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Physiological characteristics of open ocean and coastal phytoplankton communities of Western Antarctic Peninsula and Drake Passage waters



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ABSTRACT

Photophysiological processes as well as uptake characteristics of iron and inorganic carbon were studied in inshore phytoplankton assemblages of the Western Antarctic Peninsula (WAP) and offshore assemblages of the Drake Passage. Chlorophyll *a* concentrations and primary productivity decreased from in- to offshore waters. The inverse relationship between low maximum quantum yields of photochemistry in PSII (F_v/F_m) and large sizes of functional absorption cross sections (σ_{PSII}) in offshore communities indicated iron-limitation. Congruently, the negative correlation between F_v/F_m values and iron uptake rates across our sampling locations suggest an overall better iron uptake capacity in iron-limited pelagic phytoplankton communities. Highest iron uptake capacities could be related to relative abundances of the haptophyte *Phaeocystis antarctica*. As chlorophyll *a*-specific concentrations of humic-like substances were similarly high in offshore and inshore stations, we suggest humic-like substances may play an important role in iron chemistry in both coastal and pelagic phytoplankton assemblages. Regarding inorganic carbon uptake kinetics, the measured maximum short-term uptake rates ($V_{max(CO_2)}$) and apparent half-saturation constants ($K_{1/2(CO_2)}$) did not differ between offshore and inshore phytoplankton. Moreover, $V_{max(CO_2)}$ and $K_{1/2(CO_2)}$ did not exhibit any CO_2 -dependent trend over the natural pCO_2 range from 237 to 507 μatm . $K_{1/2(CO_2)}$ strongly varied among the sampled phytoplankton communities, ranging between 3.5 and 35.3 $\mu mol L^{-1} CO_2$. While in many of the sampled phytoplankton communities, the operation of carbon-concentrating mechanisms (CCMs) was indicated by low $K_{1/2(CO_2)}$ values relative to ambient CO_2 concentrations, some coastal sites exhibited higher values, suggesting down-regulated CCMs. Overall, our results demonstrate a complex interplay between photophysiological processes, iron and carbon uptake of phytoplankton communities of the WAP and the Drake Passage.

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1. Introduction

The Western Antarctic Peninsula (WAP) is a productive region of the Southern Ocean, accounting for an annual average primary production of $\sim 182 g C m^{-2} y^{-1}$ (Vernet and Smith, 2006). Early in the season, primary productivity of this region is thought to be mainly controlled by light availability. In early spring, when day length and solar radiation increase, phytoplankton growth sets in. The bloom development also depends on water column stability

(Moline, 1998; Garibotti et al., 2003). Shallow mixed layers could be related to low wind speeds and high phytoplankton concentrations due to favourable light conditions (Mitchell and Holm-Hansen, 1991; Moline, 1998; Garibotti et al., 2005; Vernet et al., 2008). Freshwater input from melting sea ice plays an important role in stabilizing the upper water column, thereby enhancing phytoplankton growth (Garibotti et al., 2005). From spring until the end of summer, large phytoplankton blooms occur along the shelf and coastal environments of the WAP, mainly consisting of large diatoms and less frequently of cryptophytes as well as the haptophyte *Phaeocystis antarctica* (Ducklow et al., 2012). Even at the end of the summer season, macronutrient concentrations are still relatively high and do not appear to limit phytoplankton growth in WAP waters (Garibotti et al., 2005). Departing from shelf and coastal regions, phytoplankton productivity and biomass strongly decrease towards offshore waters

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of the Drake Passage. The negative gradients in productivity and chlorophyll *a* concentrations result from limiting concentrations of iron (Martin et al., 1990; Hopkinson et al., 2007). Furthermore, strong winds in this region usually cause a deep vertical mixing of the upper surface layer leading to a reduced overall light availability. Therefore, the availability of iron, but also of light as well as interactions between these limiting factors, control phytoplankton growth and productivity in offshore waters (Alderkamp et al., 2011; García-Muñoz et al., 2014). Sporadically occurring elevated phytoplankton concentrations in surface pelagic waters have been associated with upwelling of iron-rich bottom water. Similarly, deep chlorophyll maxima have been observed in the Drake Passage resulting from intrusion of winter water with higher iron concentrations (Garibotti et al., 2005; Holm-Hansen et al., 2005).

To understand the environmental factors that control phytoplankton distribution and productivity patterns in the WAP and Drake Passage region, previous studies mainly characterized phytoplankton community composition and primary production (Prézelin et al., 2000; Varela et al., 2002; Garibotti et al., 2005). Studies on physiological characteristics of phytoplankton are still scarce, even though they can help to gain a better understanding on phytoplankton ecology. To date, most knowledge has been gained about photophysiological characteristics of natural phytoplankton assemblages (e.g. Hopkinson et al., 2007; Huang et al., 2012; Smith et al., 2013). As iron is essential for photosynthesis, chlorophyll *a* fluorescence techniques are often used to resolve the spatial and temporal distribution of iron-limitation in the field (Behrenfeld and Kolber, 1999; Sosik and Olson, 2002; Hopkinson et al., 2007; Behrenfeld and Milligan, 2012). Although chlorophyll *a* fluorescence can be affected by other factors such as light (Suggett et al., 2009; Smith et al., 2013) and phytoplankton community structure (Suggett et al., 2009), iron limitation is considered to have the strongest influence on chlorophyll *a* fluorescence in the High Nutrient Low Chlorophyll (HNLC) regions of the Southern Ocean (Boyd and Abraham, 2001). Next to chlorophyll *a* fluorescence, information on the degree of iron limitation can also be gained through the assessment of the phytoplankton's cell capacity to take up iron. In laboratory and field studies, iron limitation has been shown to induce high affinity transporters for iron uptake in phytoplankton (Maldonado and Price, 1999; Maldonado and Price, 2001; Hassler and Schoemann, 2009). As most of the dissolved iron pool is complexed to strong organic ligands, Antarctic phytoplankton need to access organic iron using reductases located on their cell surface (Maldonado et al., 2006; Strzepak et al., 2011; Shaked and Lis, 2012). Siderophores, porphyrins, and saccharides are all iron-binding ligands that can be present *in situ* (Hutchins et al., 1999; Maldonado and Price, 1999; Hassler et al., 2011a). Recent data suggest that oceanic iron chemistry is controlled by humic substances-like (HS-like) compounds, including exopolymeric substances (Laglera and van den Berg, 2009; Hassler et al., 2011b). Unfortunately, information on iron uptake capacities, ligands and HS-like compounds is generally scarce for Antarctic phytoplankton (Hassler and Schoemann, 2009) and, to date, does not exist for phytoplankton of WAP and Drake Passage waters.

Inorganic carbon uptake characteristics of natural phytoplankton assemblages were found to depend on ambient CO₂ concentrations, which thus influence the physiological ecology of natural phytoplankton assemblages (Tortell et al., 2008, 2010; Neven et al., 2011). In addition, surface concentrations of dissolved CO₂ can greatly vary as a result of biological activity. Antarctic phytoplankton growth can result in pCO₂ values less than ~100 μatm towards the end of a bloom (Arrigo et al., 1999; Cassar et al., 2004; Moreau et al., 2012; Tortell et al., 2013). The sensitivity of phytoplankton to varying pCO₂ is mainly resulting from the poor affinity of the carbon-fixing enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) for its substrate CO₂. To ensure efficient carbon fixation rates also under low CO₂ conditions, phytoplankton cells employ carbon concentrating mechanisms (CCMs) that enrich CO₂ at the catalytic

site of RubisCO (Reinfelder, 2011). In laboratory CO₂-perturbation experiments, bloom-forming Antarctic phytoplankton species were found to have highly efficient CCMs irrespective of the pCO₂ during acclimation (Trimborn et al., 2013). Along natural pCO₂ gradients, CO₂-dependent regulation of the CCM activity was found in phytoplankton assemblages of the Ross, Weddell and Amundsen Sea (Neven et al., 2011; Tortell et al., 2010, 2013). To date, inorganic carbon uptake characteristics of phytoplankton along the WAP region have not yet been examined.

To better understand the physiological ecology of open ocean and coastal phytoplankton, which experiences different controlling environmental factors (e.g. iron, CO₂), inshore communities of the WAP and offshore communities of the Drake Passage were physiologically characterized during the research cruise ANT XXVII-2 onboard RV *Polarstern*. Next to the characterisation of the phytoplankton community composition and primary productivity, photophysiological processes as well as uptake characteristics of iron and inorganic carbon were studied.

2. Materials and methods

2.1. Field sampling

Field sampling was conducted during cruise ANT XXVII-2 onboard R.V. *Polarstern* from the 9th to the 27th January 2011. From 15 stations in total, seawater samples were collected in coastal (inshore, bathymetric depth < 500 m) and open ocean (offshore, bathymetric > 500 m) waters of the Western Antarctic Peninsula (Fig. 1). Using Niskin bottles (3–5 bottles à 12 L) attached to a sampling rosette with conductivity, temperature and depth as well as transmission sensors (CTD rosette), seawater samples were collected either from the chlorophyll maximum when present or, in case of a uniform surface mixed layer, from the depth at which transmission-based estimates of biomass appeared highest (Table 1).

2.2. Macronutrients

Macronutrients (nitrate, phosphate and dissolved silicate) of the sampled stations were determined colorimetrically onboard with a Technicon TRAACS 800 Auto-analyzer following procedures improved after Grasshoff et al. (1999). Samples for the determination of biogenic silica were taken, filtered through a cellulose acetate filter (Sartorius, 0.4 μm) and stored at –20 °C until further analysis at the home laboratory. Before analysis each filter was dried at 85 °C overnight and biogenic silicate was determined using the method by Koroleff (1983).

2.3. Seawater carbonate chemistry

For the determination of the seawater carbonate chemistry from each station, samples for alkalinity, dissolved inorganic carbon (DIC) and pH were collected. Total alkalinity (TA) samples were taken from the filtrate (Whatman GFF filter, ~0.6 μm), fixed with 0.03% HgCl₂ and stored in 100-mL borosilicate flasks at 4 °C until further analysis. TA was estimated from duplicate potentiometric titration (Brewer et al., 1986) back in the home laboratory using a TitroLine alpha plus (Schott Instruments) and calculated from linear Gran Plots (Gran, 1952). Dissolved inorganic carbon (DIC) samples were gently sterile-filtered (Sartorius stedim, 0.2 μm), fixed with 0.03% HgCl₂ and stored in 5-mL borosilicate flasks free of air bubbles at 4 °C until they were measured with a QuAatro Autoanalyzer (Seal Analytical). Seawater pH was measured on board using a pH/ion meter (model 713, Metrohm) that was calibrated (three-point calibration) using National Institute of Standards and Technology-certified buffer systems. Seawater carbonate chemistry (including pCO₂) was calculated from

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