both the Ross Sea and near east Antarctica, waters that are highly stratified generally contain high concentrations of diatoms, whereas well-mixed regions are associated with *P. antarctica* (Arrigo et al., 1999, 2000; Wright and Van den Enden, 2000). These data suggest that light availability plays a major role in defining where and when these different phytoplankton taxa bloom. Moreover, the in situ light climate for phytoplankton is

highly variable, due to changes in sea ice, solar angle, cloud cover, and wind driven vertical mixing in the upper mixed layer. Early data also showed that phytoplankton employ a number of strategies for dealing with short-term changes in irradiance. Experiments in which phytoplankton were acclimated to irradiance regimes simulating vertical mixing suggest that phytoplankton do not simply respond to average irradiance conditions in the water column, but rather acclimate to the dynamic irradiance conditions (Van Leeuwe et al., 2005; Van de Poll et al., 2007). If light becomes supersaturating and photosystems become reduced, photochemistry can be suppressed by decreasing the amount of photosynthetic pigments (mainly chlorophyll *a*). In addition, excess energy can be thermally dissipated when the xanthophyll cycle pigment diadinoxanthin is de-epoxidated to diatoxanthin (Olaizola and Yamamoto, 1994). This conversion is regulated within seconds of irradiance changes so that excess energy can be rapidly dissipated. Therefore, the ratio of protective xanthophyll pigments to photosynthetic pigments is an important indicator of the photoprotective status of the phytoplankton.

Laboratory experiments showed that photoprotection by xanthophyll cycle pigments occurs in both Antarctic diatoms (e.g. *Fragilariopsis cylindrus*) and *P. antarctica* when they are exposed to excess light (Van Leeuwe and Stefels, 2007; Kropuenske et al., 2009, 2010; Arrigo et al., 2010; Van de Poll et al., 2011), but acclimation strategies differ for the two taxa. Diatoms rely heavily on photoprotective pigments and xanthophyll cycling as a way to dissipate excess energy and are adapted to grow in shallow mixed layers near the well-lit surface ocean (Kropuenske et al., 2009; Arrigo et al., 2010; Mills et al., 2010; Van de Poll et al., 2011). In contrast, *P. antarctica* relies much less on energy dissipation and more on repair of photodamage and maintenance of excess photosynthetic capacity. This allows *P. antarctica* to grow well both within a deeply mixed water column and when exposure to high irradiance near the sea surface is followed by a recovery period when they are mixed to greater depths (Kropuenske et al., 2009; Arrigo et al., 2010; Mills et al., 2010; Van de Poll et al., 2011).

While early evidence points to the importance of light regime in controlling phytoplankton community composition in Southern Ocean polynyas, the abundance of trace metals such as iron (Fe) may also play a role. Primary productivity throughout much of the Southern Ocean is limited by low Fe concentrations (e.g. Martin et al., 1990; De Baar et al., 1995). Specifically, primary productivity in many coastal shelf regions may be seasonally limited towards the end of the phytoplankton blooms (Sedwick and DiTullio, 1997; Arrigo et al., 2003; Sedwick et al., 2000, 2011). Fe limitation directly affects phytoplankton photophysiology due to the high Fe requirements of the photosynthetic apparatus and electron transport pathways.

The Fe requirements of Antarctic phytoplankton differ depending on cell size (Timmermans et al., 2001; Strzepek et al., 2011) and photosynthetic architecture (Strzepek and Harrison, 2004; Lavaud et al., 2007). Moreover, the ability to assimilate organically complexed Fe may differ between phytoplankton taxa (Tagliabue and Arrigo, 2005; Strzepek et al., 2011). Because of the high Fe content of the photosynthetic apparatus, the Fe requirement of phytoplankton increases at low irradiance because of their need to build more photosynthetic reaction centers (Maldonado et al., 1999; Strzepek and Price, 2000). Moreover, Fe limitation may affect photoprotection and photodamage; since Fe-limited phytoplankton generally contain less chlorophyll *a*, the potential to absorb excess irradiance and thus become damaged is decreased (Greene et al., 1992; Van de Poll et al., 2005; Van Leeuwe and Stefels, 2007). However, because Fe-limitation also decreases the synthesis of photosynthetic proteins such as the D1 reaction center protein that are prone to photodamage (Greene et al., 1992; Vassiliev et al., 1995), repair of photodamage may be decreased as well. Finally, Fe effects

on xanthophyll cycle pigment content are usually less pronounced than on chlorophyll *a*, thereby increasing the ratio of photoprotective to photosynthetic pigments in both Fe-limited Antarctic diatoms (Van de Poll et al., 2005) and *P. antarctica* (Van Leeuwe and Stefels, 1998, 2007; Alderkamp et al., 2012a). Thus, the net effect of Fe-limitation on photoinhibition is unclear since culture studies have shown evidence of both increased sensitivity and increased tolerance to excess irradiance when phytoplankton were Fe-limited (Van de Poll et al., 2005; Alderkamp et al., 2012a).

3. The DynaLiFe program

The primary objective of the dynamic light and Fe (DynaLiFe) program was to improve our understanding of the synergistic and antagonistic interactions between dynamic light and Fe in controlling the abundance and distributions of *P. antarctica* and diatoms in the Southern Ocean. The central hypothesis of the study was that the interaction between Fe availability and dynamic irradiance governs phytoplankton distributions and community composition. The rapidly thinning ice sheets that directly flow into the Amundsen Sea were hypothesized to affect both Fe availability through input of glacially derived Fe (Raiswell et al., 2006) and the light climate through meltwater input affecting water column stability.

Prior to field sampling, a comprehensive effort to characterize the dynamics of the phytoplankton blooms in the Amundsen Sea was carried out, including the Pine Island Polynya and the Amundsen Polynya. Using data from a number of satellite sensors, the relationship between changes in phytoplankton biomass and rates of NPP were related to interannual changes in sea ice distribution (Arrigo et al., 2012). This study helped target likely sites for in situ sampling and has provided a larger temporal and spatial context within which we interpret the results of our oceanographic campaign.

Using the RV/IB *Nathaniel B. Palmer* (NBP 09-01) as a research platform, the DynaLiFe program sampled the Pine Island Polynya, Amundsen Polynya, and the sea ice zone in the vicinity of the polynyas. The water column in these regions was sampled for nutrients, concentrations of total and dissolved Fe, dissolved gases, as well as phytoplankton composition and biomass during January and February of 2009. The sampling strategy was designed to allow us to characterize the amount of nutrients (including Fe) that advected onto the continental shelf and how these nutrient distributions were modified by the resident ice shelves as they upwelled to the ocean surface and were subsequently modified by phytoplankton growth. The Fe distributions are presented in the paper by Gerringa et al. (2012), who specifically showed that Fe released from the PIG was the main source of Fe for the phytoplankton bloom in the Pine Island Polynya. The phytoplankton blooms were described by Alderkamp et al. (2012b) in greater detail, who showed that the polynyas were dominated by *P. antarctica*, whereas the waters in the sea ice zone harbored a mixed community of diatoms and *P. antarctica*. Rates of NPP and nutrient depletion were high and the Fe from melting glaciers and sea ice stimulated additional nitrate uptake in the polynyas, particularly when mixed layers were shallow. In conjunction with the in situ chemical and biological measurements, we also conducted discrete bioassay experiments at a number of stations to assess phytoplankton nutrient demand, paying particular attention to possible growth limitation by both ligand-bound and free dissolved Fe, as described by Mills et al. (2012). Taking a more chemical perspective, the importance of organic ligands in enhancing the bioavailability of Fe for the phytoplankton community was measured by Thuróczy et al. (2012), who showed that ligands released during the *P. antarctica*

bloom can extend the lifetime of the bloom by retaining Fe in bioavailable form. Finally, Tortell et al. (2012) present the first simultaneous measurements of surface water partial pressure of CO₂, biological oxygen saturation ($\Delta O_2/Ar$) and dimethylsulfide concentrations in both polynya waters and the sea ice zone of the Amundsen Sea.

Although the polynyas in the Amundsen Sea are relatively small, they provide a unique opportunity to investigate how coastal regions of the Antarctic are likely to respond to increased nutrient input from melting glaciers and ice sheets. As the polar oceans continue to warm, glacial melt will become more widespread around the periphery of the Antarctic continent, potentially resulting in enhanced delivery of trace metals that currently limit phytoplankton growth. The DynaLiFe program has provided some of the first glimpses of how primary production in coastal polynyas may change in the coming decades.

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