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Phytoplankton and pigment patterns across frontal zones in the Atlantic sector of the Southern Ocean

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ABSTRACT

Phytoplankton distribution and concentrations of macronutrients and iron were studied in the Polar Frontal Zone (PFZ) and the eastern Weddell Gyre of the Southern Ocean, during austral autumn. HPLC analysis of algal pigments was combined with microscopy observations to assess algal distribution. Patterns of algal distribution were dictated by the frontal systems. Travelling from north to south, four distinctively different algal communities were observed, the composition of which could be explained by variations in nutrients, light climate and grazing pressure. North of the PFZ, low silicate levels (<3 μM) were limiting diatom growth, and the algal community was dominated by prasinophytes. Silicate concentrations increased over the PFZ, which coincided with the dominance of diatoms. South of the PFZ, the open waters of the Weddell Gyre are characterised as a high-nutrient low-chlorophyll area. Low iron concentrations (<0.4 nM on average) supported an algal community that was dominated by smaller size algae (<20 μm). Deep wind-mixed layers (>100 m depth) together with low incident irradiance in autumn were likely limiting algal growth. At the Marginal Ice Zone (MIZ), the phytoplankton community consisted mainly of low numbers of flagellates (Chlorophyceae and haptophytes) and high numbers of microzooplankton, indicating phytoplankton control by grazing. The phytoplankton distribution patterns presented here and the relation with potential growth-controlling factors provides more insight in the mechanisms that control carbon fluxes from the atmosphere into the ocean interior.

1. Introduction

In the Southern Ocean, high algal productivity, associated with increased fluxes of carbon from the atmosphere into the deep ocean, has been related to frontal systems (de Baar et al., 1995; Lancelot et al., 2000). The Polar Frontal Zone (PFZ) is a complex system that consists of various meandering currents (Orsi et al., 1995; Sokolov and Rintoul, 2007). On the north side, downwelling of watermasses is related to convergence zones; on the southern boundary of the PFZ upwelling of nutrient-rich watermasses is associated with divergence. Especially along the northward-propagating currents of divergence microalgae may travel for prolonged periods along the surface, thus profiting from favourable light conditions (Strass et al., 2002; Tremblay et al., 2002).

Similar beneficial conditions for algal growth may be encountered in the Marginal Ice Zone (MIZ). Over the course of the season ice melt, associated with the gradual retreat of the ice edge, can provide a stable water column and a continuous replenishing of nutrients that may be consumed during algal growth (Smith and Nelson, 1985; Lancelot et al., 1991).

In contrast, the open ocean areas south of the PFZ and large parts of the Weddell Gyre are characterised by low algal biomass, with chlorophyll *a* concentrations generally below 0.3 μg l^{-1} (Banse, 1996). In this high-nutrient low-chlorophyll (HNLC) area, iron and light synergistically control growth (de Baar et al., 2005). Iron is an essential trace element in photosynthesis. Various protein–pigment complexes that are part of the photosystems require iron for synthesis (cytochromes and FeS-proteins). Under iron limitation, impairment of those protein complexes results in a decrease in the efficiency of electron transport (Greene et al., 1991). At the same time, persistently strong winds create deep vertical mixing of the water column (Mitchell and Brody, 1991; Lancelot et al., 2000). Iron and light limitation proved to be growth-controlling factors in a number of studies in the Antarctic Circumpolar Current (ACC) (Alderkamp et al., 2013; van Leeuwe et al., 1997).

In the Southern Ocean, algal productivity is characterised by a strong seasonality, as the availability of light and nutrients varies throughout the year (see Boyd, 2002 and references therein). Light conditions are primarily controlled by the annual solar cycle. In winter, light levels are too low to allow the build-up of algal biomass. In spring, growth conditions improve with the increase in sunlight. Algal blooms may

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then develop in areas of sufficient nutrient supply, like the frontal jets in the ACC. Over the course of these blooms, iron and silicate may be reduced until nutrient concentrations drop beneath saturation levels (Boyd, 2002; Pasquer et al., 2005). In autumn, both light levels and nutrient supply may become limiting for algal growth. However, few in situ data are available this late in the season, leaving phytoplankton dynamics in autumn largely unexplored.

Carbon fluxes in the Southern Ocean strongly depend on the algal species composition. The sequestration of carbon from the atmosphere into the ocean interior is not only determined by carbon uptake rates but also depends on the fate of the microalgae (Assmy et al., 2013; Tremblay et al., 2002). The biogeochemical cycles that determine carbon fluxes vary with species; in the Southern Ocean diatoms and *Phaeocystis antarctia* are prominent players that follow distinctively different biogeochemical pathways (Arrigo et al., 1999). To improve insight in the functioning of the biological pump, it is required to improve our knowledge on the seasonal variation in phytoplankton abundance and its controlling mechanisms. Pigment analyses by high-performance liquid chromatography (HPLC) are widely applied to study algal distributions on a large scale (Roy et al., 2011). The development of software that is designed to convert pigment patterns into algal groups (CHEMical TAXonomy: CHEMTAX) has further promoted the application of HPLC analyses (Wright et al., 1996). Accurate estimations of algal abundance can be obtained in combination with microscopy.

We present here data from a study performed in the PFZ at 20° E and in the eastern section of the Weddell Gyre in the Southern Ocean in autumn. We studied phytoplankton distribution and pigment patterns in relation to iron and macronutrients to ascertain which factors govern growth of the in situ algal population in autumn. Cell volume was converted to carbon biomass, to estimate the carbon contribution of the various plankton groups to total carbon. The major aim was to extend the knowledge on the seasonal phytoplankton development in the Southern Ocean and to gain insight in the controls of carbon fluxes in the Southern Ocean in autumn.

2. Material and methods

2.1. Field study

The Atlantic sector of the Southern Ocean was visited during the ANT-XVI/3 cruise (March–May 1999) of the German RV Polarstern. During the cruise, a transect was investigated that reached from the PFZ in the north to the MIZ in the south (Fig. 1). Within the PFZ, three major fronts were encountered (Orsi et al., 1995; Strass and Leach, 2000). The Sub-Antarctic Front (SAF) at ~47.5°S in the north was marked by the northward subduction of low-salinity water. The Antarctic Polar Front at 49°S (APF), determined by the 2 °C isotherm, was characterised by the transition to nutrient-rich waters. The Southern Polar Front at 53°S (SPF) was indicated by an increase in salinity, related to upwelling of the Circumpolar Deep Water (Strass et al., 2002).

Along the transect, macronutrient samples were taken every 20 min (in ca. 3 nmi intervals); pigment samples were taken at about every latitudinal degree going south. Samples were taken with the ship's pump (at 8 m depth). Potential damaging effects of shear stress on phytoplankton cells were checked by comparison of samples taken with the pump to samples taken with Niskin bottles, by means of PAM-fluorometry (Water-PAM, Walz). The pump showed to be safe (Kroon, pers. comm.). At the PFZ and the MIZ, samples for pigment and macronutrient analyses were taken with a Rosette sampler equipped with a CTD at 10, 20, 40, 60, 80 and 100 m depth.

Seawater for the analysis of total dissolved iron was taken with equipment adapted especially for trace metal clean work (see de Baar et al., 1999 for details). Samples were taken with Teflon coated GoFlo bottles that were deployed on a Kevlar hydrowire.

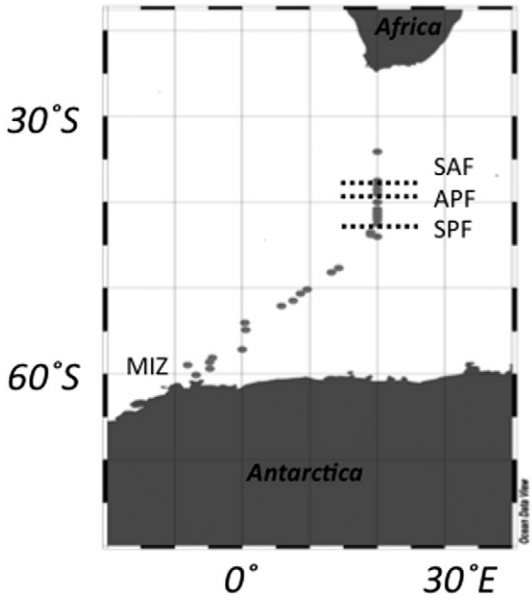

Fig. 1. Research area during ANT-XVI/3. The dots represent the stations along a transect that extended from the Sub-Antarctic Front (SAF) in the north to the Marginal Ice Zone (MIZ) in the south. The three fronts that constitute the Polar Frontal Zone are based on in situ data (Strass and Leach, 2000) and according to Orsi et al. (1995).

2.2. Nutrient analysis

The concentrations of the macronutrients, nitrate, phosphate and silicate, were determined on board using a Technicon II Autoanalyzer following standard methods (Kattner and Becker, 1991). Samples for the determination of dissolved iron were acidified with ultraclean quartz distilled nitric acid to pH < 2. Total dissolved iron was measured on board using a flow injection technique with inline pre-concentration on a chelating resin followed by chemiluminescence detection (FIA-CL; de Jong et al., 1998).

2.3. Pigment analyses and cell counts

A sample volume between 4–6 l was filtered gently (<15 kPa) onto GF/F filters (Whatman), subsequently snap-frozen in liquid nitrogen and stored at −80 °C until analysis. Before extraction in 90% acetone, filters were freeze-dried during 48 h. Pigments were analysed by high-performance liquid chromatography (HPLC) on a Waters system equipped with a photodiode array detector (van Leeuwe et al., 2006). A Waters DeltaPak reversed-phase column (C18, fully end-capped) was used. Pigment standards were obtained from DHI Water Quality Institute (Horsholm, Denmark).

CHEMTAX matrix factorization was applied to derive algal classes from pigment patterns (Wright et al., 1996). Data were analysed by separating the water column in two layers ("bins" in CHEMTAX), above and below 50 m (Table 1). The initial pigment ratio included eight algal classes. These classes were chosen based on literature information (e.g. Alderkamp et al., 2010; Wright et al., 2010) and microscopy. Two groups of diatoms were described. Diatoms_1 contained typical diatom species that are characterised by Chl $c_{1,2}$. Diatoms_2 is a separate group in which Chl c_1 is replaced by Chl c_3. This group represents *Pseudonitzschia* sp., though not exclusively. Haptophytes were also separated in two groups, representing Haptophytes 6, 7, 8 as defined by Zapata et al. (2004). The input ratios were based on Wright et al. (2010). Microscope observations showed that Haptophyceae_C mainly consisted of *Chrysomonodales*. The input ratios for Haptophyceae_P were based on pigment ratios typical for *Phaeocystis antarctica* (van Leeuwe et al., 2014). The presence of *P. antarctica* was also confirmed