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Evidence for high iron requirements of colonial *Phaeocystis antarctica* at low irradiance

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Abstract We have carried out field and laboratory experiments to examine the iron requirements of colonial *Phaeocystis antarctica* in the Ross Sea. In December 2003, we performed an iron/light-manipulation bioassay experiment in the Ross Sea polynya, using an algal assemblage dominated by colonial *Phaeocystis antarctica*, collected from surface waters with an ambient dissolved Fe concentration of ~0.4 nM. Results from this experiment suggest that *P. antarctica* growth rates were enhanced at high irradiance (~50% of incident surface irradiance) but were unaffected by iron addition, and that elevated irradiance mediated a significant decrease in cellular chlorophyll *a* content. We also conducted a laboratory iron dose–response bioassay experiment using a unialgal, non-axenic strain of colonial *P. antarctica* and low-iron (<0.2 nM) filtered seawater, both collected from the Ross Sea polynya in December 2003. By using rigorous trace-metal clean techniques, we performed this dose–response iron-addition experiment at ~0°C without using organic chelating reagents to control dissolved iron levels. At the relatively low irradiance of this experiment (~20 μE m^{-2} s^{-1}), estimated nitrate-specific growth rate as a function of dissolved iron concentration can be described by a Monod relationship, yielding a half-saturation constant with respect to growth of 0.45 nM dissolved iron. This value is relatively high compared to reported estimates for other Antarctic phytoplankton. Our results suggest that seasonal changes in the availability of both iron and light play critical roles in limiting the growth and biomass of colonial *Phaeocystis antarctica* in the Ross Sea polynya.

Keywords Iron · Light · *Phaeocystis antarctica* · Ross Sea

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Introduction

The colonial prymnesiophyte *Phaeocystis antarctica* is a keystone species on the Antarctic continental shelf, where it plays an important role in the biogeochemical cycling of carbon, sulfur and nutrient elements (Gibson et al. 1990; Smith et al. 1991; DiTullio and Smith 1995; Arrigo et al. 1999; DiTullio et al. 2000; Sweeney et al. 2000; Schoemann et al. 2005). In the polynya region of the southern Ross Sea, extensive blooms of colonial *P. antarctica* typically form during spring and early summer, then wane during the mid to late summer (Smith and

Gordon 1997; Arrigo et al. 1998; Smith et al. 2000; Mathot et al. 2001; Arrigo and van Dijken 2004). Field observations have documented a general decrease in the depth of the surface mixed layer during the growing season, from more than 100 m in early spring to less than 25 m in summer (Arrigo et al. 1998; Gordon et al. 2000; Sweeney 2003; Worthen and Arrigo 2003; Smith and Van Hilst 2003). The results of several studies suggest that this seasonal change in stratification is accompanied by a decrease in the dissolved iron concentration of surface waters, from values of around 0.5 nM or more in spring to less than 0.1 nM in late summer (Sedwick and DiTullio 1997; Fitzwater et al. 2000; Sedwick et al. 2000; Coale et al. 2005). These dissolved iron levels are low enough to limit algal community growth rates in the Ross Sea during the summer (Martin et al. 1990; Sedwick and DiTullio 1997; Sedwick et al. 2000; Coale et al. 2003). Hence it has been argued that seasonal changes in irradiance and/or iron availability—bottom-up controls—regulate the timing and location of colonial *Phaeocystis antarctica* blooms in the Ross Sea (Arrigo et al. 1998; Boyd 2002; Smith et al. 2003; Worthen and Arrigo 2003; Arrigo and Tagliabue 2005; Tagliabue and Arrigo 2005). As yet, there are few published data to support this assertion.

With regard to irradiance, the results of field and laboratory studies indicate that *P. antarctica* can readily adapt to a wide range of ambient light conditions (Palmisano et al. 1986; Matrai et al. 1995; Hong et al. 1997; Moisan and Mitchell 1999; Robinson et al. 2003; Schoemann et al. 2005). However, the field and laboratory measurements discussed by Van Hilst and Smith (2002) and Smith and Van Hilst (2003) suggest that there is little difference between the photosynthesis-irradiance characteristics of colonial *Phaeocystis antarctica* and diatoms in the Ross Sea, implying that other factors, such as iron availability and grazing, must control the spatial and temporal distribution of the two main phytoplankton taxa in this highly productive shelf region.

So far there has been only limited research addressing the iron requirements of colonial *P. antarctica*. Sedwick et al. (2000) performed a shipboard iron-addition experiment with a colonial *Phaeocystis*-dominated algal assemblage collected from the southern Ross Sea in spring 1994, with their results suggesting that the ambient dissolved iron concentrations of ~0.8 nM were sufficient to meet the growth requirements of the native *P. antarctica* colonies. Evidence for iron limitation of *Phaeocystis antarctica* was reported by Olson et al. (2000), who measured the photosynthetic competency of individual *P. antarctica* cells in the shipboard iron-addition experiments that Coale et al. (2003) performed in the Ross Sea during late summer 1997. In these experiments, Coale et al. (2003) observed an increase in the abundance of prymnesiophytes, mainly *Phaeocystis*, in response to iron addition. The dose–response experiments performed by Coale et al. (2003) in the Ross Sea allowed them to estimate half-saturation constants (with respect to growth) of 0.005–0.043 nM dissolved Fe for prymnesiophytes, suggesting that the iron requirements of *Phaeocystis* in the Ross Sea may be quite low, although their experimental results suggest similarly low values for diatoms. However, the results described by Olson et al. (2000) and Coale et al. (2003) pertain to bottle incubations performed at full surface irradiance (i.e., light levels that were probably much higher than mean surface mixed-layer irradiance), and presumably apply to solitary *Phaeocystis antarctica* cells; therefore, their results may not be representative of the colonial *Phaeocystis antarctica* that bloom in the southern Ross Sea during spring and early summer.

Here we report the results of two experiments that provide further information on the iron requirements of colonial *Phaeocystis antarctica* in the Ross Sea. The first is a shipboard iron- and light-manipulation experiment, which was performed using a native algal assemblage dominated by colonial *P. antarctica*, collected in the northern Ross Sea polynya during December 2003. The second is a laboratory dose–response iron-addition experiment in which we used a pure culture of colonial *P. antarctica* and low-iron (<0.2 nM) filtered seawater, both collected from the southern Ross Sea polynya in December 2003. To our knowledge, this experiment represents the first time a dose–response iron-addition experiment has been carried out with colonial *Phaeocystis antarctica* using realistic, sub-nanomolar